Reorganising the orchid genus Coelogyne

a phylogenetic classification based on morphology and molecules

Barbara Gravendeel

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CONTENTS

SUMMARY

The aims of this study are:

1) to reconstruct a skeleton phylogeny of the orchid genus *Coelogyne* and allied genera based on molecular and morphological characters;
2) to incorporate this phylogeny into a phylogenetic classification of the Coelogyninae;
3) to provide taxonomic revisions of a selection of species groups of *Coelogyne*.

Coelogyne comprises over 200 species distributed throughout southeast Asia with main centers of diversity in Borneo, Sumatra and the Himalayas. Most species are epiphytes and occur in primary forests. They have a fairly large number of medium-sized to large flowers with delicate colours and a sweet scent, which are pollinated by bees, beetles or wasps. The genus is placed in subtribe Coelogyninae (subfamily Epidendroideae) together with 15 other genera with a total of approximately 550 species. The subtribe is characterised by sympodial growth, pseudobulbs of one internode, terminal inflorescences, a winged column and massive caudicles. Separate maximum parsimony analyses of RFLPs, *matK* and nuclear rDNA ITS sequences, macromorphological and anatomical data collected for 27 *Coelogyne* species and 13 representatives of related genera produce largely congruent results. A total evidence analysis indicates that Coelogyninae are monophyletic and diverged early into three major clades.

Clade I comprises species of *Coelogyne* sect. *Coelogyne*, subgenus *Cyathogyne*, sect. *Rigidiformes*, *Tomentosae*, *Veitchiae* and *Verrucosae*, from which *Bracisepalum*, *Chelonistele*, *Dendrochilum*, *Entomophobia*, *Geesinkorchis* and *Nabaluia* split off. Synapomorphies for this group of species are the more than 15 flowers per inflorescence, presence of sterile bracts on the rachis and presence of hairs on the ovary. Elongate trichomes with acute top on the leaf surface, synanthous inflorescences, presence of sterile bracts at the base of the rachis, simultaneously opening flowers, persistent floral bracts, ovate-oblong petals, and hairy sepals are present in the majority of taxa in this clade. Clade II subsequently diverged into species of *Neogyna* and *Pholidota* nested within species of *Coelogyne* sect. *Bicellae*, *Brachypterae*, *Elatae*, *Flaccidae*, *Fuliginosae*, *Hologyne*, *Lentiginosae*, *Longifoliae*, *Moniliformes*, *Ptychogyne* and *Speciosae*. Synapomorphies for this group are the caducous floral bracts, glabrous ovaries, linear petals and a relatively low number of morphologically diverse keels on the hypochile. Hysteranthous inflorescences, less than 15 flowers per inflorescence, intermediate-sized flowers and a relatively low number of keels on the epichile are present in the majority of taxa in this clade. Clade III consists of species of *Pleione* and is characterised by short-living pseudobulbs, a lack of stegmata in all sclerenchymatous tissues, a hypochile without lateral lobes and an epichile apex with fimbriate margin.

The traditional circumscription of *Coelogyne* is not supported by the total evidence phylogeny presented here and should be abandoned. A redefinition of the genus is suggested by including *Neogyna* and *Pholidota* and removing the species of *Coelogyne* sect. *Coelogyne* (in part), *Cyathogyne*, *Tomentosae*, *Rigidiformes*, *Veitchiae* and *Verrucosae*. A formal proposal for the creation of a new genus for these species is not made yet, as most internal nodes of the total evidence tree are only poorly supported and need a larger taxon sampling and data from more variable genes.

The number of subgeneric groups recognised by various authors in *Coelogyne* varies between 5 and 23, which is mainly due to the relative lack of morphological characters available to define groups of species. Of the 17 sections sampled in *Coelogyne*, just three (with only two sampled species each) form strongly supported monophyletic groups in the total evidence analysis: sect. *Longifoliae*, *Moniliformes* and *Verrucosae*. This is consistent with the clear morphological synapomorphies that characterise those sections. Monophyly of *Coelogyne* sect. *Flaccidae* and *Tomentosae* is weakly supported, which is in accordance with the few and not unique synapomorphies that define these sections. *Coelogyne* sect. *Coelogyne* and sect. *Elatae* are clearly paraphyletic. This was already expected as the morphological diversity in both sections is high. A well-supported subset of species is formed by *C. fimbriata* (sect. *Fuliginosae*) and *C. stricta* (sect. *Elatae*), which 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. The species sampled of subgenus *Bicellae*, *Cyathogyne*, *Hologyne* and *Ptychogyne* seem well nested within several sections of *Coelogyne* and do not warrant the status of subgenus.

Several of the traditionally used floral traits for (sub)generic and sectional delimitation within Coelogyninae and *Coelogyne* (the ‘key’characters) were plotted on the total evidence tree. Inflorescence type, number of flowers per inflorescence, persistence of floral bracts, presence of sterile bracts on the rachis, 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 synapomorphies for major clades in Coelogyninae and *Coelogyne*. The number of leaves per pseudobulb, size of the flowers, shape of the lip base and petals and presence of stelidia and calli on the lip show many reversals and appear not to be phylogenetically informative.

With the phylogenetic boundaries of the total evidence analysis as a reference, a start with a taxonomic treatment of the whole genus is made by revisions of three different groups of species in *Coelogyne*. An integrated phylogenetic analysis of morphological and molecular characters is performed for the 16 species of sect. *Speciosae* and 8 species of sect. *Verrucosae* to check monophyly and study interspecific relationships, whereas a complex of the closely related species of sect. *Fuliginosae* is resolved with a phenetic analysis using morphological characters. The last three chapters of this thesis contain descriptions of all species (including three new ones), synonyms, photographs, drawings, distribution maps and identification keys.

SAMENVATTING

Coelogyne Lindl. is een orchideeëngeslacht van ongeveer 200 soorten, die hun verspreidingsgebied hebben door geheel zuidoost Azië, met Borneo, Sumatra en het Himalaya gebied als belangrijkste centra van diversiteit. De naam is afgeleid van het Griekse ‘koilos’ = ‘hol’ en ‘gyne’ = ‘vrouw’ hetgeen verwijst naar de holle stempel. Lindley beschreef het geslacht in 1821 en onderscheidde toen vijf soorten. Sindsdien zijn er nog zeker 400 soorten beschreven, maar daarvan zijn vele namen ongeldig of synoniem voor eerder beschreven soorten. De meeste *Coelogyne* soorten groeien in laagland- en bergbos en hebben een epifytische levenswijze (= op bomen en rotsen groeiend). Het aantal bloemen per bloeiwijze varieert van klein tot zeer groot. De bloemen zijn overwegend wit of groen/bruinachtig, met een opvallende bruine of gele tekening op de lip. Ze hebben vaak een zoete geur, wat een groot aantal verschillende bestuiverstypen aantrekt, o.a. bijen, kevers en wespen. Een beperkt aantal soorten staat bekend als de ‘necklace orchids’ vanwege de lange, hangende, veelbloemige bloeiwijzen.

Coelogyne behoort tot de Coelogyninae (onderfamilie Epidendroideae), dat daarnaast uit nog 15 andere geslachten bestaat en in totaal ongeveer 550 soorten omvat. Al deze geslachten zijn sympodiaal (= groei vanuit de okselknoppen van de hoofdas van de wortelstok en niet vanuit de top) en hebben pseudobulben (= verdikte stengeldelen), die bestaan uit één stengellid, eindstandige bloeiwijzen, een gevleugeld zuiltje (= met stijl en stempel vergroeide meeldraad) en een sterk vergroot caudiculum (= kleverige hechtschijfje, dat de stuifmeelklompjes verenigt). De omgrenzingen van de verschillende geslachten zijn niet duidelijk, en er zijn de afgelopen 150 jaar diverse indelingen gepubliceerd. Er bestaat veel verschil van mening over de relatieve belangrijkheid van bepaalde morfologische kenmerken. Wat de ene onderzoeker reden genoeg vindt voor het onderscheiden van een nieuw geslacht, doet een ander af als slechts een soortsonderscheidend kenmerk. Een aantal geslachten wordt onderscheiden op basis van de afwezigheid van kenmerken. *Coelogyne* wordt bijvoorbeeld gedefinieerd door de afwezigheid van een sterk zakvormige lipbasis, die in alle andere geslachten van de Coelogyninae wel aanwezig zou zijn.

Een fylogenetische analyse (= op basis van verwantschap) met expliciet gecodeerde morfologische kenmerken, RFLPs (Restriction Fragment Length Polymorphisms), *matK* en ribosomaal kern DNA (ITS) sequenties met 40 soorten uit de Coelogyninae staat centraal in dit onderzoek. De analyse van alle moleculaire kenmerken (Hoofdstuk 2) en een gezamelijke analyse van moleculaire en morfologische kenmerken (Hoofdstuk 3) laat zien dat de Coelogyninae monofyletisch (= ontstaan uit één voorouder) zijn en al vroeg in hun evolutie in drie groepen opgesplitst raakten.

De eerste groep bestaat uit soorten van verschillende onderverdelingen (zgn. secties en ondergeslachten) van *Coelogyne*, waaruit de geslachten *Bracisepalum*, *Chelonistele*, *Dendrochilum*, *Entomophobia*, *Geesinkorchis* en *Nabaluia* afsplitsten. Gemeenschappelijke kenmerken voor deze groep van soorten zijn de bloeiwijzen met meer dan 15 bloemen en haren op het vruchtbeginsel. Kenmerken, die aanwezig zijn in het merendeel van de soorten in deze groep zijn: haren met een spitse top op het bladoppervlak, synanthe bloeiwijzen (= bloeiwijzen, waarbij de jonge pseudobulb zich later ontwikkelt dan de bloemen) met steriele schubben aan de basis, bloemen die gelijktijdig open zijn, niet afvallende schutbladen, en eironde, behaarde bloemdekbladen.

De tweede groep bestaat uit soorten van de geslachten *Neogyna* en *Pholidota* samen met verschillende secties van *Coelogyne*. Gemeenschappelijke kenmerken voor deze groep zijn de afvallende schutbladen, onbehaarde vruchtbeginsels, lijnvormige en onbehaarde bloemdekbladen en bloeiwijzen met minder dan 15 bloemen en morfologisch sterk gedifferentieerde kielen op het bovenste deel van de lip. Kenmerken, die aanwezig zijn in het merendeel van de taxa in deze groep zijn: hysteranthe bloeiwijzen (= bovenop volgroeide pseudobulb met bladeren), bloemen van gemiddelde grootte en een relatief klein aantal kielen op het onderste deel van de lip.

De derde groep bestaat uit *Pleione* soorten en wordt gekenmerkt door kortlevende pseudobulben, de afwezigheid van silica korrels in het sklerenchym en een lip zonder duidelijke zijlobben, met een gewimperde rand.

De fylogenetische analyse van morfologische en moleculaire kenmerken laat zien dat de traditionele omgrenzing van het geslacht *Coelogyne* geen goede weergave is van evolutionaire verwantschappen. Voorgesteld wordt om soorten uit *Neogyna* en *Pholidota* met *Coelogyne* te laten samenvallen en soorten uit *Coelogyne* sect. *Coelogyne*, *Cyathogyne*, *Tomentosae*, *Rigidiformes*, *Veitchiae* en *Verrucosae* te verwijderen. Een formeel voorstel voor een nieuw geslacht voor deze *Coelogyne* soorten wordt hier nog niet gedaan, omdat de resultaten van de fylogenetische analyse van moleculaire en morfologische kenmerken samen daarvoor nog niet genoeg zijn opgelost. Hiervoor is een uitgebreidere steekproef van soorten nodig, en moeten meer genen bekeken worden.

Het aantal onderverdelingen dat binnen *Coelogyne* onderscheiden wordt varieert per onderzoeker van 5 tot 23. Dit wordt mede veroorzaakt door het relatieve gebrek aan morfologische kenmerken om groepen van soorten mee te definiëren. Van de 17 secties/ondergeslachten, die in dit onderzoek bekeken zijn, blijken er maar drie duidelijk monofyletisch te zijn: sect. *Longifoliae*, *Moniliformes* en *Verrucosae*. Deze secties worden gekenmerkt door duidelijke gemeenschappelijke morfologische kenmerken. *Coelogyne* sect. *Flaccidae* en *Tomentosae* zijn waarschijnlijk ook monofyletisch, maar statistische ondersteuning hiervoor is niet groot, wat mede veroorzaakt wordt door het kleine aantal niet unieke kenmerken, dat deze sectie definieert. *Coelogyne* sect. *Coelogyne* en sect. *Elatae* zijn duidelijk parafyletisch (= niet ontstaan uit één voorouder), wat de hoge morfologische diversiteit binnen deze groepen van soorten al deed vermoeden. Een goed ondersteunde groep van soorten wordt gevormd door *C. fimbriata* (sect. *Fuliginosae*) en *C. stricta* (sect. *Elatae*). Bij beide soorten zijn steriele schubben aanwezig op de basis van de bloeiwijze. Om te kunnen zeggen of deze groep van soorten de status van een nieuwe sectie verdient, is een grotere steekproef van *Coelogyne* soorten nodig. De ondergeslachten *Bicellae*, *Cyathogyne*, *Hologyne* en *Ptychogyne* blijken nauw verwant te zijn met soorten uit verschillende secties van *Coelogyne* en verdienen dus geen aparte status.

Voor enige traditioneel gebruikte bloemkenmerken voor het onderscheiden van onderverdelingen binnen Coelogyninae en *Coelogyne* (de zogenaamde sleutelkenmerken) werd onderzocht of zij fylogenetische informatie bevatten. Het type bloeiwijze, aantal bloemen per bloeiwijze, niet of wel afvallende schutbladen, aanwezigheid van steriele schubben aan de basis van de bloeiwijzen, aanwezigheid van haren op het vruchtbeginsel, vorm van de bloemdekbladen, aanwezigheid en vorm van de zijlobben en het aantal kielen op de lip en de aanwezigheid van een gewimperde rand aan de lip blijken goede kenmerken te zijn voor het onderscheiden van monofyletische groepen van soorten binnen de Coelogyninae en *Coelogyne*. Het aantal bladen per pseudobulb, grootte van de bloemen, vorm van de basis van de lip en bloemdekbladen en aanwezigheid van stelidia (= uitsteeksels op het zuiltje) en calli (= verdikkingen) op de lip blijken niet fylogenetisch informatief te zijn.

Met de resultaten van de gezamelijke fylogenetische analyse als referentiekader wordt een begin gemaakt met een systematische bewerking van het gehele geslacht *Coelogyne*. Een fylogenetische analyse met *matK* en ribosomaal kern DNA (ITS) sequenties en morfologische kenmerken van de 16 soorten uit sect. *Speciosae* (Hoofdstuk 4) en acht soorten uit sect. *Verrucosae* (Hoofdstuk 6) werd gebruikt om de monofylie van deze groepen vast te stellen en verwantschappen tussen de soorten te onderzoeken. Een complex van de sterk verwante soorten uit sect. *Fuliginosae* (Hoofdstuk 5) werd opgelost met behulp van een fenetische analyse (= op basis van similariteit) van morfologische kenmerken. Deze laatste drie hoofdstukken bevatten beschrijvingen van alle soorten (waaronder drie nieuwe), synoniemen, foto’s, tekeningen, verspreidingskaartjes en determinatiesleutels.

Chapter 1

GENERAL INTRODUCTION

GOAL OF SYSTEMATICS

Systematics has two fundamental aims:

1) to discover, describe and name all species – the tips of the branches of the tree of life, and
2) to document the changes on the branches that have occurred during evolution and transform these into a predictive classification system that reflects evolution (Systematics Agenda 2000). Systematics is therefore the study of the biological diversity that exists on earth today and its evolutionary history (Judd et al., 1999).

In the first half of this introduction the main aspects of the practice of systematics are briefly discussed. An overview of these aspects and the sequence in which they are performed is also presented as a flow-chart (Fig. 1.1). In the second half the main subject of this study (the orchid genus *Coelogyne*) is introduced and the aims and outlines of this thesis are explained.

Recognition of species

To describe the tips of the branches of the tree, for practical reasons it is necessary to have a clear idea of the species concept taken as a starting point. In this thesis, the morphological species concept of Van Steenis (1957) is used. Distinct species are recognised when at least two morphological character (states) indicate substantial differences. Specimens, without two clearly fixed morphological differences are considered to belong to the same species.

Recognition of two morphological characters defining a species is a personal choice: what one taxonomist considers as a good delimitation character can be dismissed as irrelevant by a colleague, who studied more material. Ideally, molecular data should be collected to provide more information about permanent decreasing gene flow between different populations in the process of speciation. However, only few living collections were available for most of the species studied in this thesis, and DNA extracted from herbarium specimens turned out to be too degraded in most of the cases.

Why is this particular species concept used? The morphological species concept has some advantages over other concepts:

1) selfing individuals (quite common in plants and also present in *Coelogyne*) do not need to be called new species, as they should according to the biological (Mayr, 1942) and recognition (Patterson, 1985) species concept;
2) evolutionary lineages can be identified by a specific morphologically based criterion, instead of only assumed to be there, like in the evolutionary species concept (Simpson, 1951);
3) the fixation of two morphological characters is easier to recognise than monophyly, the criterion of the phylogenetic species concept (Cracraft, 1983);

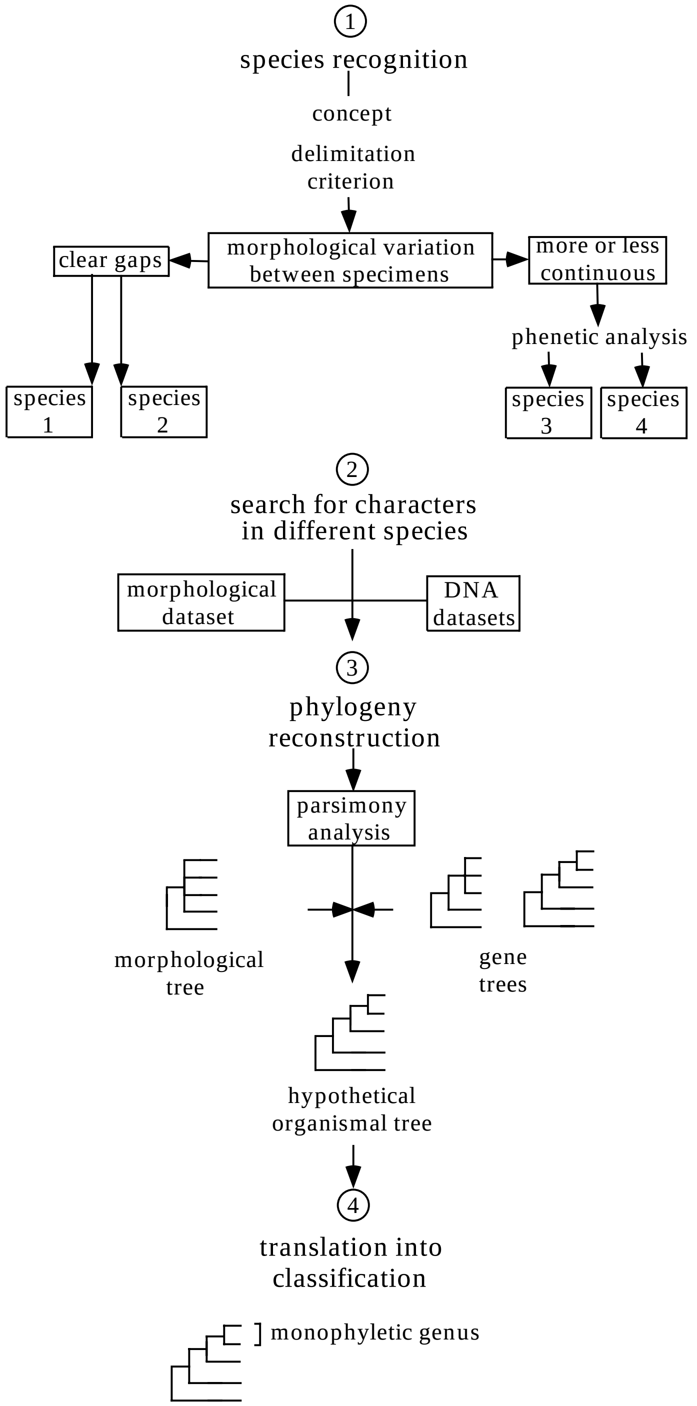

Fig. 1.1. Flow-chart of the main aspects of the practice of systematics.

4) as species are used as terminal units in phylogeny recontruction, the historical aspect should be more fundamental to a species than its morphological distinctness. However, permanence of character fixation, as required for the recognition of phylogenetic (Cracraft, 1983) or composite species (Kornet, 1993) could not be assessed in the *Coelogyne* specimens studied for this thesis, as they were all collected in the same time-slice. Moreover, these concepts require information about the permanency of splits between populations, which is difficult to assume without extra information, as many species of this study show overlaps in distribution areas.

For most of the species in this study clearly fixed morphological differences were present and species delimitation was not problematic. However, in two groups of closely related taxa, variation of most morphological characters studied appeared to be more or less continuous. Phenetic methods were used to find gaps in multivariate morphometric space and search for a good combination of delimiting characters. These methods are suitable for solving difficult species complexes, as they do not impose a rigidly hierarchical pattern on the data when none is to be expected (Crisp & Weston, 1993).

In this thesis, a species can be paraphyletic (consisting of an ancestor with only part of all its descendants). To put it more precisely, the species is not paraphyletic, but it can be a group of paraphyletic populations. Only part of the populations of one species is active in forming a new species, thus the remaining populations, which are consequently paraphyletic, remain as ancestral species. On the species level therefore, taxon names in this thesis do not solely refer to monophyletic groups (consisting of an ancestor with all its descendants), in contrast with Pleijel (1999).

Search for characters

In this thesis sequence data are the main information used for the reconstruction of evolutionary histories. This is not based on the belief that morphological information is worthless, but rather that it is extremely difficult to interpret morphological variation accurately in Orchidaceae (Chase, 1999). If sequence divergence stays below 15%, alignment is usually straightforward and the homology of a change is easily assessed (Patterson, 1988). Homology of morphological characters is often much more difficult to interpret accurately without time-consuming ontogenetic and anatomical studies. Moreover, generic delimitation in the Orchidaceae has long been based mainly on floral traits which are associated with pollinator attraction. Several recent studies show that floral characters mapped on molecular cladograms can be very homoplasious (Dressler, 1981; Chase & Palmer, 1992; Hapeman & Inoue, 1997).

Reconstructions of evolutionary histories based on sequence data are called gene trees. Caution must be exercised to directly translate these gene trees into organismal trees, as processes of introgression, gene duplication, loss and lineage sorting can cause incongruence (Page & Charleston, 1997). Congruence between different gene trees is often assumed to be strong evidence for an accurate estimate of the organismal tree (Slowinski & Page, 1999). That is why in this study information was collected from multiple DNA regions, representing both coding and non-coding as well as slowly evolving plastid and more divergent nuclear regions.

Reconstruction of the phylogeny

To reconstruct the evolutionary history of a group of organisms, a hypothesis on the genealogical relationships (a so-called phylogeny) has to be made. A phylogeny is an evolutionary chronicle. Evolutionary relationships are inferred by using various kinds of evidence: in this thesis molecular, morphological and, to a lesser extent, anatomical characters are used. A group of organisms that shares many identical states in these characters (for instance six shared mutations in the *matK* gene of the plastid genome, hairy ovaries and trichomes with acute top on the leaves) is considered to be closely related and are assumed to be derived from a common ancestor. This ancestor, together with all its descendants, forms a monophyletic group: a group that exists in nature as a result of the historical process of evolution. By comparison with outgroups (taxa assumed to be closely related with the organisms under study based on earlier collected evidence) characters are polarised: the states also occurring in the outgroup are considered to be plesiomorphic, the states in (part of) the ingroup (the group of interest) apomorphic. Presumed synapomorphies are used to investigate the relationships between taxa in the ingroup.

A phylogeny can be represented as a branching diagram, a so-called cladogram. Most optimal cladograms in this thesis are reconstructed using the parsimony criterion, in which the character transformations on the branches of a cladogram are minimised. Most current methods of phylogeny reconstruction impose hierarchical patterns, which are incompatible with reticulate patterns caused by hybridisation. However, hybridisation between both closely and more distantly related taxa frequently produces new plant species. Divergently branching phylogenetic hypotheses cannot be used to detect hybrids, as their behaviour can be identical to that of nonhybrid taxa (McDade, 1990). Few natural hybrids are known to exist among the *Coelogyne* species studied for this thesis. However, for one species incongruency was found between the phylogeny based on the uniparentally inherited plastid genome and the phylogeny based on recombined nuclear data. Incongruencies between nuclear and organellar phylogenetic trees are often attributed to introgression of a cytoplasmic genome from one species into the nuclear background of another species (Wendel & Doyle, 1998). The nuclear DNA is assumed to be eliminated through backcrossing to the other parental species, whereas the plastid DNA was retained, and is now coupled with the nuclear genome of the other species. However, introgression is not the only process that could produce incongruencies. A second cause might be coalescence of alleles antedating species divergence (lineage sorting). It is difficult to distinguish between introgression and lineage sorting, because they both may produce similar phylogenetic patterns (Hardig et al., 2000). However, there are relatively few examples of plastid DNA polymorphisms that transcend species boundaries, probably because of the generally slow rate of plastid DNA evolution (Wendel & Doyle, 1998). Therefore, hybridisation due to introgression appears to be the most probable explanation for the incongruence found in this study.

Translation into a classification

Once the phylogeny is reconstructed, the knowlegde of this part of the tree of life – of the tips and terminal branches and all their phylogenetic relationships to one another – can be translated into an unambiguous system of classification. The main aim of classifications is enabling communication by naming supra-specific categories. This has nothing to do with evolution. Naming is entirely an abstraction and can be made to fit whatever criteria we wish.

Different types of classifications exist. The traditional system is the Linnaean classification. In this system, the names of organisms are anchored by reference to a rank (species, genus, family, order). The stability of this system depends largely on taxonomists choosing to agree on the general membership of named groups (Baum et al., 1998). In this thesis, the phylogenetic classification system is used, in which only monophyletic groups are recognised: taxa are not anchored by rank but by reference to phylogenetic relationships with other taxa (De Queiroz & Gauthier, 1990). Using only monophyletic groups is impossible in the Linnaean classification system, because of its mandatory ranks: at one level all groups in this system would cause an enormous proliferation of ranks and ancestral species cannot be included (Brummitt, 1997; Van Welzen, 1997). Maintaining the Linnaean classification system therefore inevitably leads to acceptance of paraphyletic taxa (Sosef, 1997).

In this thesis, classifications are strictly based on monophyletic groups. This is done because the criterium of common descent is objective and makes the system defendable instead of intuitive (Líden et al., 1997; Van Welzen, 1998), in contrast with traditional classifications, which are guided by authority and convention (Baum et al., 1998). Moreover, evolution is now the unifying theory of biology, so modern biology requires taxonomy reflecting evolution (De Queiroz & Gauthier, 1994). According to Sosef (1997) reticulate patterns make the monophyletic hierarchical model unfit for classification of the world around us. On the species level, paraphyly is indeed accepted in this thesis, as hybridisation between different populations is assumed to produce new species. On higher taxonomic levels, however, hybridisation is assumed to be nearly absent and paraphyly is therefore considered unacceptable.

THE GENUS COELOGYNE

Lindley described the orchid genus *Coelogyne* in 1821, naming it *Caelogyne* (from the greek ‘koilos ’ = ‘hollow’ and ‘gyne ’ = ‘female’) because of the concave stigma. Soon after he corrected this spelling to *Coelogyne* (Lindley, 1825). *Coelogyne* is characterised by a free, never-saccate lip with high lateral lobes over the entire length of the hypochile and smooth, papillose, toothed or warty keels (Seidenfaden & Wood, 1992). The genus comprises over 200 species distributed throughout southeast Asia with main centers of diversity in Borneo, Sumatra and the Himalayas (Butzin, 1992a).

Most *Coelogyne* species are epiphytes and occur in primary forest, from sea level up to c. 3000 m elevation. For example, in the lowland Dipterocarp-dominated rainforest of Peninsular Malaysia, Sumatra and Borneo, *C. asperata*, *C. septemcostata* and *C. xyrekes* are quite common on the trunks and main branches of trees along the river banks, where the light regime is more favourable compared with the shaded forest interior (Chan et al., 1994). In the lower montane rainforest of Java, *C. flexuosa* and *C. miniata* are growing in dense clumps on mossy rocks in high light levels (Comber, 1990). In montane cloud forest of the Himalayan range, where the climate is seasonally dry and temperatures are relatively low, *C. cristata*, *C. fimbriata* and *C. flaccida* occur on trees, covered with thick coats of mosses (Sparrow, 1995). In the alpine scrub vegetations of Mount Kinabalu, *C. papillosa* can be found, growing as a lithophyte or even as a terrestrial (Wood et al., 1993). In New Guinea *C. fragrans* often grows low down on the trunks of small trees in rather open montane forest, where the plants catch large amounts of leaf-litter. At somewhat lower elevations *C. beccarii* occupies similar niches in Castanopsis-dominated forest and in forest on the ridges of limestone hills (Schuiteman, pers. comm.).

Most species are characterised by a fairly large number of medium-sized to large flowers with delicate colours and a sweet scent and are pollinated by bees (Van der Pijl & Dodson, 1966), beetles (O'Byrne, 1994) or wasps (Carr, 1928; Dressler, 1981). A selection of species with long, pendulous, multiflowered inflorescences is widely cultivated and known as the necklace orchids (De Vogel, 1992). The number of recent artifical hybrids published indicates the growing commercial interest in this group (Erfkamp & Gruß, 1996). Concerning chromosome numbers, two polyploid series are present in the genus, with n = 19 (2n = 38; 4n = 76) in several species and n = 20 (2n = 40; 4n = 80) in the majority of the species studied according to Mehra & Kashyap (1989) and Brandham (1999).

Generic and sectional delimitations of Coelogyne

Coelogyne is placed in subtribe Coelogyninae (tribe Coelogyneae, subfamily Epidendroideae) with a total of approximately 550 species (Pedersen et al., 1997). Synapomorphies of the subtribe are sympodial growth, pseudobulbs of one internode, terminal inflorescences, a winged column and massive caudicles (Dressler, 1981; De Vogel, 1986; Butzin, 1992b). Within this subtribe, 16 genera are currently recognised (Pedersen et al., 1997). However, numerous taxonomists have proposed different subdivisions. A summary of the most important opinions on the classification of subtribe Coelogyninae is given in Chapter 3. In phylogenetic analyses 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 (Chase et al., unpubl.) *Thunia alba* (Lindl.) Rchb.f. is placed as sister taxon to Coelogyninae.

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 (1907d) published an entirely new classification of 14 sections. 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 subdivisions, of which 12 are identical with those of Pfitzer & Kraenzlin. Differences of opinion are mainly due to the relative lack of morphological characters available to define groups of species. For instance, both sect. *Coelogyne* and *Ocellatae* are defined by white flowers with yellow keels. Many characters are known to intergrade among the species of different sections, too. For example, the presence of hairs on the ovary has been used to define sect. *Tomentosae* (De Vogel, 1992). However, this character is likely to have evolved convergently in section / subgenus *Coelogyne*, *Cyathogyne*, *Rigidiformes*, *Veitchiae* and *Verrucosae*. Conflicts in the assignment of species to different sections in *Coelogyne* have been present in the literature for years (see Chapter 3 for a summary of the most important opinions on infrageneric classifications in *Coelogyne*), but there was an impasse about how to proceed. The phylogenetic analyses performed with the molecular and morphological data collected for this research have provided new insights.

Aims and outlines of this thesis

The aims of this thesis are:

1) the reconstruction of a skeleton phylogeny of the orchid genus *Coelogyne* and allied genera;
2) the incorporation of this phylogeny into a phylogenetic classification and
3) a taxonomic revision of a selection of monophyletic groups of *Coelogyne* species.

Chapter 2 provides a general framework of *Coelogyne* and allied genera in the Coelogyninae based on plastid PCR RFLPs and plastid and nuclear sequences. The results of this analysis show that *Coelogyne* as currently defined is not a monophyletic group because it is composed of two unrelated groups of species. Several of the floral traits that previous authors used to recognise this concept of the genus (the 'key' characters) appear not to be phylogenetically informative. Possible taxonomic solutions are discussed and a new classification of the genus is proposed.

Chapter 3 deals with the integration of this molecular phylogeny with results of a morphological analysis. More insight is gained in the evolution of specific morphological traits by reconstructing their character state evolution on a total evidence tree. Some clades in Coelogyninae remain unresolved in the total evidence phylogeny. Others cannot be easily recognised by morphological characters yet. These are the drawbacks that often accompany new phylogenetic classifications. Still, these disadvantages are to be preferred above the traditional classification, because we now have an empirically based taxonomy in which taxa are assigned a position in a phylogenetic system. Possibilities for bringing more resolution in the unresolved groups are briefly discussed at the end of Chapter 3.

With the phylogenetic boundaries of Chapter 3 as a reference, a start with a taxonomic treatment of the whole genus is made in Chapters 4, 5 and 6, which focus on three differrent monophyletic groups of species. An integrated phylogenetic analysis of morphological and molecular characters is performed for the species of sect. *Speciosae* (Chapter 4) and sect. *Verrucosae* (Chapter 6), whereas a complex of the closely related species of sect. *Fuliginosae* is resolved with a phenetic analysis using morphological characters (Chapter 5). For the three sections, a taxonomic treatment of all species is provided, with descriptions, colour photos, drawings, distribution maps and identification keys. Three new species are described and several others are reduced to synonymy. Revisions of other monophyletic groups within the new boundaries of *Coelogyne* are planned for the near future.

Chapter 2

MOLECULAR PHYLOGENY OF COELOGYNE (EPIDENDROIDEAE, ORCHIDACEAE) BASED ON PLASTID RFLPS, *MATK* AND NUCLEAR RIBOSOMAL ITS SEQUENCES: EVIDENCE FOR POLYPHYLY

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SUMMARY

Subtribe Coelogyninae (Epidendroideae, Orchidaceae) presently comprises 16 genera. To evaluate the monophyly of one of these genera, *Coelogyne* Lindl., and reveal sectional relationships and relations to allied genera, we collected PCR RFLPs from 11 plastid regions for 42 taxa in Coelogyninae (28 *Coelogyne* species and 14 representatives of other genera) and three outgroups from Bletiinae and Thuniinae. In addition, we sequenced a large portion of the plastid *trnK* intron (mostly *matK*) and the nuclear ribosomal DNA internal transcribed spacers ITS1 and ITS2 (including the 5.8S gene). Separate phylogenetic analyses on each dataset using maximum parsimony produced mainly congruent (except for the position of *Panisea*) but weakly supported clades. Parsimony analysis of the combined data clearly identified three main clades in Coelogyninae: I) *Bracisepalum*, *Chelonistele*, *Dendrochilum*, *Entomophobia*, *Geesinkorchis* and *Nabaluia* nested within *Coelogyne*; II) *Neogyna* and *Pholidota* nested within the remainder of species of *Coelogyne* sampled; III) *Pleione*. Whereas Coelogyninae are monophyletic, *Coelogyne* is polyphyletic, with species falling into at least two well supported clades. The utility of some morphological characters used in traditional classifications was explored by reconstructing character state evolution on the combined molecular consensus tree. Lip base and petal shape appeared to be homoplasious, whereas ovary indumentum and flower number were highly congruent with well supported groups. The implications of our results for the classification of *Coelogyne* are discussed and a reorganisation of the genus by including *Neogyna* and *Pholidota* and removing several species is proposed.

Key words: Orchidaceae, Coelogyninae, *Coelogyne*, molecular phylogeny, plastid DNA RFLPs, *matK*, nuclear rDNA ITS.

INTRODUCTION

The orchid genus *Coelogyne* Lindl. comprises over 200 species distributed throughout southeast Asia with main centers of diversity in Borneo, Sumatra and the Himalayas (Butzin, 1992a). Most species are epiphytes, occuring in tropical lowland and montane rainforests. In open, humid environments, some species may also grow as lithophytes

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or even as terrestrial plants (Comber, 1990). Most species are characterised by medium-sized to large flowers with a sweet scent and are pollinated by bees (Van der Pijl & Dodson, 1966), beetles (O'Byrne, 1994) or wasps (Carr, 1928; Dressler, 1981). The number of recent artifical hybrids published indicates the growing commercial interest in this group (Erfkamp & Gruβ, 1996).

Although revisions of several sections of *Coelogyne* were published in the last decade, a comprehensive treatment of all species is still lacking. This is partly caused by the problematic delimitation of groups within the genus. Pfitzer & Kraenzlin (1907d) grouped the species of *Coelogyne* into 14 sections. In contrast, Holttum (1964) proposed only 4 and De Vogel (1994) and Clayton (in press) 23 subdivisions. These large differences in opinion are due not only to the rather large number of species in the genus, but also the relative lack of morphological characters available to define groups of species. For example, the presence of hairs on the ovary has been used to define sect. *Tomentosae* (De Vogel, 1992). However, this character is likely to have evolved convergently in section/subgenus *Coelogyne*, *Cyathogyne*, *Rigidiformes*, *Veitchiae* and *Verrucosae*. The naturalness and relationships of the sections and subgenera of *Coelogyne* were not previously examined in a phylogenetic context.

Coelogyne is one of the 16 genera in subtribe Coelogyninae (tribe Coelogyneae, subfamily Epidendroideae) with a total of approximately 550 species (Pedersen et al., 1997). Synapomorphies of the subtribe are sympodial growth, pseudobulbs of one internode, terminal inflorescences, a winged column and massive caudicles (Dressler, 1981; De Vogel, 1986; Butzin, 1992b). *Coelogyne* Lindl. is defined by a free, never-saccate lip with high lateral lobes over the entire length of the hypochile and papillose, toothed or warty keels (Seidenfaden & Wood, 1992). The genus is defined merely by the absence of characters, such as a saccate lip base (present in all other genera of the subtribe) or a lip adnate to the column (present in *Neogyna* Rchb. f. and *Gynoglottis* J.J. Sm.; Butzin, 1992b). In addition, many characters intergrade among the genera of the subtribe. For example, a lip with small, inconspicuous lateral lobes characterises both *Chelonistele* Pfitzer and *Panisea* (Lindl.) Steud. (De Vogel, 1986; Lund, 1987).

A phylogenetic survey of *Coelogyne* and related genera of Coelogyninae using molecular characters can provide a preliminary phylogenetic classification and serve as a historical framework for evaluating hypotheses of morphological character evolution. The aims of this study are to use phylogenetic analyses of molecular data to:

1) address the generic circumscription and sectional and subgeneric relationships within *Coelogyne*;
2) investigate the relationships of *Coelogyne* with its allies in subtribe Coelogyninae;
3) determine whether some previously used morphological key characters are phylogenetically informative.

To accomplish these goals, parsimony analyses were conducted on PCR RFLP data of 11 regions of the plastid genome and sequence data from both the *trnK* intron (mostly *matK*) and the nuclear rDNA ITS regions.

PCR RFLPs were expected to be useful in reconstructing phylogenetic relationships within the genus *Coelogyne* based on previous RFLP studies in Orchidaceae (Chase & Palmer, 1992; Yukawa et al., 1993; Freudenstein & Doyle, 1994). PCR RFLPs provide a rapid way of sampling many parts of the genome, which have evolved at different rates and under different constraints (Gielly & Taberlet, 1994). They provide information on multiple DNA regions, which in our view is better than having only two gene sequence data sets.

The *trnK* intron has been used for phylogeny reconstruction at a variety of taxonomic levels in angiosperms (Soltis & Soltis, 1998). In Orchidaceae, it has been used at generic (Whitten et al., in press) and species level (Ryan et al., 2000). The nuclear rDNA ITS regions have been used extensively to infer phylogenetic relationships in Orchidaceae at both tribal (Douzery et al., 1999), generic (Pridgeon et al., 1997) and species level (Cox et al., 1997).

MATERIALS AND METHODS

Plant samples

To determine the position of *Coelogyne* in subtribe Coelogyninae and relationships within *Coelogyne*, 45 taxa were analyzed. The sampling includes 18 of the 23 sections / subgenera currently recognised within *Coelogyne* and 11 of the 16 genera of Coelogyninae. Morphologically uniform sections / (sub)genera are represented by a single taxon only, whereas more variable groups are represented by several species. Not included were five small sections of *Coelogyne* (sect. *Ancipites* Pfitzer, *Fuscescentes* Pfitzer & Kraenzl., *Micranthae* Pradhan, *Ocellatae* Pfitzer and *Proliferae* Lindl.) and five mostly monotypic genera (*Bulleya* Schltr., *Dickasonia* L.O. Williams, *Gynoglottis* J.J. Sm., *Ischnogyne* Schltr. and *Otochilus* Lindl.). Outgroups were sampled from tribe Arethuseae, subtribes Bletiinae and Thuniinae, 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 (Chase et al., unpubl.). Voucher specimens are listed in Table 2.1 and deposited at K or L.

DNA extractions

Total genomic DNA was extracted from 50 mg of leaf tissue following the 2x CTAB method of Doyle & Doyle (1987). Some samples were purified through a cesium chloride / ethidium bromide gradient (1.55 g ml^{-1}). Leaf material was taken from one individual per species.

PCR RFLPs

RFLPs were detected by digesting three coding (16S, *psbA*, *psbD*) and eight non-coding regions (*trnT-trnL, trnL, trnL-trnF, trnC-trnD, trnS-psaA, atpB-rbcL, psbA-trnH, petA-psbE*) of the plastid genome using 19 restriction enzymes: *Bam*HI, *Bcl*I, *Bgl*II, *Bsm*I, *Cla*I, *Dra*I, *Eco*RI, *Eco*RV, *Hind*III, *Nde*I, *Nsi*I, *Pst*I, *Pvu*II, *Sac*I, *Sca*I, *Ssp*I, *Xba*I (six base cutters), *Dde*I (five base cutter), and *Hinf*I (four base cutter). Primers used were from Demesure et al. (1995), Fofana et al. (1997), Sang et al. (1997), Savolainen et al. (1995), Tsumura et al. (1995) and Taberlet et al. (1991). The thermal cycling protocol comprised 3 min. denaturation at 94 ºC, followed by 35 cycles, each with 45 sec. denaturation at 94 ºC, 45 sec. annealing at 50–57 ºC and an extension of 2 min. at 72 ºC, concluding with an extension of 10 min. at 72 ºC. Digested PCR products were separated on 1.5 – 2% agarose gels and stained with ethidium bromide to detect polymorphisms. The sizes of the fragments were determined with reference to two markers, a *Hind*III-*Eco*RI digested lambda bacteriophage DNA marker and a 100-bp marker.

Table 2.1. List of species analysed. Arranged by (sub)tribe, section and (sub)genus 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)
		Panisea tricallosa Rolfe		China	*Leiden cult. 970828* (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 eberhardtii Gagnep.	*Lawrenceanae*	Vietnam	*Leiden cult. 970803* (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 rochussenii de Vriese	*Tomentosae*	unknown	*Leiden cult. 27060* (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)

matK and ITS amplifications

The *trnK* intron (mostly *matK*) was amplified with the following four primers: -19F (5’-CGTTCTGACCATATTGCACTATG-3’) and 881R (5’- TMTTCATCAGAATAAGAGT-3’); 731F (5’-TCTGGAGTCTTTCTTGAGCGA-3’) and 2R (5’-AACTAGTCGGATGGAGTAG-3’). All primers were designed at the Royal Botanic Gardens, Kew, except for 2R (Johnson & Soltis, 1994). The thermal cycling protocol comprised 28 cycles, each with 1 min. denaturation at 94 ºC, 30 sec. annealing at 48 ºC, an extension of 1 min. at 72 ºC, concluding with an extension of 7 min. at 72 ºC. All PCR products were sequenced directly after purification with QIAquick purification columns (QIAGEN, Amsterdam, The Netherlands). Four sequencing reactions were performed for each completed sequence, one with each of the four PCR primers, and these generated nearly complete overlapping single strand sequences for the *trnK* intron fragments.

ITS1 and ITS2 spacers along with the 5.8S gene were amplified with the primers 17 SE (5’-ACGAATTCATGGTCCGGTGAAGTGTTCG-3’) and 26SE (5’-TAGAATTCCCCGGTTCGCTCGCCGTTAC-3’) from Sun et al. (1994). The thermal cycling protocol comprised 26 cycles, each with 10 sec. denaturation at 96 ºC, 5 sec. annealing at 50 ºC and extension of 4 min. at 60 ºC. All PCR products were cloned following the protocol of Promega’s pGEM-T Easy Vector System and then reamplified from transformed bacterial colonies by touching them with a sterile pipet tip and using that as template. Two sequencing reactions were performed for each completed sequence, one with each of the two PCR primers, and these generated nearly complete overlapping single strand sequences for the entire ITS fragments.

All amplified, double-stranded DNA fragments were purified using Wizard PCR minicolumns (Promega, Madison, Wisconsin, USA) and sequenced on an ABI 377 automated sequencer (PE Applied Biosystems, Inc.), using standard dye-terminator chemistry following the manufacturer’s protocols.

Phylogenetic analyses

Variable restriction sites were coded as present or absent. Length variations were not included as characters in the analyses. Sequences were aligned by using MegAlign version 4.03 (DNASTAR, Inc. 1999) with subsequent adjustment by hand. Characters at position 143–170 bp were excluded from the ITS sequence data due to ambiguous alignment. Sequences are deposited in GenBank (AF302692 untill AF302761) and TREEBASE (SN570). The *matK* and ITS alignments and the PCR RFLPs data set are available from the first two authors upon request: e-mail gravendeel@nhn.leidenuniv.nl or m.chase@rbgkew.org.uk.

Maximum parsimony (MP) analysis was performed on the RFLP and sequence 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 molecular characters were assessed as independent, unordered and equally weighted using Fitch parsimony (Fitch, 1971). Indels were coded as missing data only. Number of transversions and their CIs and RIs were calculated on one of the MPTs of the combined analysis by using a stepmatrix with zero weights for transitions and the TREE SCORE command (ACCTRAN optimisation). From these data the number of transitions and their CIs and RIs were calculated. To evaluate monophyly, trees were constrained using the enforce topological constraints option in PAUP*. 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. The decay index (Bremer, 1994) was also calculated using the branch and bound option to examine trees up to six steps longer than the shortest tree found for each data set. Congruence of the separate data sets was assessed by visual inspection of the individual bootstrap consensus trees. Bootstrap trees were considered incongruent only if they displayed 'hard' (i.e. bootstrap percentages > 80) incongruencies (Weins, 1998).

To explore the phylogenetic utility of some traditionally used morphological characters in classifications of the Coelogyninae, character state evolution of the shape of the lip base and petals, presence of hairs on the ovary and flower number per inflorescence was reconstructed using the assumptions of maximum parsimony with the Trace Character facility in MacClade version 3.04 (Maddison & Maddison, 1992). A complete phylogenetic analysis with morphological characters in *Coelogyne* and allied genera will be addressed in a separate publication.

RESULTS

PCR RFLP analysis

Four of the amplified regions were uninformative (16S, *psbA*, *psbD*, *trnL*-*trnF*). A total of 38 restriction sites was observed in the remaining seven regions. Of these, 15 were invariant, three were autapomorphies and the remaining 20 were potential synapomorphies (Table 2.2). MP analysis yielded >10,000 most parsimonious trees (length = 61, CI = 0.56, RI = 0.77; Table 2.3).

The RFLPs bootstrap consensus tree shows little resolution. Five weakly supported (< 50%) clades are present: *Chelonistele*, *Coelogyne foerstermannii* plus *C. sanderiana* (sect. *Coelogyne*), sect. *Verrucosae*, *C. fimbriata* (sect. *Fuliginosae*) plus *C. stricta* (sect. *Elatae*), and *Pleione*.

matK sequence analysis

Length ranges of the *matK* gene and its flanking *trnK* sequences for Coelogyninae were 1536–1544 bp and 221–245 bp respectively. Boundaries of the *matK* gene were taken from Johnson & Soltis (1994). The final alignment has a total length of 1939 sites (1554 and 385 sites, resp.), of which 272 are variable and 119 potentially phylogenetically informative; there is one autapomorphic indel of 8 bp in the *matK* gene and five synapomorphic indels in the flanking *trnK* sequences, ranging in size from 4–19 bp. The transition/transversion ratio is 0.83, higher than the ratios found in Orchidaceae so far (Whitten et al., in press), but lower than the ratios found in dicots (Soltis & Soltis, 1998). Third-codon positions contributed the most steps (163 on the combined tree), slightly more than first or second positions, but all three sites displayed equal CI and RI values (Table 2.4 & 2.5). The average number of changes per variable site is 1.4 (Table 2.3). The MP analysis yielded >10000 most parsimonious trees (length = 394, CI = 0.77, RI = 0.79; Table 2.3). The *matK* bootstrap consensus tree is congruent with the results of the RFLP data, but shows more resolution at the (sub)generic level.

Table 2.2. Restriction site data used in the phylogenetic analysis.

Region	Informative restriction enzymes	Length and variation (bp)
16S	–	1400
psbA	–	1000
psbD	–	1100
trnL-trnF	–	500 ± 50
trnC-trnD	*Bgl*I, *Cla*I, *Dde*I, *Eco*RI	4500 ± 100
trnS-psaA	*Bam*HI, *Cla*I, *Eco*RI	4200 ± 50
petA-psbE	*Bam*HI, *Cla*I, *Dde*I, *Dra*I, *Ssp*I	2000 ± 100
atpB-rbcL	*Dra*I	1400 ± 50
trnL	*Dra*I, *Eco*RI, *Eco*RV	750 ± 50
trnH-psbA	*Hinf*I	700 ± 50
trnT-trnL	*Bcl*I, *Bgl*II, *Eco*RI	670 ± 50

Therefore, all plastid data were combined in a single analysis. The bootstrap consensus topology and the corresponding bootstrap percentages and decay values of this analysis are indicated in Fig. 2.1.

According to the combined plastid data the Coelogyninae excluding *Pleione* are monophyletic, but bootstrap support for placing *Pleione* outside Coelogyninae is low (<50%). Two sister clades within the subtribe are moderately supported. The first clade consists of species of *Bracisepalum*, *Chelonistele*, *Dendrochilum*, *Entomophobia*, *Geesinkorchis*, *Nabaluia*, *Coelogyne* sect. *Coelogyne*, *Cyathogyne*, *Tomentosae*, *Veitchiae* and *Verrucosae* (60%). Four smaller sets of taxa in this first major clade are recovered in all bootstrap replicates: *Bracisepalum selebicum* together with *Dendrochilum*, *Chelonistele*, *Coelogyne dayana* plus *C. rhabdobulbon* (sect. *Tomentosae*),

Table 2.3. Values and statistics from parsimony analyses of separate and combined data matrices.

	RFLPs	*matK*	all plastid data	ITS1-5.8S-ITS	combined
number of included positions in matrix	23	1939	–	729	–
number of variable sites	23	272 (14%)	–	436 (66%)	–
number of phylogenetically informative sites	20	119	–	224	–
number of MPTs	10,000+	10,000+	174	32	4
tree length	61	394	474	1355	1729
CI	0.56	0.77	0.71	0.57	0.60
RI	0.77	0.79	0.75	0.53	0.57
average number of changes per variable site	3.4	1.4	–	2.5	–
length on combined tree	73	377	–	1092	–
number of clades in bootstrap consensus with >80% support	0	7	7	8	11

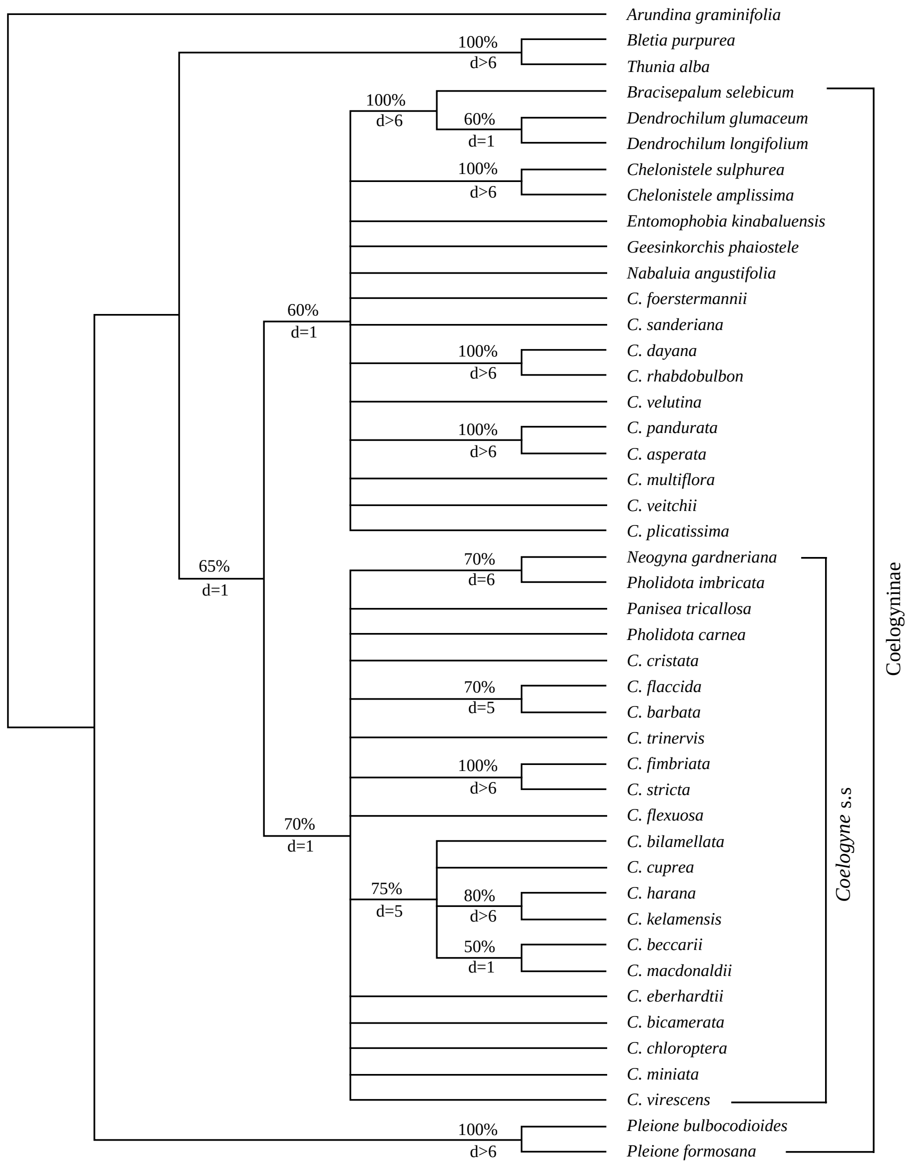


Fig. 2.1. Bootstrap consensus of 174 trees from parsimony analysis of all plastid data with bootstrap percentages and decay values (only percentages > 50% are given).

and sect. *Verrucosae*.

The second major subclade consists of species of *Neogyna*, *Panisea*, *Pholidota*, *Coelogyne* sect. *Bicellae*, *Brachypterae*, *Coelogyne*, *Elatae*, *Flaccidae*, *Fuliginosae*, *Hologyne*, *Lawrenceanae*, *Lentiginosae*, *Longifoliae*, *Moniliformes*, *Ptychogyne* and *Speciosae* (70%). Two strongly supported smaller sets of taxa are present in this second major clade: *Coelogyne fimbriata* (sect. *Fuliginosae*) plus *Coelogyne stricta* (sect. *Elatae*) (100%), and sect. *Moniliformes* (80%).

ITS sequence analysis

Length ranges of nuclear rDNA ITS sequences for Coelogyninae were 204–253 bp,159–163 bp, and 242–271 bp respectively. Boundaries from the 5.8S gene are taken from Hershkovitz & Lewis (1996). One region of 30 bp in ITS1 was considered unalignable and was excluded. The final alignment has a total length of 759 sites (286, 165, and 308 sites for ITS1, 5.8S and ITS2, resp.). Of the included positions, 436 are variable and 224 potentially phylogenetically informative, which is in accordance with variation levels in most angiosperms (Baldwin et al., 1995). The transition/transversion ratio is 1.68 in the ITS1 spacer and 1.56 in the ITS2 spacer region (Table 2.4), which is in accordance with ratios found in Orchidaceae so far (Cox et al., 1997; Pridgeon et al., 1997; Whitten et al., in press). The average number of changes per variable site is 2.5 (Table 2.3). The MP analysis yielded 32 most parsimonious trees (length = 1355, CI = 0.57, RI = 0.53; Table 2.3). The bootstrap consensus topology and the corresponding bootstrap percentages and decay values are indicated in Fig. 2.2.

The ITS bootstrap consensus tree shows less resolution than the combined plastid data. The monophyly of Coelogyninae including *Pleione* is strongly supported (90%). Six strongly supported clades are present: *Bracisepalum selebicum* together with *Dendrochilum* (100%), *Chelonistele sulphurea* plus *Entomophobia kinabaluensis* (100%), sect. *Verrucosae* (100%), sect. *Moniliformes* (100%), *C. eberhardtii* (sect. *Lawrenceanae*) plus *C. miniata* (subgenus *Hologyne*) (90%), and *Pleione* (100%). Many other clades are weakly supported (< 80%).

Combined analysis

Bootstrap consensus trees of the three individual data sets revealed no hard incongruences except for the placement of *Panisea*. To improve resolution, a combined analysis of all three data sets (excluding *Panisea*) was performed (Huelsenbeck et al., 1996). The combined matrix yielded four most parsimonious trees (length = 1729; CI = 0.60; RI = 0.57; Table 2.3). Bootstrap analyses of the combined data set (excluding *Panisea*) provided more resolution and higher internal support for relationships (> 80%) than did any of the individual data sets (Table 2.3). One of the four most parsimonious trees with the corresponding bootstrap percentages and decay values are shown in Fig. 2.3.

In the combined analysis of all molecular data, the Coelogyninae including *Pleione* receive strong support (90%). Three main clades in Coelogyninae are present. In the first major clade, species of *Bracisepalum*, *Chelonistele*, *Dendrochilum*, *Entomophobia*, *Geesinkorchis* and *Nabaluia* are nested within species of *Coelogyne* sect. *Coelogyne*, *Cyathogyne*, *Tomentosae*, *Veitchiae* and *Verrucosae* (80%). Four smaller subsets of taxa are recovered in all bootstrap replicates: *Bracisepalum selebicum* with *Dendrochilum*, *Chelonistele sulphurea* with *Entomophobia kinabaluensis*, *Coelogyne dayana* with *C. rhabdobulbon* (sect. *Tomentosae*), and sect. *Verrucosae*. In the second major clade, species of *Neogyna* and *Pholidota* are nested within species of *Coelogyne* sect. *Bicellae*, *Brachypterae*, *Coelogyne*, *Elatae*, *Flaccidae*, *Fuliginosae*, *Hologyne*, *Lawren-*

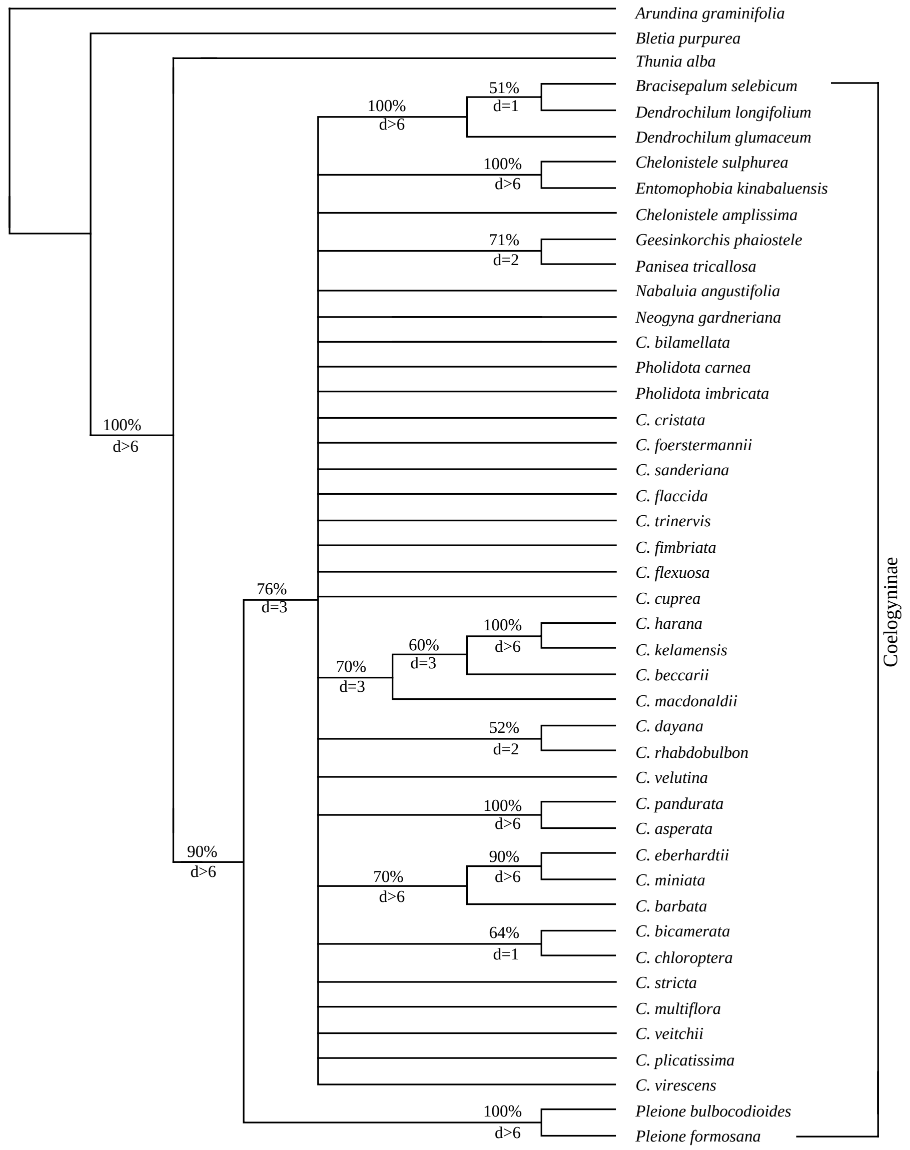


Fig. 2.2. Bootstrap consensus of 32 trees from parsimony analysis of ITS1-5.8S-ITS2 sequence data with bootstrap percentages and decay values (only percentages >50% are given).

ceanae, *Lentiginosae*, *Longifoliae*, *Moniliformes*, *Ptychogyne* and *Speciosae* (100%). Four subsets of taxa receive strong support within this second major clade: *Neogyna gardneriana* with *Pholidota imbricata* (80%), *C. fimbriata* (sect. *Fuliginosae*) with *C. stricta* (sect. *Elatae*) (90%), sect. *Moniliformes* (100%), sect. *Moniliformes* with sect. *Speciosae* (95%), and *C. eberhardtii* (sect. *Lawrenceanae*) with *C. miniata*

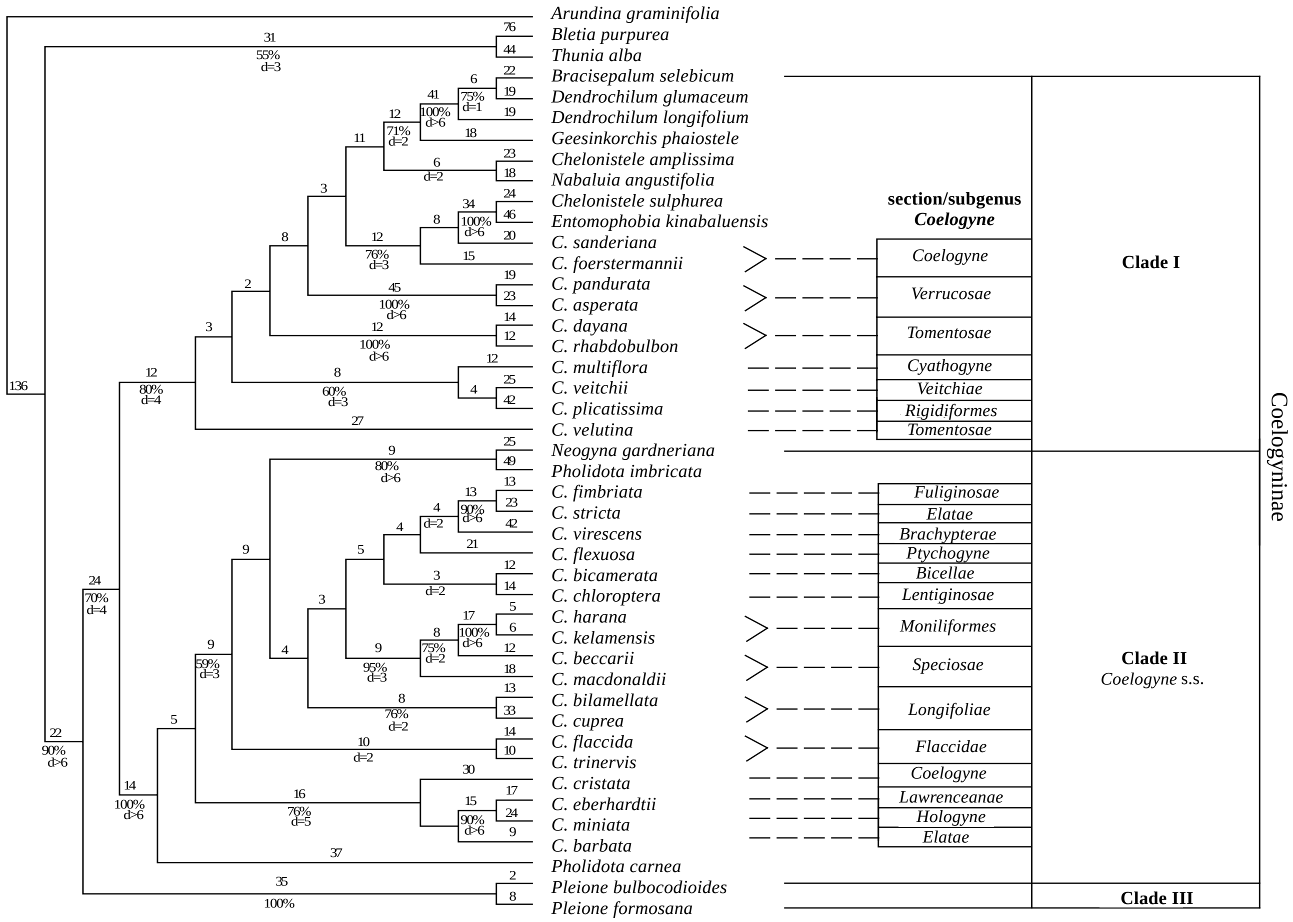


Fig. 2.3. One of the four MTPs from parsimony analysis of the combined molecular data. Branch length (number of nucleotide substitutions) is indicated above the branches and bootstrap percentages and decay values below them (only percentages > 50% are given).

Table 2.4. Number of steps, CI and RI for each codon position in *matK* based upon one of the four MPTs from the combined analysis.

Codon position	number of steps	CI	RI
1	84 (25%)	0.67	0.75
2	86 (26%)	0.74	0.75
3	163 (49%)	0.67	0.71

(subgenus *Hologyne*) (90%). The third major clade consists of species of *Pleione* (100%).

DISCUSSION

Comparative phylogenetic utility of separate data sets

The number of phylogenetically informative characters produced by the RFLPs was less succesful than predicted (20 only; Table 2.3), compared to studies of restriction enzyme digestions of PCR products in other plant groups (Tsumura et al., 1995; Mes et al., 1997; Asmussen & Liston, 1998). Apparently, the rate of plastid DNA evolution is relatively low in Coelogyninae.

The excess of transversions (Table 2.5), the excess of substitutions at third-codon positions (Table 2.4), and the multiple stop-codons present in the alignment, all indicate a loss of function for *matK* in Coelogyninae. For dicots so far, *matK* data demonstrate ts/tv ratios greater than 1.0 and a relatively even distribution of substitutions across codon positions (Xiang et al., 1998). A loss of function is also suspected for Maxillarieae (Whitten et al., in press).

The number of phylogenetic informative characters of the nuclear rDNA ITS sequences is much higher than those of the RFLPs and *matK* data (224 vs. 20 and 119, resp.; Table 2.3). However, many clades in the ITS bootstrap consensus are only weakly supported. The much lower CI and RI of the nuclear data (0.57 and 0.53) compared with the *matK* sequences (0.77 and 0.79) indicate a higher internal conflict, which might be caused by saturation at this taxonomic level of comparison. This is also consistent with the higher rate at which the variable sites in this region evolve compared with the *matK* sequences (2.5 steps/site vs. 1.4 steps/site, resp.; Table 2.3).

New generic circumscription of Coelogyne

Many recent studies have indicated that combined molecular data sets utilizing

Table 2.5. Number of steps, CI and RI for transitions and transversions for each region based upon one of the four MPTs from the combined analysis.

	matK		ITS1		ITS2	
	ts	tv	ts	tv	ts	tv
number of steps	189	228	433	258	318	203
CI	0.74	0.62	0.41	0.55	0.42	0.62
RI	0.82	0.64	0.27	0.35	0.53	0.51
ts/tv	0.83		1.68		1.56	

regions with different levels of variation provide resolution at different levels of the cladogram, and that phylogenetic resolution and bootstrap percentages are improved by directly combining independent molecular data sets (Chase & Cox, 1998; Soltis & Soltis, 1998; Whitten et al., in press). The high level of congruence among the three data sets, representing both coding and non-coding as well as plastid and nuclear regions, and the high bootstrap percentages in the combined analysis support the combined tree as a good hypothesis of phylogenetic relationships of *Coelogyne* and the Coelogyninae.

Coelogyne as currently circumscribed is polyphyletic, with species falling into at least two well-supported clades. Constrained analyses of the combined data set showed that the number of additional steps needed to achieve monophyly of *Coelogyne* is relatively great (at least 154 steps longer).

There are two possible taxonomic solutions for a new phylogenetic classification of *Coelogyne* in which only monophyletic groups are recognised. The first would be to include all sampled species of Coelogyninae (excluding *Pleione*) within a single genus. According to the rules of priority, this genus should be called *Coelogyne*. However, given the large differences in floral morphology, the creation of many synonyms in widespread horticultural use, and the high number of species *Coelogyne* would then encompass (approximately 530), this option is not satisfactory. A second possibility would be to reduce *Coelogyne* to one of the three main clades found. The type species of *Coelogyne* (*C. cristata*) belongs to clade II (*Coelogyne* s.s.). The best option for reorganising *Coelogyne* seems therefore to take the following actions:

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). All species sampled of *Neogyna* and *Pholidota* have glabrous ovaries and a hypochile with broad, erect lateral lobes. These characters are also present in the other species of the *Coelogyne* s.s. clade;
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*.

Sectional and subgeneric relationships within Coelogyne

From the 18 different sections of *Coelogyne* considered here, just two (with only two sampled species each) form strongly supported monophyletic groups in the combined analysis: sect. *Moniliformes* and *Verrucosae* (both 100% supported). This is consistent with the clear morphological synapomorphies that characterise both sections. All species of sect. *Moniliformes* have elongated, unifoliate pseudobulbs, a rhachis with distinctly swollen, short internodes and many flowers that open in succession (Carr, 1935). All species of sect. *Verrucosae* have rounded to strongly flattened bifoliate pseudobulbs, inflorescences with many, simultaneously opening flowers and a rhachis with a few sterile bracts at the base and scattered minute scale-like hairs, which are also present on the pedicel, ovary and the abaxial side of the sepals and petals (Sierra et al., 2000).

Coelogyne sect. *Longifoliae* is also monophyletic, although support for this clade is weak (76%). The species of sect. *Longifoliae* all have bifoliate pseudobulbs, long and stiff inflorescences, a rhachis with long internodes, and intermediate-sized flowers that open in succession (Clayton, in press). *Coelogyne* sect. *Flaccidae* is monophyletic in all shortest trees, but bootstrap support for this clade is low (< 50%). This is in accordance with the few and not unique synapomorphies that define this section. *Coelogyne* sect. *Flaccidae* is characterised by a low number of simultaneously opening flowers with deciduous floral bracts and undulating keels on the lip, a combination of characters that also defines sect. *Ocellatae* (Clayton, in press).

Coelogyne sect. *Tomentosae* is not monophyletic, but none of the branches separating its two parts receives even low internal support.

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. *Cristatae* 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.

Coelogyne sect. *Lawrenceanae* and sect. *Speciosae* are well separated, which is not in accordance with Seidenfaden (1975), who suggested they should be combined. Molecular data support our view that they should be considered different sections because of their clear morphological differences. All species of sect. *Lawrenceanae* have shiny green, smooth pseudobulbs, hysteranthous inflorescences and flowers with deeply incised, glabrous keels on the lip. All species of sect. *Speciosae* are characterised by angular, dull green pseudobulbs, synanthous or proteranthous inflorescences and flowers with hairy or warty keels on the lip (Gravendeel & de Vogel, 1999).

A well-supported subset of species is formed by *C. multiflora* (subgenus *Cyathogyne*), *C. plicatissima* (sect. *Rigidiformes*) and *C. veitchii* (sect. *Veitchiae*). Morphological synapomorphies for this clade are the hairy ovaries, persistent floral bracts and small flowers. Another clade with high support consists of *C. fimbriata* (sect. *Fuliginosae*) and *C. stricta* (sect. *Elatae*). Both species have sterile bracts on the scape and intermediate-sized flowers. A third group of taxa supported by high bootstrap percentages is made up of *C. eberhardtii* (sect. *Lawrenceanae*) and *C. miniata* (subgenus *Hologyne*). Both species have bifoliate pseudobulbs and deciduous floral bracts. However, in other characters, such as plant size, leaf texture, inflorescence type and keel morphology, they show considerable differences. To investigate whether these three clades warrant the status of new sections, a much larger sampling within *Coelogyne* is needed.

Naturalness and content of subtribe Coelogyninae

Analysis of the combined RFLP, *matK* and ITS data set indicates that Coelogyninae are monophyletic and diverged early into three major clades. Clade I comprises species of *Coelogyne* sect. *Coelogyne*, *Cyathogyne*, *Rigidiformes*, *Tomentosae*, *Veitchiae* and *Verrucosae*, from which *Bracisepalum*, *Chelonistele*, *Dendrochilum*, *Entomophobia*, *Geesinkorchis* and *Nabaluia* were split by various authors. Synapomorphies for this group of species are the simultaneously opening flowers (with the exception of *Geesinkorchis*) and inflorescences with relatively many flowers. Many other characters, such as small flower size, persistent floral bracts, hairy ovaries, ovate-oblong petals and a hypochile with inconspicuous lateral lobes, although present in most taxa of clade I, are not perfectly coincident, probably due to considerable convergent evolution in this group of species. The presence of many different generic names in clade I can be explained by the high number of autapomorphies present, such as the presence of stipes in *Geesinkorchis* and a transverse callus on the lip of *Entomophobia*. *Bracisepalum selebicum* and both *Dendrochilum* species sampled form a well-supported subset of taxa in clade I. These three species have unifoliate pseudobulbs, pendulous inflorescences with sterile bracts on the base of the rhachis and small flowers with a hypochile with inconspicuous lateral lobes. Another well-supported subclade in clade I comprises *Chelonistele sulphurea* and *Entomophobia kinabaluensis*. Both species have erect inflorescences with sterile bracts on the base of the rhachis and small flowers with a relatively short column. Generic boundaries within clade I are not clear yet, as most internal nodes of this clade are only poorly supported. More data should be collected to improve resolution. Additional taxon sampling is also needed to find the limits of new monophyletic groups.

Clade II (*Coelogyne* s.s.) subsequently diverged into species of *Neogyna* and *Pholidota* nested within species of *Coelogyne* sect. *Bicellae*, *Brachypterae*, *Elatae*, *Flaccidae*, *Fuliginosae*, *Hologyne*, *Lawrenceanae*, *Lentiginosae*, *Longifoliae*, *Moniliformes*, *Ptychogyne* and *Speciosae*. Synapomorphies for this group of species are the glabrous ovaries, linear petals (with the exception of *Pholidota*) and broad, erect lateral lobes of the hypochile. Many other characters, such as a small flower number, deciduous floral bracts and large flower size are not present in all taxa of clade II. *Neogyna gardneriana* and *Pholidota imbricata* form a strongly supported subset of taxa in clade II. Both species have an epichile with semi-orbicular, widely retuse lateral lobes.

Clade III consists of species of *Pleione*. The relatively isolated position of *Pleione* is consistent with the purplish pink colour of the flowers, short-lived pseudobulbs and annually deciduous leaves of many species in this genus, which do not occur in any of the other Coelogyninae (Cribb et al., 1983).

The position of *Panisea* differs in the plastid and the ITS trees. In all of the plastid cladograms, *Panisea* is placed in the *Coelogyne* s.s. clade (clade II), in some of them as sister species to *C. fimbriata* and *C. stricta*. In contrast, *Panisea* appears as sister species to *Geesinkorchis* in the majority of the ITS trees (clade I). A combined analysis including *Panisea* (not shown) results in a nearly complete loss of internal support for clades I and II, an indication that its position is incongruent in the trees from each genome. Therefore, we removed *Panisea* so that clear patterns could be discerned. Hard incongruencies between nuclear and organellar phylogenetic trees are often attributed to introgression of a cytoplasmic genome from one species into the nuclear background of another species (Wendel & Doyle, 1998). *Panisea tricallosa*, *C. fimbriata* and *C. stricta* show an overlap in distribution area in northern India and Nepal. We suggest that *Panisea tricallosa* shares a similar *matK* sequence with these species as a result of introgression. However, introgression is not the only process that could produce such incongruence. A second cause might be coalescence of alleles antedating species divergence (lineage sorting). There are relatively few examples of plastid DNA polymorphisms that transcend species boundaries, probably because of the generally slow rate of plastid DNA evolution (Wendel & Doyle, 1998). Therefore, introgression due to hybridisation appears to be the most probable explanation for the incongruence caused by *Panisea*. However, it is difficult to distinguish between introgression and lineage sorting, because they both may produce similar phylogenetic patterns (Hardig et al., 2000).

Phylogenetic utility of traditionally used key characters

The shape of the lip base and petals, presence of hairs on the ovary and number of flowers per inflorescence have been used for diagnosing genera within Coelogyninae and sections / subgenera within *Coelogyne* (Pfitzer & Kraenzlin, 1907b, d; De Vogel, 1992; Pedersen et al., 1997; Clayton, in press). To evaluate their phylogenetic significance, we reconstructed their distribution on the strict consensus of the four cladograms from the combined analysis.

Lip base shape

A saccate lip base is present in all Coelogyninae sampled except for the species of *Coelogyne*. Fig. 2.4A shows the most parsimonious derivation of a saccate lip base. A saccate lip base is gained at least four times and appears not to be phylogenetically useful at the generic level. The evolutionary lability of this character might be caused by a close association with pollination systems, which can be homoplasious in Orchidaceae (Dressler, 1981; Chase & Palmer, 1992; Hapeman & Inoue, 1997). Moreover, lip bases in Coelogyninae might not be derived from the same structure for all taxa studied. For instance, in *Bracisepalum* the base of the lip has two sac-like extensions, which might not be homologous with the saccate lip base of the other Coelogyninae. Studies of floral development may give additional insight as to whether different lip base types are derived by common descent or as a result of parallelism.

Petal shape

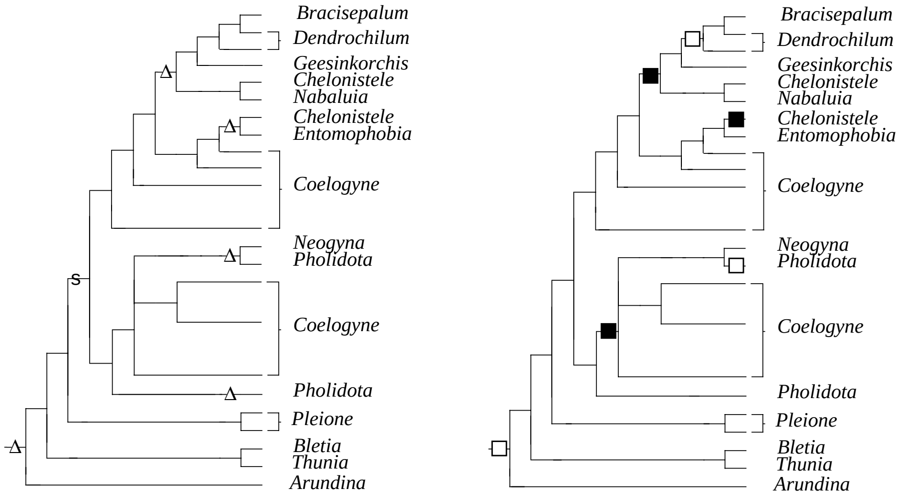
Petals are ovate-oblong in *Bracisepalum*, *Dendrochilum*, *Entomophobia*, *Pholidota*, *Pleione* and species of *Coelogyne* sect. *Coelogyne*, *Cyathogyne*, *Rigidiformes*, *Tomentosae*, *Veitchiae* and *Verrucosae*. All other taxa sampled in Coelogyninae have linear petals. The ancestral habit for the Coelogyninae seems to be ovate-oblong petals, and linear petals are gained in *Coelogyne* s.s., *Chelonistele*, *Geesinkorchis* and *Nabaluia* (Fig. 2.4B). Linear petals are derived at least three times and appear not to be phylogenetically useful at the generic level within the principal lineages of Coelogyninae.

Ovary indumentum

Hairy ovaries are present in all species of clade I except for *Geesinkorchis*, whereas all other Coelogyninae have glabrous ovaries (see also Fig. 2.4C). The presence of hairs on the ovary is a uniquely derived character state supporting the view of clade I as a separate group in Coelogyninae.

Flower number

A clear gap is present in the number of flowers per inflorescence of the taxa analyzed.



A. Evolution of lip base shape

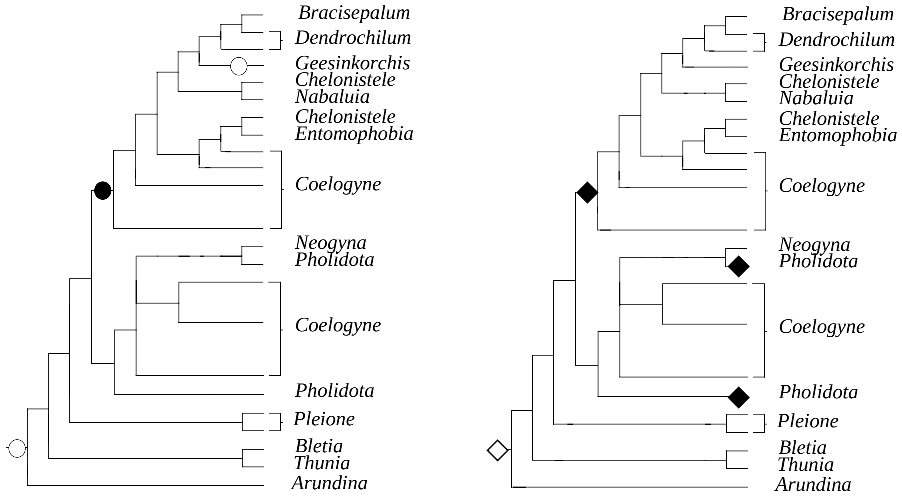
Δ lip base saccate

s lip base not saccate

B. Evolution of petal shape

☐ petal ovate-oblong

■ petal linear



C. Evolution of ovary indumentum

○ ovary glabrous

● ovary hairy

D. Evolution of flower number

◇ inflorescence with less than 15 flowers

◆ inflorescence with more than 15 flowers

Fig. 2.4. A most parsimonious reconstruction of character state evolution for three characters used in traditional classifications of *Coelogyne* and the Coelogyninae. — A. Lipbase shape; B. petal shape; C. ovary indumentum; D. flower number.

Inflorescences with 15 or more flowers are present in all species of clade I, whereas all other Coelogyninae (with the exception of *Pholidota*) have much lower flower numbers (see also Fig. 2.4D). A high flower number represents a good synapomorphy for clade I.

Reorganisation of Coelogyne

The traditional generic circumscription of *Coelogyne* is mainly based on the absence of a saccate lip base, which is present in all other genera of Coelogyninae. Absence of characters often indicates symplesiomorphy and generally makes the group defined by such a character paraphyletic. Sectional delimitations were previously based on such characters, which also intergrade considerably among closely related species. The poly- and paraphyletic nature of *Coelogyne* and several of its sections according to molecular data clearly shows how convergent floral morphology has confounded traditional taxonomy. Traditionally used classifications of *Coelogyne* and Coelogyninae are not supported by the molecular data presented here and should be abandoned.

When plotted on the molecular cladograms, some of the traditionally used key characters for generic delimitation in Coelogyninae, such as lip base and petal shape, seem unacceptably homoplasious. In contrast, ovary indumentum and flower number are good diagnostic characters. We propose to redefine the genus *Coelogyne* by the following two actions:

1) inclusion of *Neogyna* and *Pholidota*. These two genera fit perfectly in *Coelogyne* when a new definition of the genus consists of glabrous ovaries only, a lip with a saccate or flat base, and a hypochile with broad, erect lateral lobes;
2) removal of the species of *Coelogyne* sect. *Coelogyne* (in part), *Cyathogyne*, *Tomentosae*, *Rigidiformes*, *Veitchiae* and *Verrucosae*. These species fit better in clade I, because they share several synapomorphies with other genera in this clade, such as a relatively high number of simultaneously opening flowers with persistent floral bracts and hairy ovaries. Our phylogenetic analyses indicate that approximately 160 species would be left in *Coelogyne*.

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 molecular cladograms due to a substantial amount of convergent evolution in this group. In addition, generic boundaries within clade I are not yet clear, as most internal nodes have only low support. Additional sampling in clade I is needed to find the limits of new monophyletic groups, and to justify any formal proposals for nomenclatural changes.

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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.

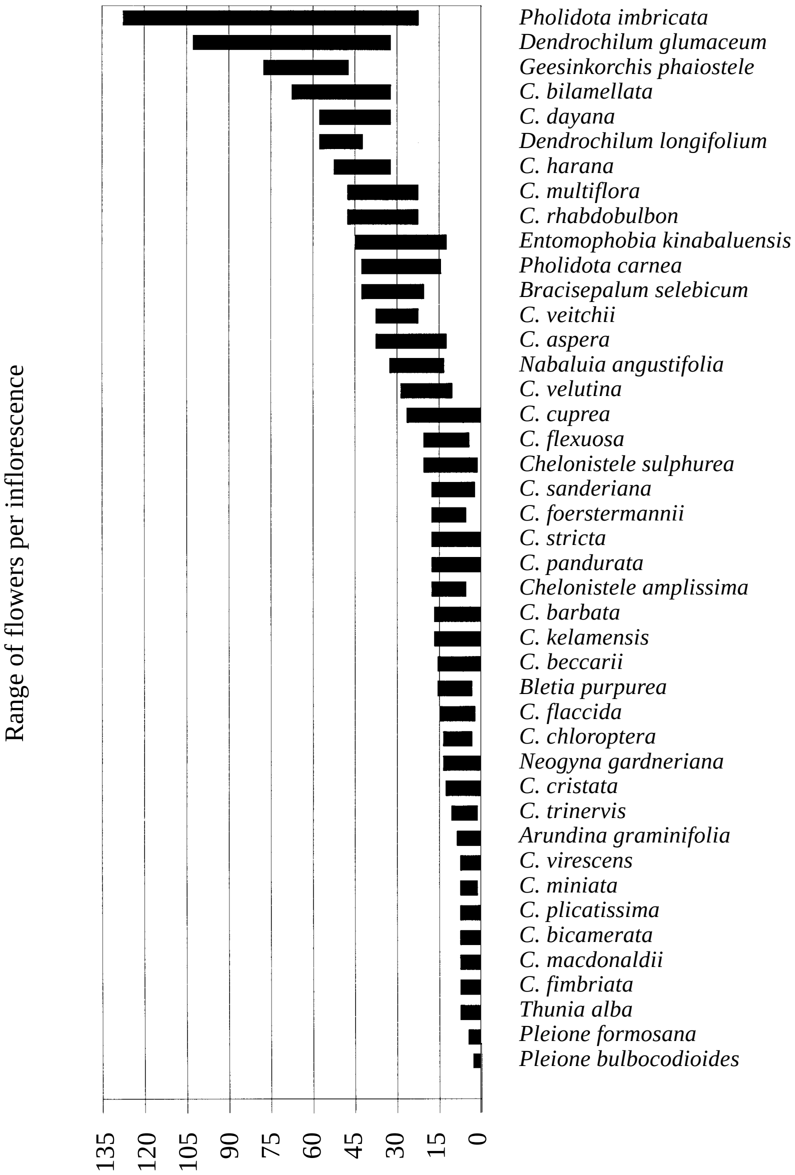


Fig. 3.1. Range of number of flowers per inflorescence for taxa studied.

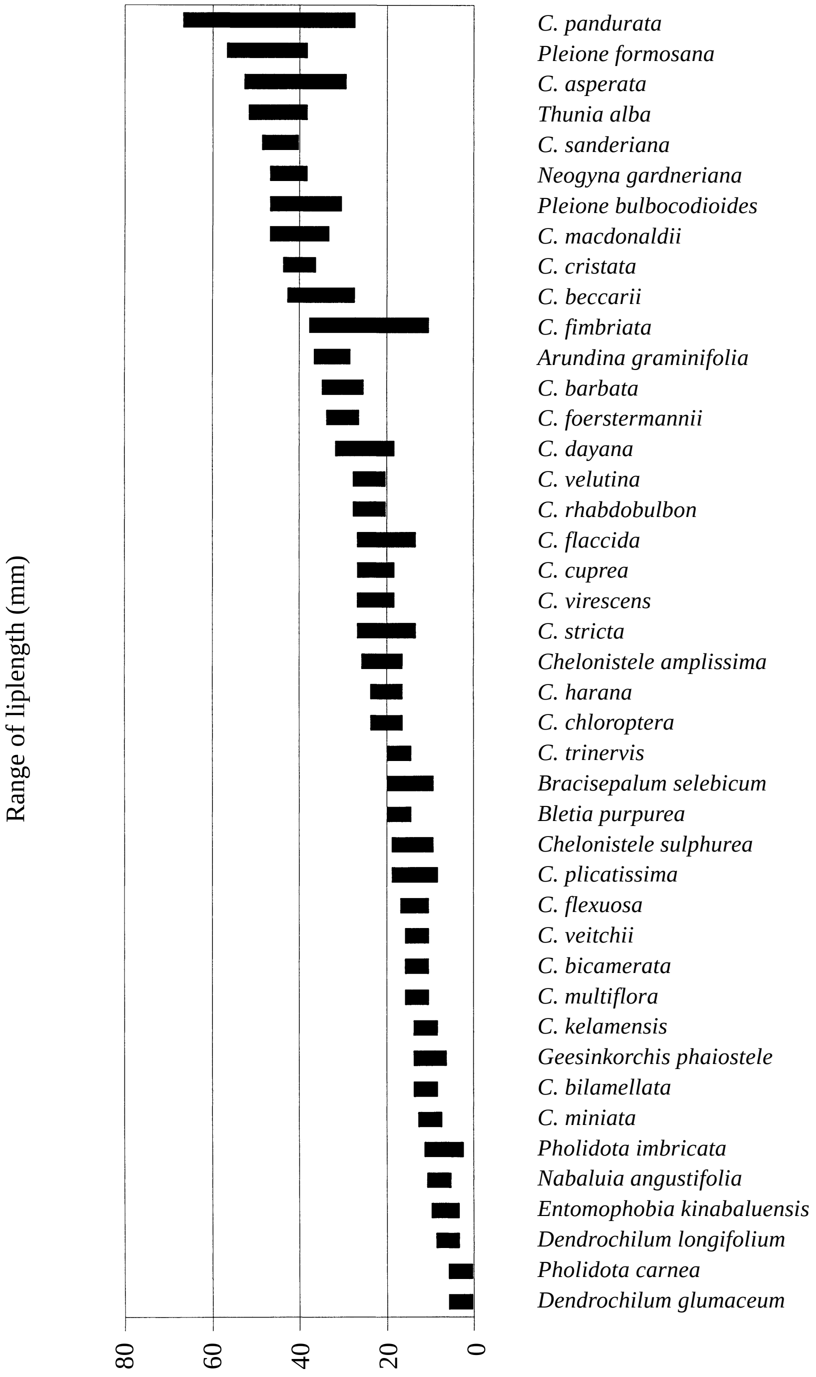


Fig. 3.2. Range of lip length (mm) for taxa studied.

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.

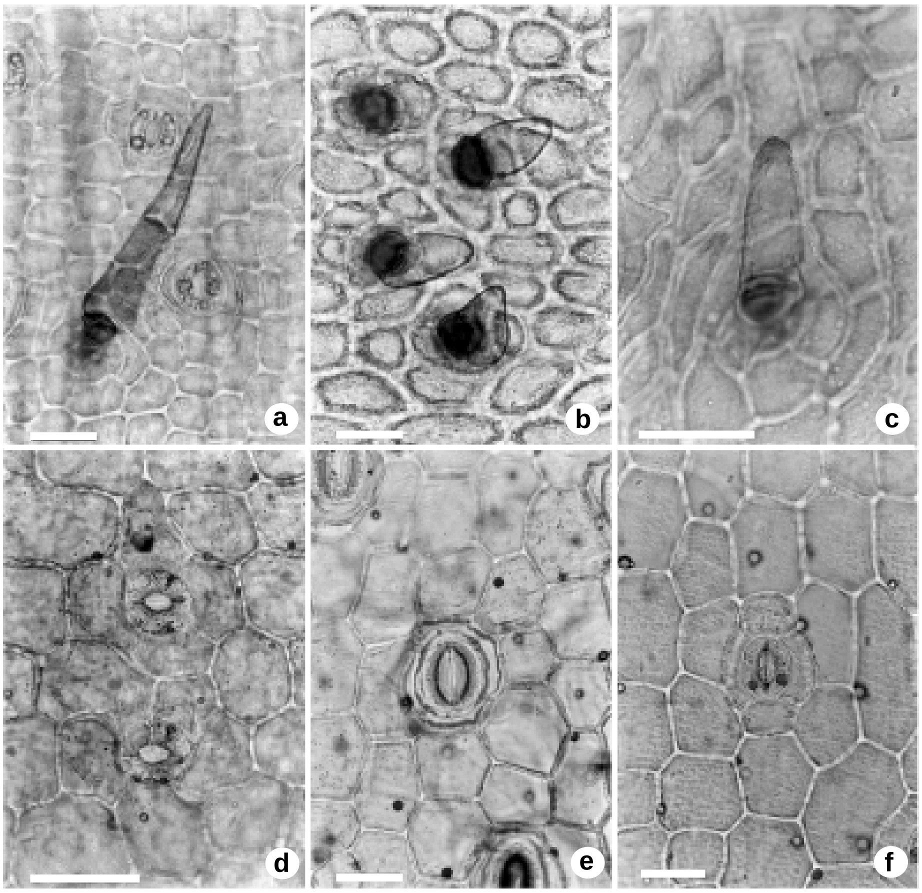


Plate 3.1. Leaf anatomical characters. – a. Elongate trichome with narrow base and acute top. *Coelogyne multiflora* Schltr. [*Leiden cult. 215747*]. – b. Short trichome with broad base and acute top. *Pholidota imbricata* Hook. [*Leiden cult. 21540*]. – c. Short trichome with broad base and broadly 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%).

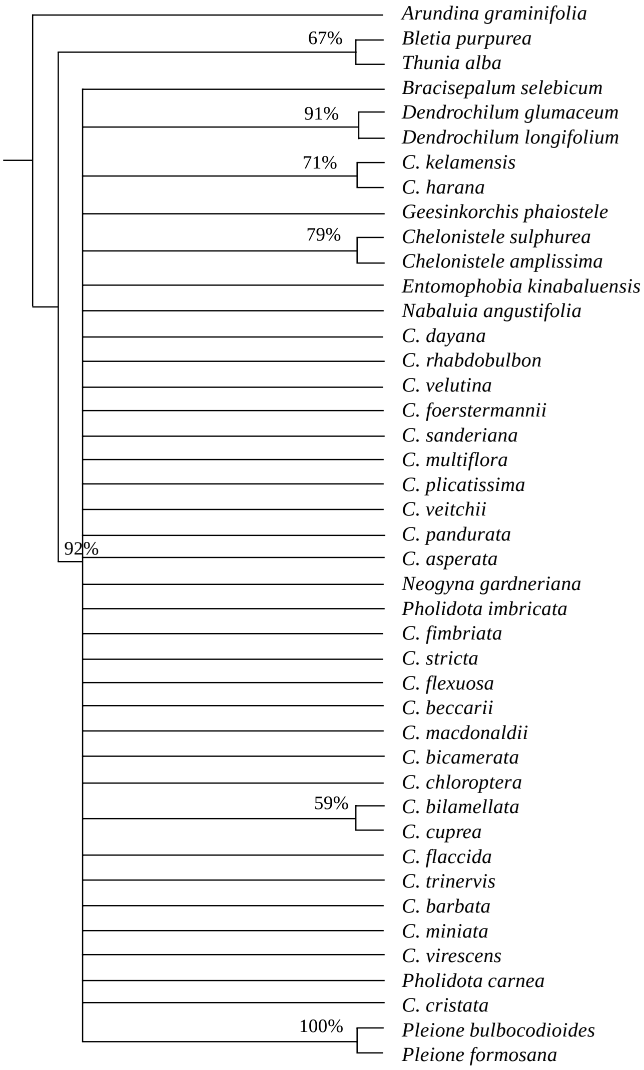


Fig. 3.3. Bootstrap consensus of 198 trees from parsimony analysis of macromorphological and anatomical data with bootstrap percentages (only percentages >50% are given).

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

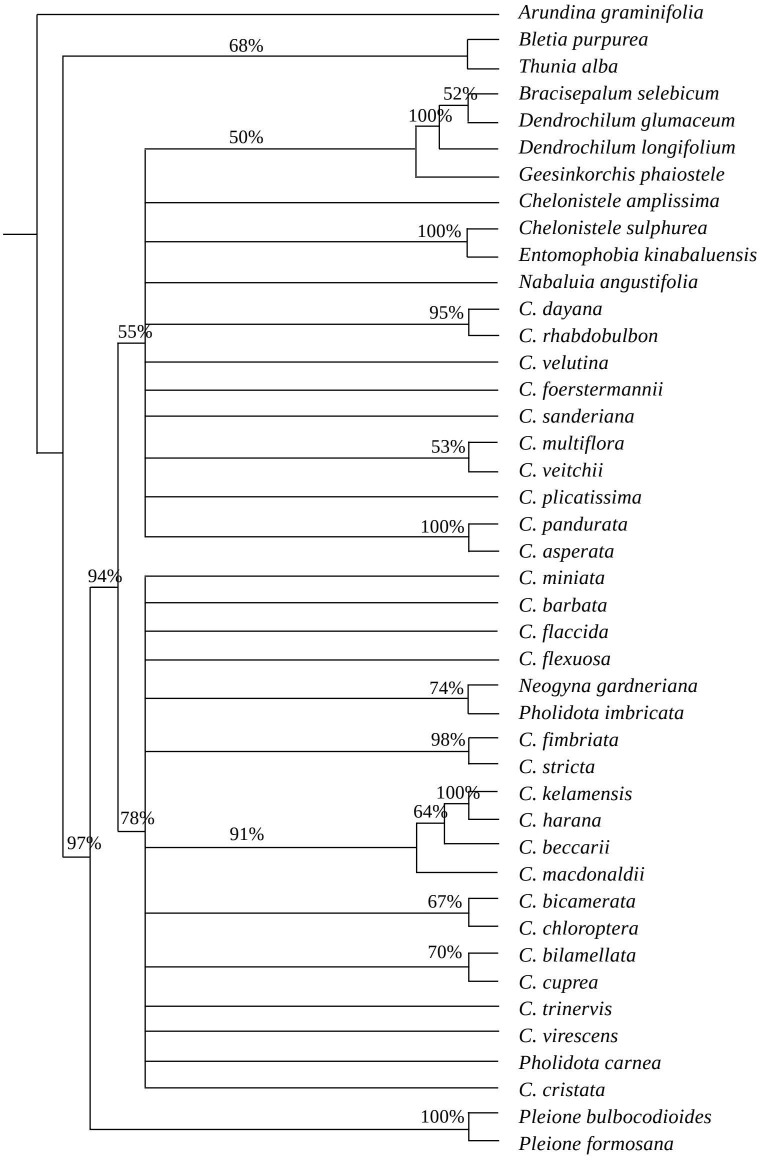
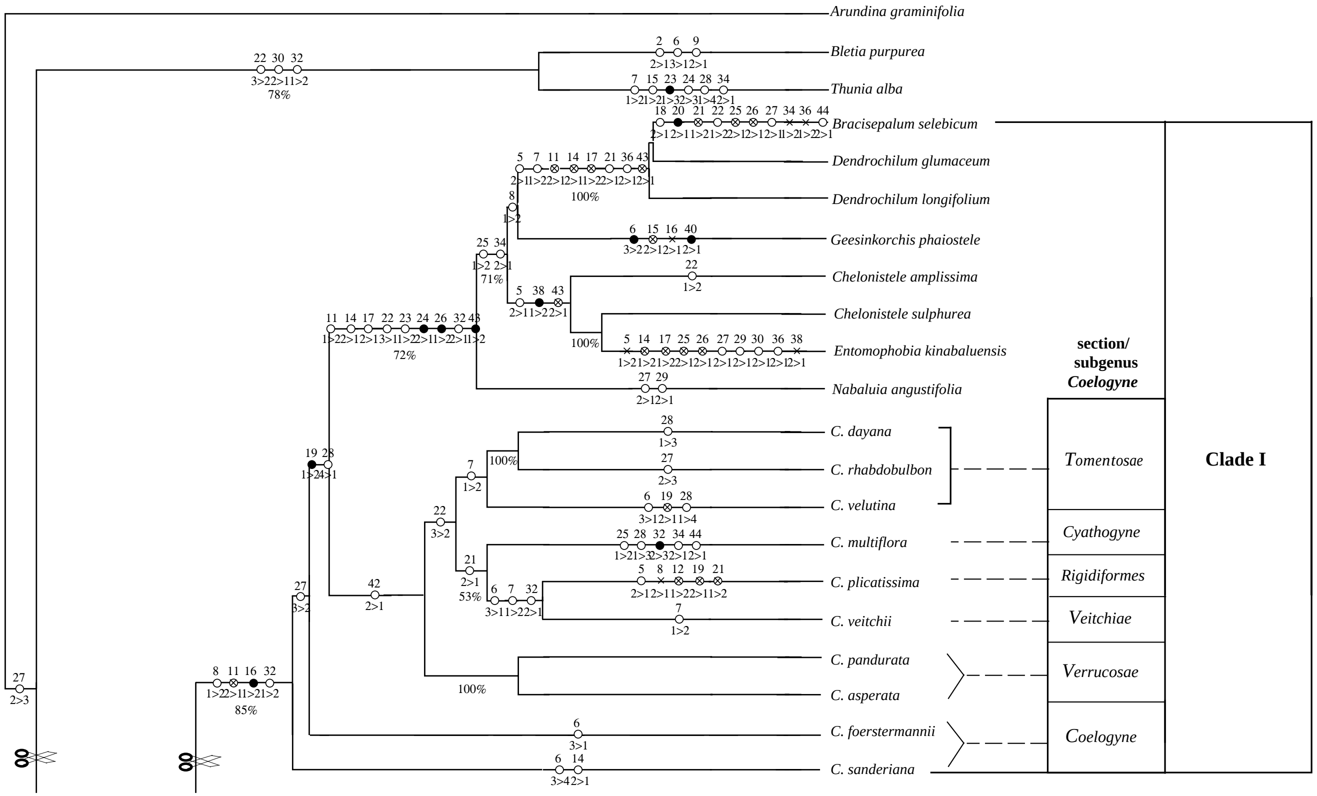


Fig. 3.4. Bootstrap consensus of five trees from parsimony analysis of combined molecular data with bootstrap percentages (only percentages > 50% are given).


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
78%
100%
71%
72%
100%
100%
53%
100%
85%
section/ subgenus Coelogyne
Tomentosae
Cyathogyne
Rigidiformes
Veitchiae
Verrucosae
Coelogyne
Clade I

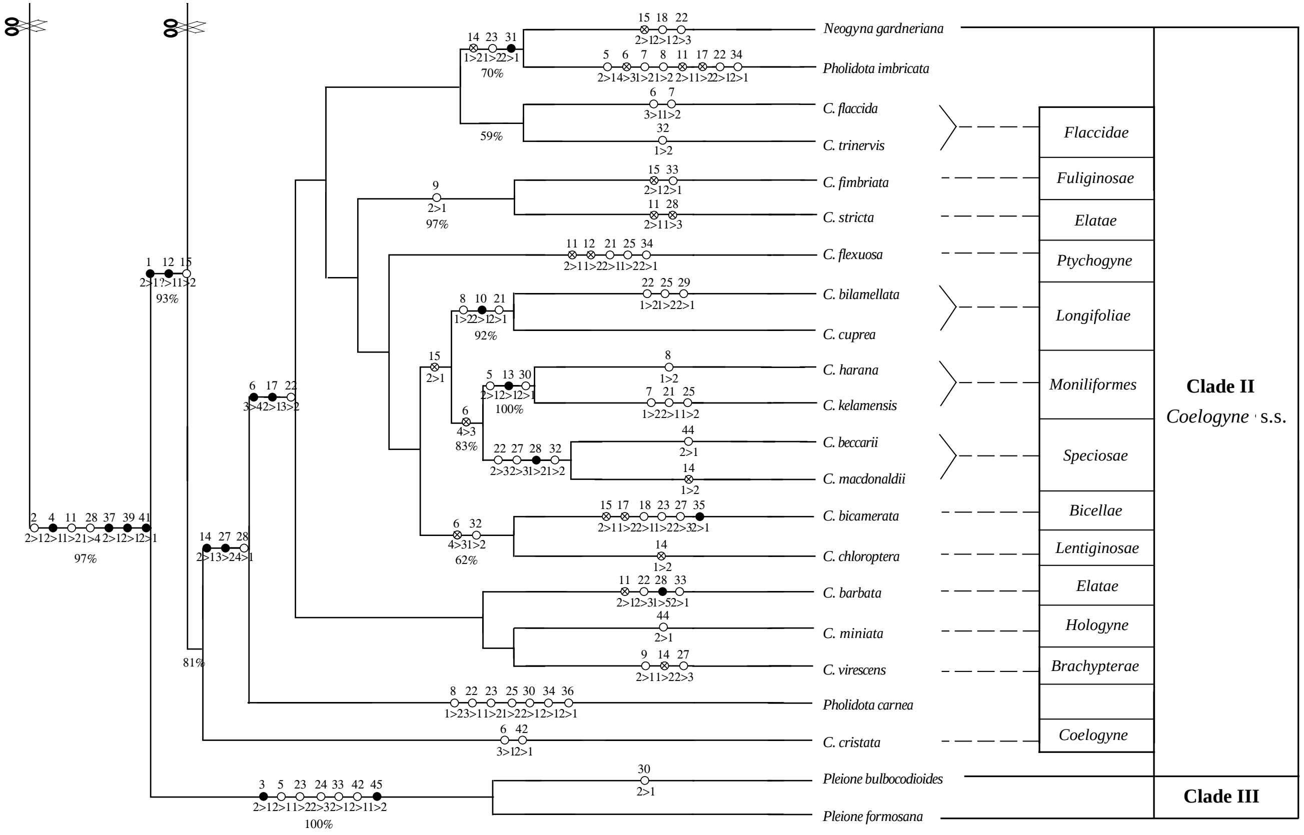


Fig. 3.5. One of the two MPTs from the total evidence analysis (only bootstraps > 50%). The state changes of the morphological characters used were traced with MACCLADE version 3.04 (Maddison & Maddison, 1992). Legends: ● = unique apomorphy; ○ = parallelism; x = reversal; ⊗ = parallel reversal.

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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Chapter 4

REVISION OF COELOGYNE SECTION SPECIOSAE (ORCHIDACEAE)*

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SUMMARY

Section *Speciosae* Pfitzer & Kraenzl. of the genus *Coelogyne* Lindl. is revised using morphological and molecular characters. Sixteen species are recognised, including one new (*C. tommii*) and one dubious species (*C. dichroantha*). Three former varieties are raised to subspecies level (*C. speciosa* subsp. *speciosa*, subsp. *incarnata* and subsp. *fimbriata*). Two species formerly included in sect. *Speciosae* by several authors are excluded (*C. eberhardtii* and *C. lawrenceana*). A total evidence analysis of morphological characters and ITS and *matK* sequence data supports the monophyly of the section as here recognised. Two major clades in the section are identified: the first one consists of species from Peninsular Malaysia, Sumatra, Java, Borneo, Sulawesi and the Moluccas; the second one comprises species of Sulawesi, New Guinea and the Pacific islands.

Key words: *Coelogyne* sect. *Speciosae,* orchids, systematics, phylogeny, *matK*, nuclear rDNA ITS.

INTRODUCTION

Within the subtribe Coelogyninae sixteen genera are presently recognised (Pedersen et al., 1997). One of these genera is *Coelogyne* Lindl., which contains over 200 species, distributed from mainland southeast Asia, Malaysia, Singapore, Indonesia, Philippines, Brunei and Papua New Guinea to the Pacific Islands.

Lindley (1821) described the genus, naming it *Caelogyne* (from the Greek ‘koilos’ = ‘hollow’, and ‘gyne’ = ‘female’) because of the concave stigma. Soon after he corrected this spelling to *Coelogyne* (Lindley, 1825) and later subdivided the genus into five sections: *Erectae, Filiferae, Flaccidae, Flexuosae* and *Proliferae* (Lindley, 1854). Reichenbach f. (1861) also used this subdivision. Pfitzer & Kraenzlin (1907c) published thirteen new section names: *Ancipites, Carinatae, Cristatae, Elatae, Fuliginosae, Fuscescentes, Lentiginosae, Longifoliae, Ocellatae, Speciosae, Tomentosae, Venustae* and *Verrucosae*. They maintained only one section of Lindley: *Proliferae.* Section *Speciosae* of Pfitzer & Kraenzlin was maintained by nearly all later authors. Only Smith (1933a), followed by Comber (1990), included sect. *Speciosae* and *Fuliginosae* in sect. *Longifoliae*. Holttum (1953, 1964) just used numbered, nameless sections.

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* Part of this chapter was published in Blumea 44 (1999): 253–320. The text is expanded with phylogenetic analyses.

In this study sect. *Speciosae* is partly recognised according to Pfitzer & Kraenzlin (1907c). They distinguished sect. *Speciosae* from the other sections by the following characters: few, showy and large flowers which open in succession; lip with few (rarely many) interrupted, hairy, warty or lobed keels; floral bract which covers the entire flower bud; peduncle with naked base. Not all of these characters appeared to apply to all species within the section. Therefore, we abandoned some of the characters of Pfitzer & Kraenzlin and transformed the remaining into the combination: average lip length larger than 32 mm (with the exception of *C. carinata*); no sterile bracts at the base of the scape; all or only the apical internodes of the rhachis slightly curved.

Pfitzer & Kraenzlin (1907c) listed a total of 11 species in sect. *Speciosae* of which three are reduced to synonymy here. Schlechter (1911) added *C. fragrans* and Smith (1917) suggested that *C. celebensis* should be included. Holttum (1953) included *C. xyrekes* and *C. tiomanensis* and according to Butzin (1974) *C. guamensis* should also be a member of this section. Lewis & Cribb (1991) added *C. susanae* and O'Byrne (1995) assumed *C. tomiensis* to belong to the section as well. We think that *C. dichroantha* should be placed in the section because of the absence of sterile bracts at the base of the peduncle and rhachis and the few, large flowers. In our view, all these species are more related to each other than to any other *Coelogyne* species. Therefore, we include them in sect. *Speciosae*.

Pfitzer & Kraenzlin (1907c) included *C. lawrenceana*, in which they were followed by Butzin (1974, 1992a) and Seidenfaden (1975). In addition the latter author included *C. eberhardtii*. However, both species have completely white flowers with yellow, completely plate-like, incised keels and shining green, smooth pseudobulbs. The species here recognised as belonging to sect. *Speciosae* have cream coloured, yellowish, greenish or salmon coloured flowers with papillose, warty or partly plate-like keels which are hairy or glabrous, and dull green, angular pseudobulbs.

Coelogyne carinata was included in sect. *Longifoliae* by Pfitzer & Kraenzlin (1907d) and Butzin (1974) and in sect. *Lentiginosae* by Schlechter (1911) and nearly all later authors because of the small, simultaneously opening flowers. In this study, however, *C. carinata* individuals appeared to have successively opening flowers as well, varying in size from small to medium-sized. Moreover, the species is in its floral characters very similar to *C. fragrans*; hence, it is included in sect. *Speciosae*.

The sectional classifications of *Coelogyne* in current use are based on a few diagnostic characters only, and no phylogenetic analyses with all species assigned to sect. *Speciosae* were performed so far. The main objectives of this study were:
1) to check the monophyly of sect. *Speciosae* as here recognised;
2) to study interspecific relationships within the section.

A taxonomic revision was made, and phylogenetic analyses were performed based on morphological and molecular characters obtained by sequencing the plastid *matK* gene and the nuclear rDNA ITS regions. The *matK* gene was chosen because of its proven utility at the generic and subgeneric level in Orchidaceae (Ryan et al., 2000). The nuclear rDNA ITS regions have been used extensively to infer phylogenetic relationships in Orchidaceae at both generic (Pridgeon et al., 1997; Douzery et al., 1999) and species level (Cox et al., 1997).

MATERIALS AND METHODS

Sampling

To determine the monophyly and interspecific relationships of sect. *Speciosae*, 20 taxa were analysed. The sampling includes 13 of the 16 species here recognised within the section. No living material was available of *C. dichroantha*, *C. guamensis* and *C. salmonicolor*. Four species of putatively allied sections were analysed, too. Unfortunately, *C. eberhardtii* and *C. lawrenceana* could not be included in the analyses performed for this chapter, due to lack of material for the collection of a morphological data set. The following characters and character states were used:

1. Pseudobulbs: 1 = ovate; 2 = oblong; 3 = cylindrical.
2. Pseudobulbs: 1 = 1-leafed; 2 = 2-leafed.
3. Scape: 1 = with sterile bracts on its base; 2 = without sterile bracts on its base.
4. Rhachis: 1 = slightly curved; 2 = distinctly curved at the apex; 3 = zigzagging; 4 = straight.
5. Rhachis: 1 = internodes flat; 2 = internodes swollen.
6. Floral bract: 1 = ovate; 2 = oblong.
7. Floral bract: 1 = caducous; 2 = persistent.
8. Lip: 1 = 8–32 mm long; 2 = longer than 32 mm.
9. Flowers: 1 = opening in succession; 2 = opening nearly simultaneously.
10. Hypochile base: 1 = straight; 2 = slightly saccate; 3 = extremely saccate; 4 = spurred.
11. Hypochile apex: 1 = straight; 2 = slightly saccate.
12. Hypochile lateral lobes: 1 = rounded in front; 2 = obtuse to acute in front.
13. Hypochile keels, number: 1 = 2–3; 2 = more than 3.
14. Hypochile keels, number of projections: 1 = consisting of 1 transverse row of projections; 2 = consisting of 2 transverse rows of projections; 3 = consisting of 5 transverse rows of projections.
15. Hypochile keels, indument: 1 = covered with hairs; 2 = covered with small papillae; 3 = covered with elongate papillae.
16. Hypochile keels, shape: 1 = plate-like with straight margin; 2 = consisting of warts; 3 = consisting of ridges; 4 = consisting of rounded projections; 5 = longitudinally grooved; 6 = consisting of tapering, branched projections with stellately arranged hairs at their apices; 7 = plate-like with undulating margin; 8 = plate-like with fimbriate margin.
17. Epichile, shape: 1 = ovate; 2 = elliptic.
18. Epichile, apex: 1 = clearly raised; 2 = flat.
19. Epichile, apex ornamentation: 1 = covered with warts; 2 = glabrous.
20. Epichile lateral lobes: 1 = cleary pronounced; 2 = absent.
21. Epichile keels, number: 1 = 0–3; 2 = more than 3.
22. Epichile keels, shape: 1 = consisting of warts; 2 = plate-like with straight margin; 3 = plate-like with undulating margin; 4 = longitudinally grooved.
23. Epichile, apex: 1 = extremely recurved; 2 = not or only slightly recurved.
24. Column: 1 = straight; 2 = bent.
25. Pollinia: 1 = all obliquely elliptic; 2 = abaxial pair obliquely elliptic, adaxial pair orbicular; 3 = all orbicular.

Table 4.1. List of species analysed. Arranged by (sub)tribe and genus according to Dressler (1990).

Subtribe	Genus and species	Section	Geographic origin	Voucher
Thuniinae	*Thunia alba* (Lindl.) Rchb.f.		unknown	*Chase 589* (K)
Coelogyninae	*Pleione bulbocodioides* (Franch.) Rolfe		unknown	*Leiden cult. 990010* (L)
	Pleione formosana Hayata		unknown	*Leiden cult. 91051* (L)
	Coelogyne cristata Lindl.	*Coelogyne*	unknown	*Leiden cult. 2214* (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 beccarii Rchb.f.	*Speciosae*	PNG, Kutubu	*Leiden cult. 32230* (L)
	Coelogyne carinata Rolfe	*Speciosae*	unknown	*Leiden cult. 30725* (L)
	Coelogyne celebensis J.J. Sm.	*Speciosae*	Sulawesi	*Leiden cult. 950057* (L)
	Coelogyne fragrans Schltr.	*Speciosae*	PNG, Tari	*Leiden cult. 32320* (L)
	Coelogyne lycastoides F. Muell. & Kraenzl.	*Speciosae*	Fiji	*Leiden cult. 914325* (L)
	Coelogyne macdonaldii F. Muell. & Kraenzl.	*Speciosae*	Vanuatu	*Leiden cult. 25836* (L)
	Coelogyne rumphii Lindl.	*Speciosae*	Buru	*Leiden cult. 24505* (L)
	Coelogyne septemcostata J.J. Sm.	*Speciosae*	Kalimantan, Apo Kayan	*Leiden cult. 970678* (L)
	Coelogyne susanae P.J. Cribb & B.A. Lewis	*Speciosae*	Bougainville	*Cribb & Morrison 1922* (K)
	Coelogyne speciosa (Blume) Lindl.	*Speciosae*	Java	*Leiden cult. 950058* (L)
	Coelogyne tiomanensis M.R. Hend.	*Speciosae*	Malaysia, Pulau Tioman	*Leiden cult. 990047* (L)
	Coelogyne tommii Gravendeel & O'Byrne	*Speciosae*	unknown	*Leiden cult. 21526* (L)
	Coelogyne xyrekes Ridl.	*Speciosae*	Malaysia, Bukit Larut	*Leiden cult. 960160* (L)

Outgroups were sampled from subtribe Thuniinae and Coelogyninae, 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 (Chase et al., unpubl.; Gravendeel et al., in prep.). Plant material was obtained from the living orchid collections of the Hortus Botanicus Leiden, Royal Botanic Gardens Kew, Kebun Raya Bogor and private collections in Australia, England en Singapore. Plants were collected during several expeditions to Peninsular Malaysia, Sumatra, Borneo, Java, Buru, New Guinea and Bougainville. Voucher specimens of accessions surveyed, with their origins, are listed in Table 4.1 and deposited at K or L.

Herbarium material was studied from the following herbaria: AAU, AMES, B, BM, BO, BRI, BSIP, C, CAL, CANB, CBG, G, HBG, K, KEP, L, LAE, MEL, NY, P, S, SAN, SAR, SING, W, WA and WRSL. The dimensions given in the descriptions are based on spirit collections and living material only due to degradation of flower structures in dried specimens. When only herbarium material was measured this is mentioned.

Maps were made with the program KORT (© Bertel Hansen, C). Coordinates were partly found with the COOR database (© Peter van Welzen, L).

DNA extractions

Total genomic DNA was extracted from 50 mg of fresh young leaf tissue following the CTAB method of Doyle & Doyle (1987). Some samples were purified through a cesium chloride / ethidium bromide gradient (1.55 g ml^{-1}). Leaf material was taken from one individual per species.

matK and ITS amplifications

The *trnK* intron (mostly *matK*) was amplified with the following four primers: -19F (5'-CGTTCTGACCATATTGCACTATG-3') and 881R (5'-TMTTCATCAGAATAAGAGT- 3'); 731F (5'-TCTGGAGTCTTTCTTGAGCGA-3') and 2R (5'-AACTAGTCG-GATGGAGTAG-3'). All primers were designed at the Royal Botanic Gardens, Kew, except for 2R (Johnson & Soltis, 1994). The thermal cycling protocol comprised 28 cycles, each with 1 min. denaturation at 94 ºC, 30 sec. annealing at 48 ºC, an extension of 1 min. at 72 ºC, concluding with an extension of 7 min. at 72 ºC. All PCR products were sequenced directly after purification with QIAquick purification columns (QIAGEN, Amsterdam, The Netherlands). Four sequencing reactions were performed for each completed sequence, one with each of the four PCR primers, and these generated nearly complete overlapping single strand sequences for the *trnK* intron fragments.

ITS1 and ITS2 spacers along with the 5.8S gene were amplified with the primers 17 SE (5'-ACGAATTCATGGTCCGGTGAAGTGTTCG-3') and 26SE (5'-TAGAATTCCCCGGTTCGCTCGCCGTTAC-3') from Sun et al. (1994). The thermal cycling protocol comprised 26 cycles, each with 10 sec. denaturation at 96 ºC, 5 sec. annealing at 50 ºC and extension of 4 min. at 60 ºC. All PCR products were cloned following the protocol of Promega's pGEM-T Easy Vector System and then reamplified from transformed bacterial colonies by touching them with a sterile pipet tip and using that as template. Two sequencing reactions were performed for each completed sequence, one with each of the two PCR primers, and these generated nearly complete overlapping single strand sequences for the entire ITS fragments.

All amplified, double-stranded DNA fragments were purified using Wizard PCR minicolumns (Promega, Madison, Wisconsin, USA) and sequenced on an ABI 377 automated sequencer (PE Applied Biosystems, Inc.), using standard dye-terminator chemistry following the manufacturer's protocols.

Phylogenetic analyses

All characters were assessed as independent, unordered and equally weighted, using Fitch parsimony (Fitch, 1971). For the morphological characters multistate coding was used. When multiple states occurred within one species, they were treated as polymorphisms. Sequences were aligned with MegAlign version 4.03 (DNASTAR, Inc. 1999) and subsequent adjustment by hand. Gaps in the sequence data were coded as missing values. The morphological data matrix and *matK* and ITS alignments are available from the first author upon request (gravendeel@nhn.leidenuniv.nl). Maximum parsimony analyses were performed on the morphological and sequence data with PAUP* version 4.0b64 (Swofford, 1999) using random additions and the MULPARS option. *Thunia alba*, *Pleione bulbocodioides* and *Pleione formosana* were used as outgroups in all analyses. The relative robustness for clades found in each parsimony

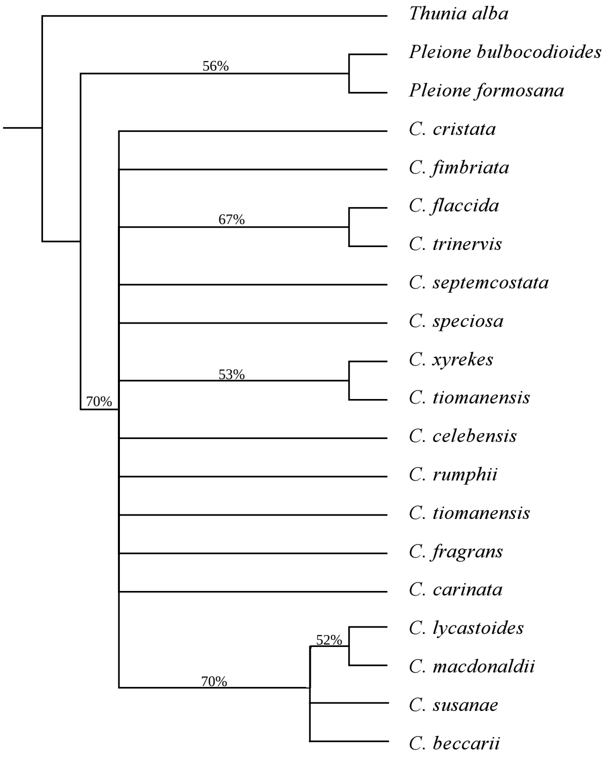


Fig. 4.1. Bootstrap consensus of 25 trees from parsimony analysis of morphological data (only percentages >50% are given).

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. Congruence of the separate data sets was assessed by visual inspection of the individual bootstrap consensus trees. Bootstrap trees were considered incongruent only if they displayed hard (>80% supported) incongruencies (Wiens, 1998). Character state evolution of all morphological characters was reconstructed using the assumptions of maximum parsimony with the Trace Character facility in MACCLADE version 3.04 (Maddison & Maddison, 1992).

SPECIES DELIMITATION

Distinct species are recognised when at least two morphological characters indicate differences. These criteria follow from the rules and recommendations for taxonomists as stated by Van Steenis (1957). For most of the species in the section this appeared not to be problematic. However, between *C. carinata* and *C. fragrans* the variation in most morphological characters studied appeared to be more or less continuous. Principal Component and cluster analyses were used to find gaps in multivariate morphometric space and search for a good combination of delimitating characters.

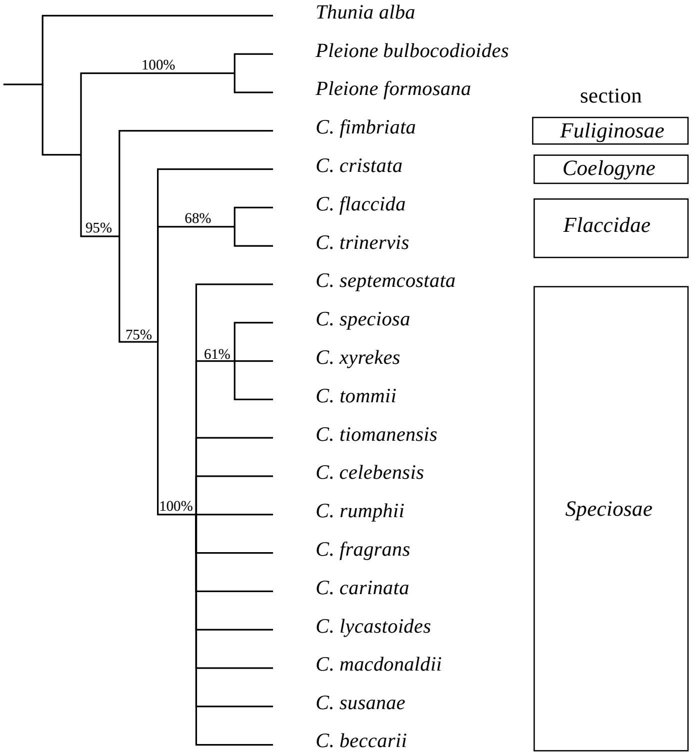


Fig. 4.2. Bootstrap consensus of 1877 trees from parsimony analysis of *matK* sequence data (only percentages >50% are given).

RESULTS

Morphology

All 25 characters scored were phylogenetic informative. The MP analyses yielded 25 most parsimonious trees (MPTs) (length = 82, CI = 0.48, RI = 0.65; Table 4.2). The bootstrap consensus topology and the corresponding branch supports are indicated in Fig. 4.1.

The morphological consensus tree shows little resolution. All Coelogyninae species are united in a weakly supported clade (70%). Other weakly supported clades unite *C. lycastoides* plus *C. macdonaldii* (52%), *C. lycastoides*, *C. macdonaldii*, *C. susanae* and *C. beccarii* (70%), *C. tiomanensis* plus *C. xyrekes* (53%), all species sampled of sect. *Flaccidae* (67%) and *Pleione* (56%).

matK and ITS sequences

Boundaries of the *matK* gene were taken from Johnson & Soltis (1994). The •nal alignment has a total length of 1844 sites (1544 bp for the *matK* gene and 300 bp in the flanking *trnK* sequences), of which 113 are variable and 47 phylogenetically informative, and contains one autapomorphic indel of nine bp in the *matK* gene and four synapomorphic indels in the flanking *trnK* sequences, ranging in size from

1–9 bp. The MP analysis yielded 1877 MPTs (length = 129, CI = 0.91, RI = 0.92; Table 4.2). The bootstrap consensus topology and the corresponding branch supports are indicated in Fig. 4.2.

The *matK* bootstrap consensus tree shows more resolution than the morphological bootstrap consensus. Monophyly of *Pleione, Coelogyne* and sect. *Speciosae* is strongly supported (100%, 95% and 100% resp.). Two weakly supported clades unite the species sampled of sect. *Flaccidae* (68%) and *C. speciosa*, *C. tommii* plus *C. xyrekes* (61%). Length ranges of nuclear rDNA ITS sequences were 213–240 bp, 159–160 bp, and 222–261 bp, resp. Boundaries from the 5.8S gene are taken from Hershkovitz & Lewis (1996). The final alignment has a total length of 683 sites (249, 162 and 272 sites for ITS1, 5.8S and ITS2, respectively). Of the included positions, 243 are variable and 106 phylogenetically informative, which is in accordance with variation levels in most angiosperms (Baldwin et al., 1995). The MP analysis yielded 24 MPTs (length = 393, CI = 0.74, RI = 0.73; Table 4.2). The bootstrap consensus topology and the corresponding branch supports are indicated in Fig. 4.3.

The ITS bootstrap consensus tree shows more resolution than either the morphological or *matK* bootstrap consensus. Three clades receive strong support: all *Pleione* species sampled (100%), *C. celebensis*, *C. rumphii*, *C. tiomanensis* plus *C. xyrekes* (86%) and *C. fragrans*, *C. carinata*, *C. beccarii*, *C. susanae*, *C. lycastoides* plus *C. macdonaldii* (84%). Weakly supported clades unite *C. celebensis* plus *C. rumphii* (58%), *C. tiomanensis* plus *C. xyrekes* (52%), *C. celebensis*, *C. rumphii*, *C. tiomanensis*, *C. xyrekes* plus *C. speciosa* (69%), *C. carinata* plus *C. beccarii* (66%),*C. fragrans*, *C. carinata*, *C. beccarii* plus *C. susanae* (55%), *C. lycastoides* plus *C. macdonaldii* (53%), *C. tommii, C. fragrans, C. carinata*, *C. beccarii*, *C. susanae*, *C. lycastoides* plus *C. macdonaldii* (72%) and *C. fimbriata*, *C. flaccida*, *C. trinervis*, *C. tommii*, *C. fragrans, C. carinata*, *C. beccarii*, *C. susanae*, *C. lycastoides* plus *C. macdonaldii* (73%).

Table 4.2. Values and statistics from parsimony analyses of morphology, *matK* and nuclear rDNA ITS sequences, and combined data.

	Morphology	*matK*	ITS1-5.8S-ITS2	Total evidence
Total number of characters	25	1844	683	2552
Number of variable characters	25 (100%)	113 (6%)	243 (36%)	381 (15%)
Number of phylogenetically informative characters	24	47	106	177
Average number of changes per variable site	3.7	1.1	3.7	–
Number of MPTs	25	1877	24	1
Tree length (steps)	82	129	393	642
CI	0.48	0.91	0.74	0.70
RI	0.65	0.92	0.73	0.70
Number of clades in bootstrap consensus with >80% support	0	3	3	10

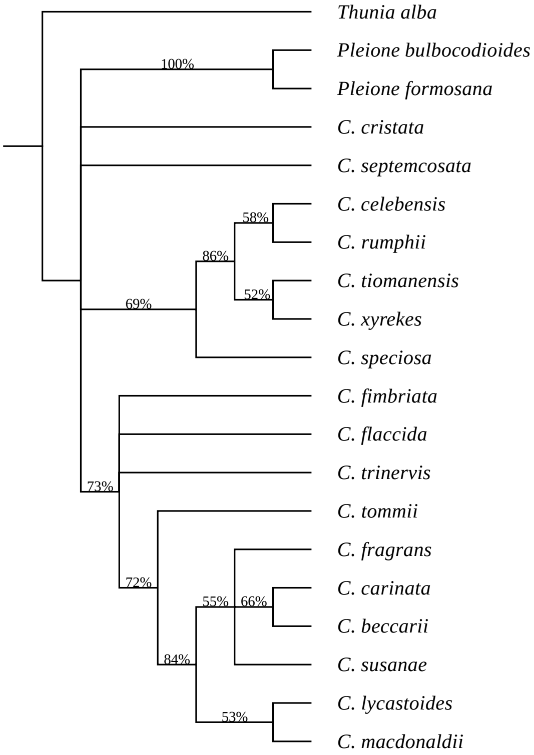


Fig. 4.3. Bootstrap consensus of 24 trees from parsimony analysis of ITS1-5.8S-ITS2 sequence data (only percentages >50% are given).

Total evidence analysis

Bootstrap consensus trees of the three individual data sets revealed no hard incongruences. To improve sampling, a combined analysis of all three data sets was performed. The combined matrix yielded a single MPT (length = 642, CI = 0.70; RI = 0.70). Bootstrap analyses of the combined data set provided more resolution and higher internal support for relationships than did any of the individual data sets (Table 4.2). The bootstrap consensus topology and the corresponding branch supports are shown in Fig. 4.4.

Strongly supported clades unite all species of *Coelogyne* and *Pleione* sampled (80% and 100% respectively), all species sampled of sect. *Flaccidae* (92%), sect. *Flaccidae* plus sect. *Fuliginosae* (99%) and all species sampled of sect. *Speciosae* (86%). Two major clades within sect. *Speciosae* are strongly supported:

1) *C. septemcostata*, *C. speciosa*, *C. xyrekes*, *C. tiomanensis*, *C. celebensis* plus *C. rumphii* (88%); and
2) *C. fragrans*, *C. carinata*, *C. lycastoides*, *C. macdonaldii*, *C. susanae* plus *C. beccarii* (97%). Within the first major clade *C. celebensis* plus *C. rumphii* (93%) and *C. xyrekes* plus *C. tiomanensis* (92%) form strongly supported subclades. Weaker supported subclades unite *C. xyrekes*, *C. tiomanensis*, *C. celebensis* plus *C. rumphii*

(85%) and *C. speciosa*, *C. xyrekes*, *C. tiomanensis*, *C. celebensis* plus *C. rumphii* (65%). Within the second clade *C. lycastoides* plus *C. macdonaldii* and *C. susanae* plus *C. beccarii* form weakly supported subclades (65% and 79% respectively). Another weakly supported subclade unites *C. beccarii*, *C. lycastoides*, *C. macdonaldii* plus *C. susanae* (64%). One strongly supported subclade unites *C. carinata* with *C. fragrans* (84%). *Coelogyne tommii* is placed at the base of the second major clade in sect. *Speciosae*, although support for this position is weak (64%).

DISCUSSION

Separate and combined analyses of morphological and molecular data of almost all species indicate that sect. *Speciosae* as here recognised is monophyletic. Unfortunately, not all putatively allied species (such as *C. eberhardtii* and *C. lawrenceana*) could be included in the analyses performed for this chapter. However, the molecular phylogeny constructed in Chapter 2 indicates that at least *C. eberhardtii* is clearly separated from the other species of sect. *Speciosae* sampled.

The species of sect. *Speciosae* as here recognised have the following unique character combination in *Coelogyne*: average lip length larger than 32 mm (with the exception of *C. carinata*); no sterile bracts at the base of the scape; all or only the apical internodes of the rhachis slightly curved. All other *Coelogyne* species analysed have an average lip length smaller than 32 mm, sterile bracts at the base of the scape and/or a rhachis with zigzagging or straight internodes.

Within sect. *Speciosae*, two strongly supported major clades are present. The first major clade consists of *C. septemcostata*, *C. speciosa*, *C. xyrekes*, *C. tiomanensis*, *C. celebensis* plus *C. rumphii*, which occur in Peninsular Malaysia, Sumatra, Java, Borneo, Sulawesi and the Moluccas. These species all have unifoliate pseudobulbs (with the exception of *C. celebensis* and *C. speciosa*, which can also have some bifoliate pseudobulbs), successively opening flowers and keels on the hypochile, which are longitudinally grooved, plate-like with undulating margin or shaped like rounded or tapering projections with stellately arranged hairs at their apices. A well supported group within this first major clade consist of *C. tiomanensis* and *C. xyrekes*, which share a hypochile with slightly saccate base and apically rounded lateral lobes, and a row of undulating plate-like projections on the hypochile and epichile. Another well supported subclade unites *C. celebensis* and *C. rumphii*, which both have oblong floral bracts, rounded projections on the hypochile and warts on the epichile.

The second major subclade consists of *C. fragrans*, *C. carinata*, *C. lycastoides*, *C. macdonaldii*, *C. susanae* plus *C. beccarii*, which occur in Sulawesi, New Guinea and the Pacific islands. These species all have longitudinally grooved keels or warts or ridges on the hypochile and warts on the epichile. A well supported group within this second major clade consists of *C. carinata* and *C. fragrans*. Both species have a slightly saccate hypochile apex, longitudinally grooved keels on the hypochile and an epichile with glabrous apex. A subclade within this second major clade with weak support consists of *C. beccarii* and *C. susanae*, *C. lycastoides* and *C. macdonaldii*. These four species all have a rhachis with incrassate internodes, warts or ridges on the hypochile and a bent column. Another weakly supported subclade unites *C. lycastoides* with *C. macdonaldii*, which share persistent floral bracts, a relatively

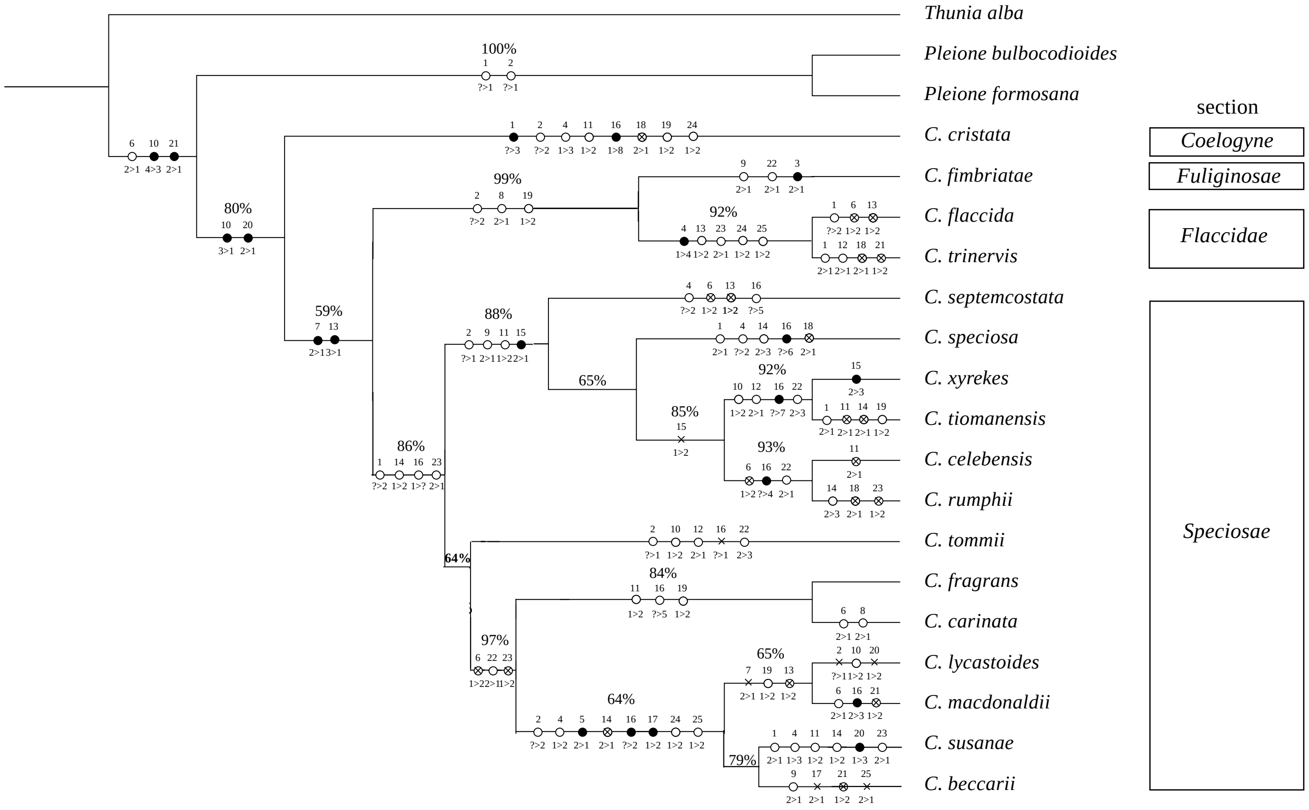


Fig. 4.4. Single MTP from total evidence analysis with bootstrap support values (only percentages >50% are given). The character state changes of the morphological characters used were traced with MACCLADE version 3.04 (Maddison & Maddison, 1992). Legends: ● = unique apomorphy; ○ = parallelism; x = reversal; ⊗ = parallel reversal.

high number of keels on the hypochile and an epichile with glabrous apex. A third subclade within the second major clade in sect. *Speciosae* unites *C. beccarii* with *C. susanae*. This subclade is based on sequence data only, and no morphological synapomorphies are present to characterise this group of species.

The results of the total evidence analysis identified *C. fimbriata*, *C. flaccida* and *C. trinervis* as nearest neighbours to the species of sect. *Speciosae*. These species share the caducous floral bracts with most of the species of sect. *Speciosae* and differ from them by the intermediate-sized flowers and the straight internodes of the rhachis (*C. flaccida* and *C. trinervis*) or sterile bracts on the base of the scape (*C. fimbriata*).

To determine whether traditionally used key characters for sectional delimitation in *Coelogyne* are phylogenetically informative, their character state evolution was reconstructed on the single MPT from the total evidence analysis (see Fig. 4.4). Characters with high phylogenetic potential are the diameter of the internodes of the rhachis, length of the lip and number and shape of the keels on the hypochile. Shape and number of leaves of the pseudobulbs show many parallelisms and reversals and appear not to be phylogenetically useful for the set of taxa analysed.

CHARACTERS

The general morphology of *Coelogyne* is described in Butzin (1992a), De Vogel (1992) and Dressler (1993). For easy reference, the most important diagnostic characters for the species within sect. *Speciosae* will be discussed here.

Pseudobulbs

When fresh the pseudobulbs of nearly all species of the section are obtusely 4-angled. *Coelogyne salmonicolor* and *C. xyrekes* can be recognised by the distinctly ribbed pseudobulbs (Fig. 4.13f, 4.19f). The shape of the pseudobulbs varies from ovoid to oblongoid, sometimes within one species as in *C. carinata* and *C. tommii*. The number of leaves on the pseudobulb is either one or two; both states may occur within one species as in *C. carinata*, *C. celebensis* and *C. fragrans* and even within a single specimen, as in *C. speciosa* (Fig. 4.15a).

Inflorescence

Synanthous inflorescences are predominant in the section: the inflorescence-bearing shoot has an immature pseudobulb hidden in the basal scales and the young leaf or leaves on top of this bulb are partly hidden and partly extending from the scales. After anthesis the pseudobulb starts swelling and the leaf or leaves fully develop. When the pseudobulb is fully grown the remainder of the decayed inflorescence (sometimes with fruits) is often persistent on top. The dry remnants of the scales of the inflorescence-bearing shoot envelope the pseudobulbs (Fig. 4.5f).

Coelogyne tommii is the only species within the section with 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 (Fig. 4.18f).

Coelogyne eberhardtii and *C. lawrenceana* have hysteranthous inflorescences: the inflorescence develops on top of a pseudobulb in full-grown state, with full-grown leaves.

Rhachis

The rhachis of the inflorescence varies from (sub)erect (about two thirds of the species studied) (Fig. 4.18f) to semi-pendulous (Fig. 4.10f). *Coelogyne septemcostata* is easily recognised by the strongly curved internodes of the rhachis (Fig. 4.14f). The internodes of the rhachis may be slightly swollen (majority of the species studied) (Fig. 4.19f) or incrassate as in *C. beccarii, C. guamensis, C. lycastoides, C. macdonaldii* and *C. susanae* (Fig. 4.11f).

Floral bracts

Usually the floral bracts are deciduous just after anthesis, although persistent bracts also occur (*C. lycastoides*, *C. macdonaldii* and *C. salmonicolor*). *Coelogyne carinata* and *C. fragrans* are variable in this character.

Flowers

Few [2–7(–22)], medium-sized to large flowers are typical for *Coelogyne* sect. *Speciosae*. Diagnostic characters can be found in the floral parts, mainly in the lip. The flowers open in succession (starting with the basal flowers) in most of the species of the section. Flowers which open more or less simultaneously occur in *C. lycastoides*, *C. macdonaldii*, *C. salmonicolor* and *C. tommii*. In *C. carinata* and *C. fragrans* both character states are present.

Hypochile — number of keels

The number of keels on the hypochile varies from 2 or 3 (most of the species studied) to 5–8 (*C. beccarii*, *C. guamensis*, *C. lycastoides* and *C. septemcostata*) to 9–13 (*C. macdonaldii* and *C. susanae*).

Hypochile — ornamentation of keels

The following keel ornamentations are found: a thick callus (*C. beccarii*) (Plate 4.1n); a decurrent and undulating plate with entire margin (*C. guamensis*, *C. tiomanensis*, *C. tommii* and *C. xyrekes*) (Plate 4.1m, 4.1o) or interrupted margin (*C. dichroantha*) (Plate 4.5a); more or less fused irregularly shaped, rounded warts or ridges (*C. lycastoides, C. macdonaldii* and *C. susanae*) (Plate 4.1j–l); elongate rounded projections, sometimes with a longitudinal groove in between (*C. celebensis* and *C. rumphii*) (Plate 4.1c, 4.1f); two, often interrupted undulating rows of irregularly rounded warts on each side of the crest, with a broad longitudinal groove in between (*C. carinata*, *C. fragrans*, *C. salmonicolor* and *C. septemcostata*) (Plate 4.1a, 4.1b, 4.1d, 4.1e); elongate tapering projections with stellately arranged hairs at their apices (*C. speciosa*) (Plate 4.1g–i). All species have minute papillae on the keels. Some species have elongate projections (also minutely papillose) (*C. xyrekes*) (Plate 4.1m) or multi- or unicellular hairs of various length (*C. salmonicolor*, *C. septemcostata*, *C. speciosa*) (Plate 4.1d, 4.1e, 4.1g–i) on the keels as well.

Hypochile — number of keel projections per row

The number of keel projections per row, counted in cross section is also informative. This number varies from 1 (one third of the species studied) to 2 (half of the species studied) to 5 (*C. rumphii* and *C. speciosa*).

Epichile

On the basal part of the epichile (claw and plate) the ornamentation of the keels is often identical to the ornamentation on the hypochile. On the apical part the keels vary from tightly packed irregularly rounded warts (most species) (Plate 4.1a) to irregularly undulating plate-like projections (five of the species studied) (Plate 4.1o) to an irregular semi-orbicular plate-like projection (*C. tiomanensis* and *C. xyrekes*) (Plate 4.1m). Scattered warts on the lateral lobes and epichile apex are typical for nearly two thirds of the species studied (Fig. 18a). About one third of the species has glabrous epichile apices. The margin of the claw epichile varies from entire (*C. tiomanensis*) (Fig. 17a) to erose (*C. rumphii*, *C. speciosa* subsp. *speciosa* and subsp. *incarnata*, and *C. xyrekes*) (Fig. 12a) to fimbriate (*C. speciosa* subsp. *fimbriata*) (Fig. 15b).

Fruit

In most cases, remnants of the perianth are still attached to the fruit (Fig. 15a). When some details of the keels are visible these can be good identification tools.

SYSTEMATIC TREATMENT

Coelogyne section Speciosae

Coelogyne Lindl. sect. *Speciosae* Pfitzer & Kraenzl. in Engl., Pflanzenr. 32 (1907) 28; Schltr., Feddes Repert. Beih. 1 (1911) 101; J.J. Sm., Feddes Repert. Spec. Nov. Regni Veg. 32 (1933) 168; Butzin, Willdenowia 7 (1974) 247; Seidenf., Dansk Bot. Ark. 29 (1975) 9; Butzin in Brieger et al., Die Orchideeen 1A (1992) 923; De Vogel, Proc. 14th World Orch. Conf. (1994) 203. — Type species: *Coelogyne speciosa* (Blume) Lindl.

Creeping, medium-sized to large epiphytes, sometimes terrestrials or lithophytes. Roots along the entire rhizome, rather slender to sturdy. Rhizome short, creeping, terete; rhizome scales 1– 6, soon eroding. Inflorescence-bearing shoot covered with scales at the base; scales tightly imbricate, 5 or 6. *Pseudobulbs* 1- or 2-leafed (in some species 1- and 2-leafed pseudobulbs may occur on the same plant). *Leaves* stiff herbaceous. Petiole short to long, almost orbicular in section and channelled. Blade oblong to linear-lanceolate, striate and plaited, small to large; base decurrent onto the petiole, sometimes laterally notched; apex acute, acuminate or cuspidate. *Inflorescence* erect, proteranthous or synanthous with the partially to entirely developed leaves, 2–7(–22)-flowered, glabrous. Peduncle ovoid in section, broadening to the apex, during flowering at the base enclosed by the leafblade(s) and/or scales of the young shoot, in a later stage by the petiole(s), usually long and elongating after anthesis. Rhachis (sub)erect to curved, terete, zigzag, with slightly to distinctly curved internodes, each with a swollen base bearing a flower. *Floral bracts* deciduous or persistent, attached around the base of the petiole, the lowest bract longer and broader than the higher bracts; lanceolate to ovate to oblong; apex acute or acuminate or cuspidate. *Flowers* widely open, opening in succession or (nearly) simultaneously, distichous, medium-sized to large, finely papillose. Pedicel terete, slightly twisted, glabrous; ovary twisted, 6-ribbed, glabrous. *Median sepal* boat-shaped, broadly sessile, ovate or (ovate-)oblong or (obovate-)lanceolate, glabrous; apex obtuse, acute, acuminate or apiculate; nerves 7–15, often with smaller cross veins, the midrib a rounded keel. *Lateral sepals* oblique, boat-shaped, ovate, (ovate-)oblong or ((ob)ovate-)lanceolate, glabrous; apex emarginate, obtuse, acute, acuminate or cuspidate; nerves 7–17, often with smaller cross veins, the midrib a rounded keel. *Petals* slightly to extremely recurved, with (a)centric midrib, linear, glabrous; apex emarginate, obtuse, acute, acuminate, cuspidate, apiculate or mucronate; nerves 1–5, midrib prominent. *Lip* immobile, boat-shaped, 3-lobed, when flattened pandurate in outline, nerves 9–21. *Hypochile* broadly attached, flat or slightly saccate at the base; flat or slightly saccate towards the apex; lateral lobes erect, with acute, broadly rounded or obtuse sinus which is sometimes absent, in front rounded, obtuse or acute, slightly converging or diverging, with slightly to extremely irregularly erose front margin; keels 2–13, mostly widened along the crest, a thick callus by fusion of the keels (*C. beccarii*), a decurrent and undulating plate with entire margin (*C. guamensis, C. tiomanensis, C. tommii* and *C. xyrekes*) or interrupted margin (*C. dichroantha*), more or less fused irregularly rounded warts or ridges (*C. lycastoides, C. macdonaldii* and *C. susanae*), elongate rounded projections (*C. celebensis* and *C. rumphii*), two, often interrupted, undulating rows of irregularly shaped rounded warts on each side of the crest, with a broad longitudinal groove in between (*C. carinata*, *C. fragrans*, *C. salmonicolor* and *C. septemcostata*) or elongate tapering projections with stellately arranged hairs at their apices (*C. speciosa*); all keels have minute papillae, some have elongate projections (also minutely papillose) (*C. xyrekes*) or hairs as well (*C. salmonicolor*, *C. septemcostata*, *C. speciosa*). *Epichile* convex, when flattened obrhomboid, (ob)ovate, orbicular, elliptic or broadly spathulate, with or without a broad, short claw; base broadly attached; apex emarginate, retuse, rounded, obtuse or acute, (slightly) raised, with an obtuse, acute or acuminate apex; margin (slightly) erose or entire, recurved; sides either or not pronounced as lateral lobes, with or without warts; keels 2–9, on the claw and plate either identical with the ornamentations on the hypochile or changing into more or less tightly packed irregularly rounded warts towards the apex of the hypochile. *Column* curved to the front, when flattened spathulate; hood with winged margins, widest below the apex, gradually narrowing to the base, its apical margin more or less truncate or dentate, laterally notched where the wings are attached and sometimes with an additional notch or cuneate projection above, the middle part (slightly) rounded, recurved. Filament short. Anther basiversatile, broadly, oblongly or elongately bell-shaped in outline, near the place of attachment with a rounded, elongate or acute projecting apex; apex with or without notch. Pollinia four, flattened to one side, obliquely elliptic or obliquely orbicular, each with an oblique, earshaped depression which becomes shallower towards the caudicle, all connate at the apex by a caudicle; caudicle flattened, broadly triangular in outline, granular. *Stigma* cup-shaped, semi-orbicular with elevated, recurved margin; margin apex with or without an apical notch; rostellum more or less triangular, lateral margins incurved, with a truncate, obtuse, broadly rounded or acute apex with or without apical notch. *Fruit* body ellipsoid, beaked by the persistent column and remnants of the perianth; valvae keeled, keels plate-like; juga band-like with a pronounced longitudinal ridge, with or without incisions.

Distribution — The sixteen species of the section are distributed from mainland southeast Asia (Thailand), all over Malesia to the islands in the Pacific Ocean (Marianas, Solomon Islands, Vanuatu, New Caledonia, Fiji, Tonga, Samoa). No main centres of diversity can be distinguished.

Habitat & Ecology — Epiphytes, sometimes terrestrials or lithophytes in shady to exposed environments. Most species grow in lowland to montane forests or sometimes in secondary vegetations, usually in the range of 400–1500 m.

Cultivation — Only *Coelogyne fragrans, C. speciosa* subsp. *speciosa* and subsp. *incarnata* are widely cultivated. Within *Coelogyne,* three groups can be distinguished, based on the temperature requirements: a warm group (the real tropical species), which should be cultured at 18–23 °C; an intermediate group, which should be cultured at 15–18 °C; and a cool group (the species from higher altitudes), which should be cultured at 10–18 °C, but which can survive lower temperatures. The species of the cool group have a resting period of sometimes several months before new roots emerge. During this resting period, it is recommended to stop watering.

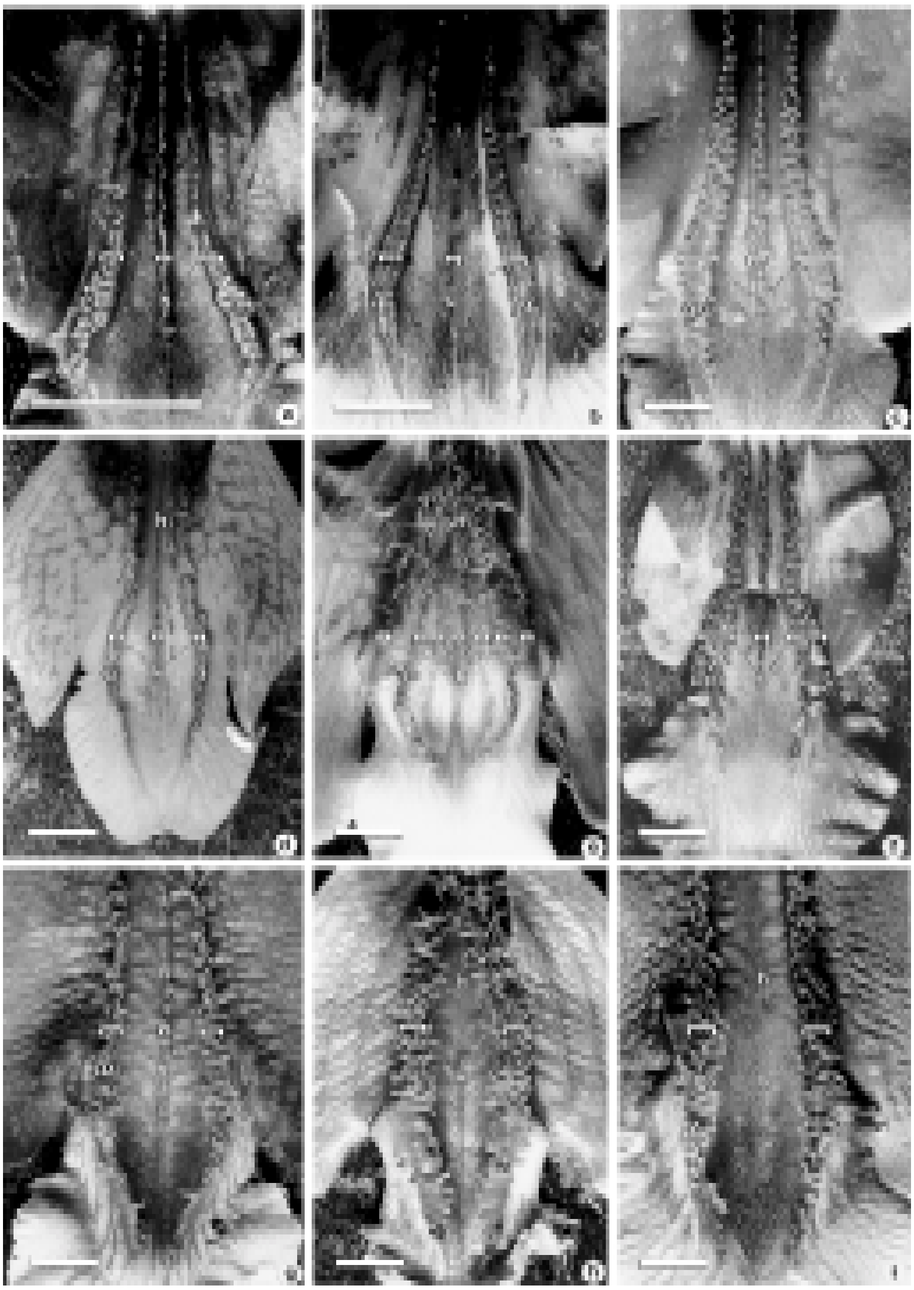
A loose mixture of fern root and hardwood bark or charcoal with *Sphagnum* is recommended for a good drainage as all *Coelogyne* species are very intolerant of wet roots. Watering should be regular and atmospheric humidity should be rather high. Spraying of the leaves is beneficial for the plants. When developing new shoots the plants require more water and diluted manure. Repotting or division of plants is best done in this growing stage and only when absolutely necessary as the plants often require several years to recover from repotting before flowering again. The plants prefer moderate shade and flower for several days to a week (after Hawkes, 1965).

Artificial hybrids — Many attempts have been made to cross species of sect. *Speciosae* with *Coelogyne* species of other sections. Curtis (1950) mentions *C. x colmanii*, a cross between *C. speciosa* var. *major* and *C. cristata* var. *alba*, made by Colman in 1900. Butzin (1992a) reports *C. x gattonensis*, a hybrid between *C. speciosa* and *C. sanderae*. Erfkamp & Gruß (1996) mention several hybrids: *Green Magic,* a hybrid between *C. parishii* and *C. speciosa*, made by Stevenson in 1986; *Memoria Soedjana Kassan*, a hybrid between *C. speciosa* and *C. asperata*, made by Parnata in 1976; *Shibata*, a hybrid between *C. flaccida* and *C. speciosa*, made by Sibata in 1923; *Speciosa-colmanii*, a hybrid between *C. speciosa* and *C. x colmanii*, made by Colman in 1918. Crosses between species within sect. *Speciosae* have also been made. *Neroli Cannon*, a hybrid between *C. speciosa* and *C. fragrans* was made by Cannon in 1981. In 1996, *C. x Andrée Millar*, a cross between *C. beccarii* and *C. speciosa* was produced by Spence (Royal Horticultural Society, 1996).

KEY TO THE SPECIES

1a. Keels on the lip with hairs or with elongate papillae (Fig. 4.19a); flowers opening in succession 2
b. Keels on the lip with minute papillae; flowers opening in succession or (nearly) simultaneously 5
2a. Keels on the lip with elongate papillae (0.1–0.25 mm long); keels plate-like, undulating (Plate 4.1m) . . . . **15. C. xyrekes**
b. Keels on the lip with hairs; keels with 2 projections over the width of the keel, separated by a longitudinal groove (Fig. 4.14a) or with up to 5 projections over the width of the keel (Fig. 4.15a) 3

3a. Number of keels on the lip 5–8; hairs on these keels 0.7–1.5 cm long . . . . **10. C. septemcostata**
b. Number of keels on the lip 2 or 3; hairs on these keels 0.1–0.5 mm long . . . 4
4a. Keels on the lip with 2 projections over the width of the keel; hairs implanted on the rims of the longitudinal groove of each keel (Plate 4.1d); lip 27–34 mm long . . . . **9. C. salmonicolor**
b. Keels on the lip with up to 5 elongate projections over the width of the keel; hairs more or less stellately arranged at the apex of the elongated projections of the keels (Plate 4.1g–i); lip 33–61 mm long . . . . **11. C. speciosa**
5a. Number of keels on the lip 2–13; pseudobulbs at least twice as wide as long 6
b. Number of keels on the lip 2–4; pseudobulbs up to twice as wide as long . . . 8
6a. Leaves of the flowering shoot (partly) developed or still undeveloped during anthesis; keels on the lip plate-like (Plate 4.1o) or with (un)interrupted margin (Plate 4.5a) 7
b. Leaves of the flowering shoot (partly) developed during anthesis; keels on the lip plate-like or consisting of callus patches (Plate 4.1j–l, 4.1n) 12
7a. Leaves 2 per pseudobulb; keels on the lip with interrupted margin and white . . . . **16. C. dichroantha**
b. Leaves 1 per pseudobulb; keels on the lip with uninterrupted margin and brown . . . . **14. C. tommii**
8a. Keels on the lip with 5 elongate projections over the width of the keel (Plate 4.1f) or plate-like (Fig. 4.17a) 9
b. Keels on the lip with 1 projection or with 2 projections over the width of the keel, separated by a longitudinal groove (Fig. 4.7a, 4.8a) 10
9a. Keels on the lip with 5 elongate projections over the width of the keel (Fig.4. 12a); midlobe of lip warty; lip 32–42 mm long . . . . **8. C. rumphii**
b. Keels on the lip plate-like, undulating (Fig. 4.17a); midlobe of lip smooth; lip 24–37 mm long . . . . **13. C. tiomanensis**
10a. Hypochile 1.5 times as long as epichile; midlobe of lip with scattered warts . . . . **3. C. celebensis**
b. Hypochile as long as epichile; midlobe of lip smooth 11
11a. Lip shorter than 28 mm; lateral sepals shorter than 33 mm; flowers not fragrant . . . . **2. C. carinata**
b. Lip longer than 28 mm; lateral sepals longer than 33 mm; flowers fragrant . . . . **4. C. fragrans**
12a. Flowers opening simultaneously; number of leaves per pseudobulb 1 or 2 . 13
b. Flowers opening in succession; number of leaves per pseudobulb 2 14
13a. Leaves 1 per pseudobulb; sidelobes of lip not projecting in front (Fig. 4.10a) . . . . **6. C. lycastoides**
b. Leaves 2 per pseudobulb; sidelobes of lip clearly projecting in front (Fig. 4.11a) . . . . **7. C. macdonaldii**
14a. Keels on the base of the lip plate-like (Fig. 9a); hypochile about as long as epichile . . . . **5. C. guamensis**
b. Keels on the lip consisting of low callus patches (Plate 4.1n) or many warts (Plate 4.1l); hypochile much shorter than epichile 15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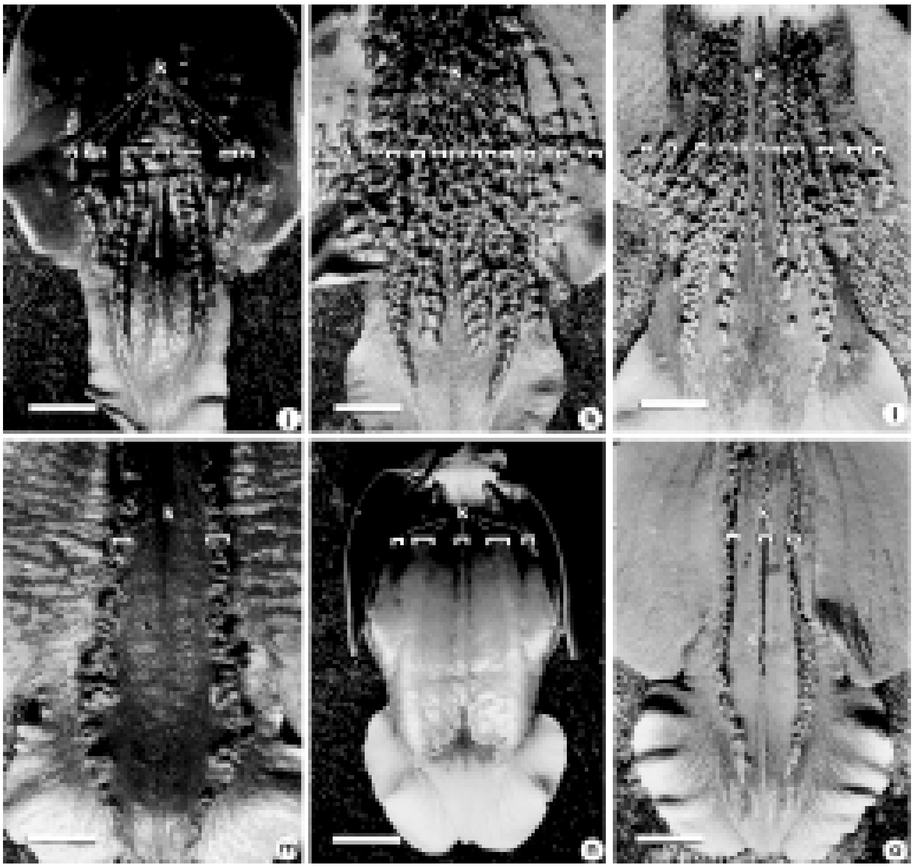

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Plate 4.1. Details of keels on lip. – a. *Coelogyne carinata* Rolfe [*Leiden cult. (De Vogel) 30714*]. – b. *C. fragrans* Schltr. [*Leiden cult. (De Vogel) 30720*]. – c. *C. celebensis* J.J. Sm. [*Leiden cult. (De Vogel) 27369*]. – d. *C. salmonicolor* Rchb. f. [*Leiden cult. (De Vogel) 24393*]. – e. *C. septemcostata* J.J. Sm. [*Leiden cult. (Nooteboom) 23187*]. – f. *C. rumphii* Lindl. [*Leiden cult. (De Vogel) 24505*]. – g. *C. speciosa* (Blume) Lindl. subsp. *speciosa* [*Leiden cult. (De Vogel) 19930*]. – h. *C. speciosa* subsp. *fimbriata* (J.J. Sm.) Gravendeel *(Bogor cult. 992-XI-311)*. – i. *C. speciosa* subsp. *incarnata* Gravendeel [*Leiden cult. (De Vogel) 950058*]. – j. *C. lycastoides* F. Muell. & Kraenzl. [*Leiden cult. (De Vogel) 914325*]. – k. *C. macdonaldii* F. Muell. & Kraenzl. [*Leiden cult. (Cribb & Morrisson) 25836*]. – l. *C. susanae* P.J. Cribb & B.A. Lewis *(Cruttwell 3185)*. – m. *C. xyrekes* Ridl. [*Leiden cult. (Roelfsema, Vogel & Van Balgooy) 960160*]. – n. *C. beccarii* Rchb. f. [*Leiden cult. (Schuiteman, Mulder & Vogel) 32078*]. – o. *C. tommii* Gravendeel & O'Byrne [*Leiden cult. (De Vogel) 21524*]. – Scale bar = 5 mm; g = longitudinal groove, h = hair, k = keel, p = projection.

15a. Main nerves of leaves 3–5; keels on the lip consisting of low, broad and large callus patches (Fig. 4.5a); lip 29–41 mm long . . . . **1. C. beccarii**
b. Main nerves of leaves 5–7; keels on the lip consisting of many rows of small warts (Fig. 4.16a); lip 40–55 mm long . . . . **12. C. susanae**

1. Coelogyne beccarii Rchb. f. — Fig. 4.5, Map 4.1, Plate 4.1n, 4.2a

Coelogyne beccarii Rchb. f., Bot. Centralbl. 28 (1886) 344; Pfitzer & Kraenzl. in Engl., Pflanzenr. 32 (1907) 32; J.J. Sm., Nova Guinea 8 (1911) 136; Schltr., Feddes Repert. Beih. 1 (1914) 103; Ridl., Trans. Linn. Soc. London 2, 9 (1916) 202; Schltr., Feddes Repert. Beih. 21 (1923) f. 137; Andrée Millar, Orchids of Papua New Guinea (1978) 74; Howcroft, Orchadian 7 (1983) 154, f. 1–2; O'Byrne, Lowland Orchids of Papua New Guinea (1994) 74. — Type: *Beccari P.P. 888* (holo FI), Papua New Guinea, Mt Arfak.

Coelogyne beccarii var. *tropidophora* Schltr., Feddes Repert. Beih. 1 (1914) 103. — Lectotype (here chosen): *Schlechter 19110* (holo B†; iso AMES, G, K, L), Papua New Guinea, Finisterre Mts.

Coelogyne micholitziana Kraenzl., Gard. Chron. 3, 10 (1891) 300 '*micholicziana*'; Xenia Orchid. 3 (1892) 100, t. 256; Rolfe, Kew Bull. 4 (1900) 104; Pfitzer & Kraenzl. in Engl., Pflanzenr. 32 (1907) 32, f. 8A–E; Sander's Orch. Guide (1927) 125. — *Coelogyne beccarii* var. *micholitziana* Schltr., Orchideen (1915) 135. — Type: *Micholitz s.n.* (holo K), Papua New Guinea.

Roots 1.8–3 mm diam. Rhizome 7–12.2 mm thick. Scale-covered part of the inflorescence-bearing young shoot 7.5–14.3 cm long. *Pseudobulbs* up to 0.9 cm apart, oblongoid, obtusely 4-angled when fresh, 4.8–8.5 cm long. *Leaves* two per pseudobulb. Petiole 2.3–8.5 cm long. Blade linear to linear-lanceolate, 22–35.4 by 1.9–6 cm; apex acuminate; main nerves 3–5. *Inflorescence* synanthous with the partially to entirely developed leaves, 2–7(–13)-flowered. Peduncle during flowering at the base enclosed by the petiole and scales of the young shoot, 18.5–44 cm long. Rhachis (sub)erect, zigzag, 1.9–7 cm long; internodes 15.5–28 mm long, slightly to distinctly curved, incrassate. *Floral bracts* lanceolate to ovate-lanceolate, 40–54 by 10.5–18 mm, deciduous; apex acuminate; nerves 11–13. *Flowers* opening in succession. Pedicel 5–8 by 2.5–2.7 mm; ovary 10–20 by 4–7 mm. *Median sepal* ovate, 34.5–44 by 18–22 mm; apex acute; nerves 9–13, the midrib a rounded keel 0.5–1 mm high. *Lateral sepals* ovate, 34–44 by 14–19 mm; apex acuminate; nerves 9–12, the midrib a rounded keel 0.3–1 mm high. *Petals* slightly recurved, 32–43 by 3.6–5.5 mm; apex acuminate; nerves 5, midrib centric. *Lip* 29–41 by 26–28 mm, nerves 11–15. *Hypochile* when flattened 15–18 by 26–28 mm; base attached over 6–19 mm, not saccate; lateral lobes in front rounded to obtuse, extending 2.8–3.5 mm in front and slightly converging, front margin at the base irregularly erose; with acute sinus; apex not saccate; keels 3–7, widened along the crest, more or (rarely) less fused together into a thick callus 1.9–3.1 mm high (Plate 4.1n), with papillae but without hairs, all keels starting at the base of the lip and there 0.5–0.9 mm high, developed on the hypochile and the apical half of the epichile, the median keel lower than the lateral ones. *Epichile* highly convex, when flattened obrhomboid to orbicular, 15–22 by 15–19 mm, with a broad, short claw 2–2.9 mm thick; base attached over 12.5–14 mm; apex acute, slightly raised, with an acute apex with warts 0.4–0.75 mm high; margin slightly erose, recurved; sides pronounced as lateral lobes, with warts 0.5–1 mm high, centre 0.48–0.5 mm thick, margin 0.2–0.3 mm thick; keels 5–7, ending 4–8 mm from the apex of the

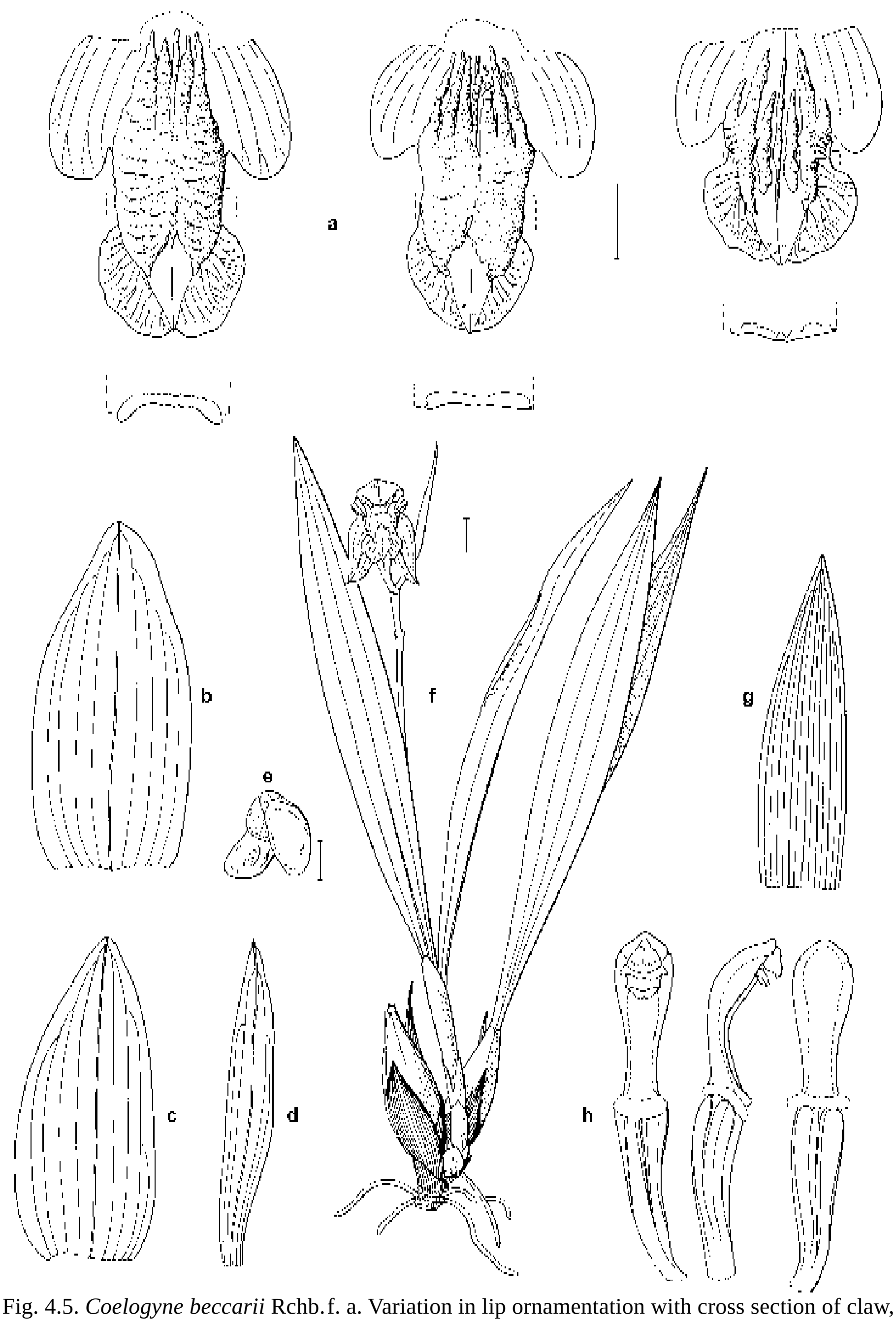


Fig. 4.5. *Coelogyne beccarii* Rchb.f. a. Variation in lip ornamentation with cross section of claw, from left to right: *Leiden cult. (Schuiteman, Mulder & Vogel) 31883*, *Leiden cult. (Woods) 22059*, *Leiden cult. (Reeve) 22284*; b. median sepal; c. lateral sepal; d. petal; e. pollinia; f. habit; g. floral bract; h. column: front, lateral and rear view [*Leiden cult. (Schuiteman, Mulder & Vogel) 32230*]. — Scale bars: 1 cm (a–d, f–h); 1 mm (e).

epichile, on the claw identical with the keels on the hypochile, on the plate changing into a row of tightly packed irregularly rounded warts, with papillae but without hairs. *Column* 19–23 by 7–8 mm; hood with more or less acute apical margin, laterally notched or with two small cuneate projections where the wings are attached and with an additional notch above, the middle part rounded, recurved. Anther broadly bell-shaped in outline, 3–5 by 4.9–5 mm, near the place of attachment with a little rounded projecting apex; apex with or without notch. Pollinia obliquely ellipsoid, 2.1–3 by 1.2–1.9 mm; caudicle 1.3–1.5 by 0.8–1.1 mm. *Stigma* 3.9–4 by 4.6–6 mm; margin apex notched; rostellum 3–4 by 5.5–6.7 mm, with an obtuse apex with or without notch. *Fruit* body 58–65 by 24–36 mm; valvae keels 8.5–9 mm high; juga with a pronounced longitudinal ridge 5–5.5 mm high without incisions.

Distribution — Irian Jaya, Papua New Guinea, New Britain, Solomon Islands (Guadalcanal).

Habitat & Ecology — Epiphyte, rarely terrestrial in rain forest and secondary vegetations. Altitude 26–1500 m. Flowering: January, March, April, June, August–December (June–November in greenhouse).

Notes — 1. Ovary light green. Sepals and petals pale green to yellowish white. Lip white, lateral lobes, margin of the claw of the midlobe and base of the midlobe blackish brown, base of hypochile red brown, callus cream coloured to light brown to reddish orange to purplish brown, bordered with brownish red. Column white, base blackish brown to brownish red. Anther cream coloured to pale ochre. Stigma inside light green. No smell.

2. The epithet *beccarii* refers to O. Beccari, who collected the type specimen in the Arfak mountains in W Papua New Guinea.

3. As the variation in the number and structure of the keels on the lip of the specimens studied appeared to be continuous, it is concluded that *C. beccarii* var. *tropidophora* and *C. beccarii* var. *micholitziana* are synonyms of *C. beccarii*.

4. The species is easily recognised by the thick callus on the lip, the broad lateral lobes of the hypochile with obtuse to rounded front margin and the linear-lanceolate leaves.

2. Coelogyne carinata Rolfe — Fig. 4.6, Map 4.1, Plate 4.1a, 4.3a

Coelogyne carinata Rolfe, Kew Bull. (1895) 191. — Type: *Sander & Co. s.n.*, 1895 (holo K), unknown locality.

Coelogyne sarasinorum Kraenzl. in Engl., Pflanzenr. 4 (1907) 29. — Type: *Sarasin & Sarasin 700* (holo B†), Celebes, near Tomohon.

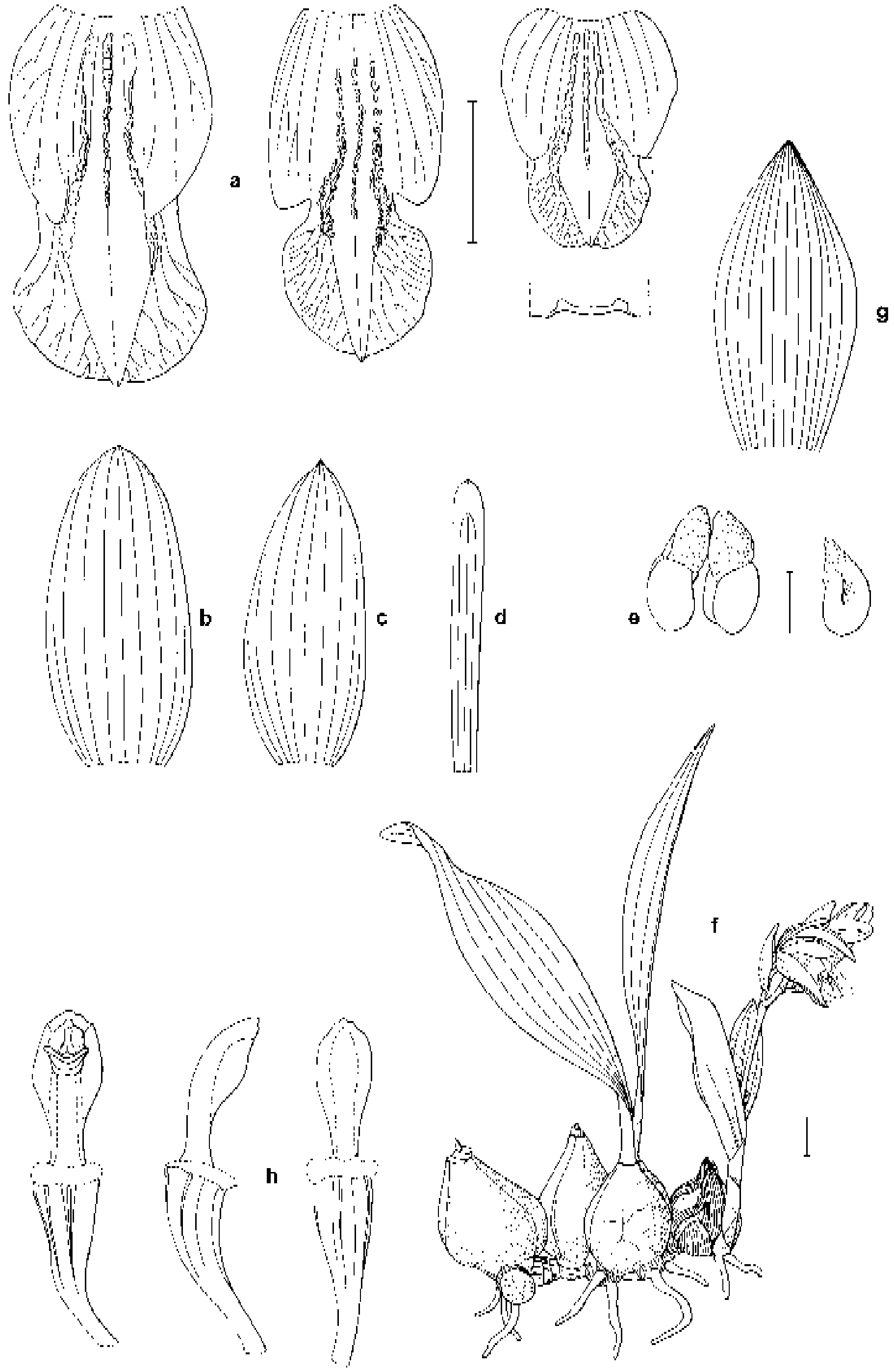
Coelogyne truncicola Schltr., Feddes Repert. Beih. 1 (1914) 104; 21 (1923) 138, t. 40; O'Byrne, Lowland Orchids of Papua New Guinea (1994) 72. — Type: *Schlechter 19618* (holo B†), Papua New Guinea, Kaiser Wilhelm Mts, Govidjoa.

Coelogyne oligantha Schltr., Feddes Repert. Beih. 16 (1919) 44. — Type: *Kempf s.n.* (holo B†), Papua New Guinea, Waria.

Coelogyne alata Andrée Millar, Orchids of Papua New Guinea (1978) 75, nom. nud.

∅

Fig. 4.6. *Coelogyne carinata* Rolfe. a. Variation in lip ornamentation with cross section of claw, from left to right: *Leiden cult. (De Vogel) 30725, NGF (Millar) 23543, Leiden cult. (De Vogel) 30714*; b. median sepal; c. lateral sepal; d. petal; e. pollinia; f. habit; g. floral bract; h. column: front, lateral and rear view [*Leiden cult. (De Vogel) 30714*]. — Scale bars: 1 cm (a–d, f–h); 1 mm (e).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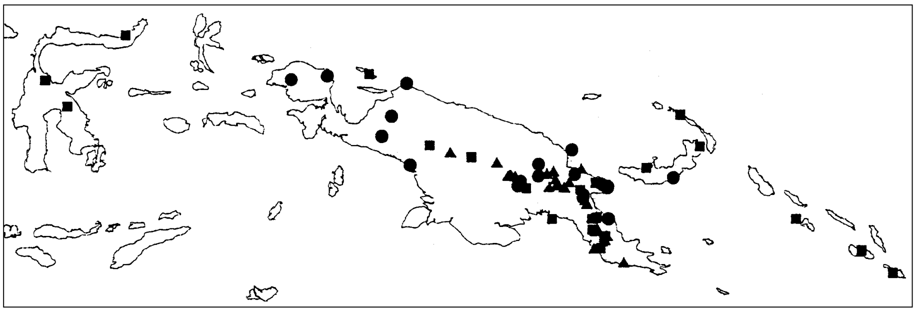


Map 4.1. Distribution of *Coelogyne beccarii* Rchb.f. (l), *C. carinata* Rolfe (n) and *C. fragrans* Schltr. (s).

Roots 1–2.8 mm diam. Rhizome 5.1–11 mm thick. Scale-covered part of the inflorescence-bearing young shoot 3.5–16 cm long. *Pseudobulbs* up to 1–2.3 cm apart, ovoid to oblongoid when fresh, 4.8–11 cm long. *Leaves* one or two per pseudobulb. Petiole 0.9–5 cm long. Blade obovate-lanceolate, 8.1–37 by 3.1–7.2 cm; apex acuminate; main nerves 5–7. *Inflorescence* synanthous with partially to entirely developed leaves, 2–8-flowered. Peduncle during flowering at the base enclosed by the petiole and scales of the young shoot, 6.4–29 cm long. Rhachis (sub)erect, zigzag, 1–9.5 cm long; internodes 8–20.5 mm long, slightly curved, (slightly) thickened. *Floral bracts* ovate, 16.2–61 by 7–14 mm, deciduous or persistent; apex acute; nerves 11–15. *Flowers* opening in succession. Pedicel 4–10 by 1.2–2.7 mm; ovary 9–13 by 3–4.4 mm. *Median sepal* ovate, 18.5–22.5 by 5.5–9.5 mm; apex apiculate; nerves 9, the midrib a rounded keel 0.5–0.7 mm high. *Lateral sepals* ovate-oblong, 16–33 by 4–7.5 mm; apex acuminate; nerves 8 or 9, the midrib a rounded keel 0.5– 0.6 mm high. *Petals* slightly recurved, 15–20 by 1–2.5 mm; apex apiculate; nerves 3, midrib centric. *Lip* 16–28 by 5–12 mm, nerves 9–11. *Hypochile* when flattened 7–12 by 5–12 mm; base attached over 4–13 mm, not saccate; lateral lobes in front obtuse, extending 0.5–1.4 mm in front and slightly diverging, front margin at the base irregularly erose, with acute sinus; apex slightly saccate; keels 3, widened along the crest, consisting of two, often interrupted, undulating rows of irregularly rounded warts on each side of the crest 0.2–0.3 mm high, with papillae but without hairs, separated by a longitudinal groove (Plate 4.1a); all keels starting at the base of the lip and there 0.1–0.2 mm high, diverging towards the apex of the hypochile, converging again on the epichile, the lateral keels up to 1 mm high, the median keel lower than the lateral ones. *Epichile* convex, when flattened circular to elliptic, 5–7.5 by 3.5–9 mm, with a broad, short claw 0.15–0.2 mm thick; base broadly attached over 3–7.5 mm; apex acute, slightly raised, with an obtuse apex; margin slightly elevated, recurved; sides pronounced as lateral lobes, without warts, centre 0.15–0.2 mm thick, margin 0.1–0.3 mm thick; keels 3, ending 3.1–5.5 mm from the apex of the epichile, on the claw identical with the ornamentations on the hypochile, on the plate sometimes changing into a row of tightly packed irregularly rounded warts c. 1 mm high, with papillae but without hairs. *Column* 11.5–13 by 3–4.5 mm; hood with more or less truncate apical margin, laterally notched where the wings are attached and with an additional notch above, the middle part rounded, recurved. Anther broadly bell-shaped in outline, 2.2–2.5 by 2.5–3 mm, near the place of attachment with a rounded projecting apex; apex without notch. Pollinia obliquely ellipsoid, 1.2–1.5 by 0.8–1 mm; caudicle 1–1.5 by 1.5–1.8 mm. *Stigma* 2.2–3 by 2–2.3 mm; margin apex (slightly) notched; rostellum 1.7–2 by 2–2.2 mm, with an obtuse apex without notch. *Fruit* body 44–46 by 23–32 mm; valvae keels 6–7.5 mm high; juga with a pronounced longitudinal ridge 3.5–4.5 mm high with up to 4 incisions up to 1.5 mm deep.

Distribution — Sulawesi, Biak, Irian Jaya, Papua New Guinea, New Britain, New Ireland, Solomon Islands (New Georgia, Guadalcanal, San Cristobal).

Habitat & Ecology — Epiphyte in oak forest, rubber tree plantations, primary rain forest along rivers, in logged areas, coastal vegetation on limestone rock and flood plains, rarely terrestrial. Altitude 105–2300 m. Flowering: March, May–July, September, October (February, April–June in greenhouse).

Notes — 1. Sepals and petals pale green. Hypochile very pale green to green, lobes inside with orange brown open reticulate markings, keels with light orange brown sides and much paler crest, between the keels orange brown. Epichile base as on hypochile, front part white, median tinged greenish. Column whitish green, stigma with faint pale brownish markings. Anther pale yellowish green. No smell.

2. The epithet *carinata* refers to the keels on the lip.

3. In some cases, the species is difficult to keep apart from *C. fragrans*. Especially specimens from the surroundings of Morobe tend to have intermediate floral sizes and may be hybrids between the two species. *Coelogyne carinata* can be distinguished from *C. fragrans* by a lip length shorter than 28 mm and nonfragrant flowers.

3. Coelogyne celebensis J.J. Sm. — Fig. 4.7, Map 4.2, Plate 4.1c, 4.3c

Coelogyne celebensis J.J. Sm., Bull. Jard. Bot. Buitenzorg II, 25 (1917) 3; Burkill, Gard. Bull. Straits Settlem. 3 (1924) 292; Bouman-Houtman, Trop. Natuur 15 (1926) 95, f. 1. — Lectotype (here chosen): *Bogor cult. (Elbert) s.n.* (L), Kolaka, Sulawesi. Paratypes: *Bogor cult. (Elbert) 4; Van Vuuren 1912, 1913; Noerkas 388; Rachmat 29, 678* (BO?, not found).

Coelogyne platyphylla Schltr., Feddes Repert. Beih. 21 (1925) 129. — Type: *Becker cult. (native collector) s.n.* (holo B†), Sulawesi, Dongala.

Roots 1.5–1.8 mm diam. Rhizome 7.8–13 mm thick. Scale-covered part of the inflorescence-bearing young shoot 8–15 cm long. *Pseudobulbs* 0–2.5 cm apart, oblongoid, distinctly 4-ridged when fresh, 5.7–14 cm long. *Leaves* one or two per pseudobulb. Petiole 1.1–4 cm long. Blade obovate-lanceolate, 33–62 by 8.1–14 cm; apex acuminate; main nerves 7. *Inflorescence* synanthous with the partially to entirely developed leaf or leaves, 3–7-flowered. Peduncle during flowering at the base enclosed by the petiole and scales of the young shoot, 27–30.5 cm long. Rhachis (sub)erect, zigzag, 3.5–11.5 cm long; internodes 15.5–24 mm long, slightly curved, hardly thickened. *Floral bracts* ovate-lanceolate, 49–69 by 13–18 mm, deciduous; apex acuminate; nerves 17–19. *Flowers* opening in succession. Pedicel 4–8 by 1.9–2.2 mm; ovary 7.4–13 by 3.3–5 mm. *Median sepal* oblong, 49–56 by 16–21 mm; apex acuminate; nerves 11–15, the midrib a rounded keel 0.6–1 mm high. *Lateral sepals* oblong, 44–53 by 13–16 mm; apex acuminate; nerves 10–16, the midrib a rounded keel 0.5–0.7 mm high. *Petals* slightly recurved, 49–54 by 2.8–3.5 mm; apex acuminate; nerves 3,

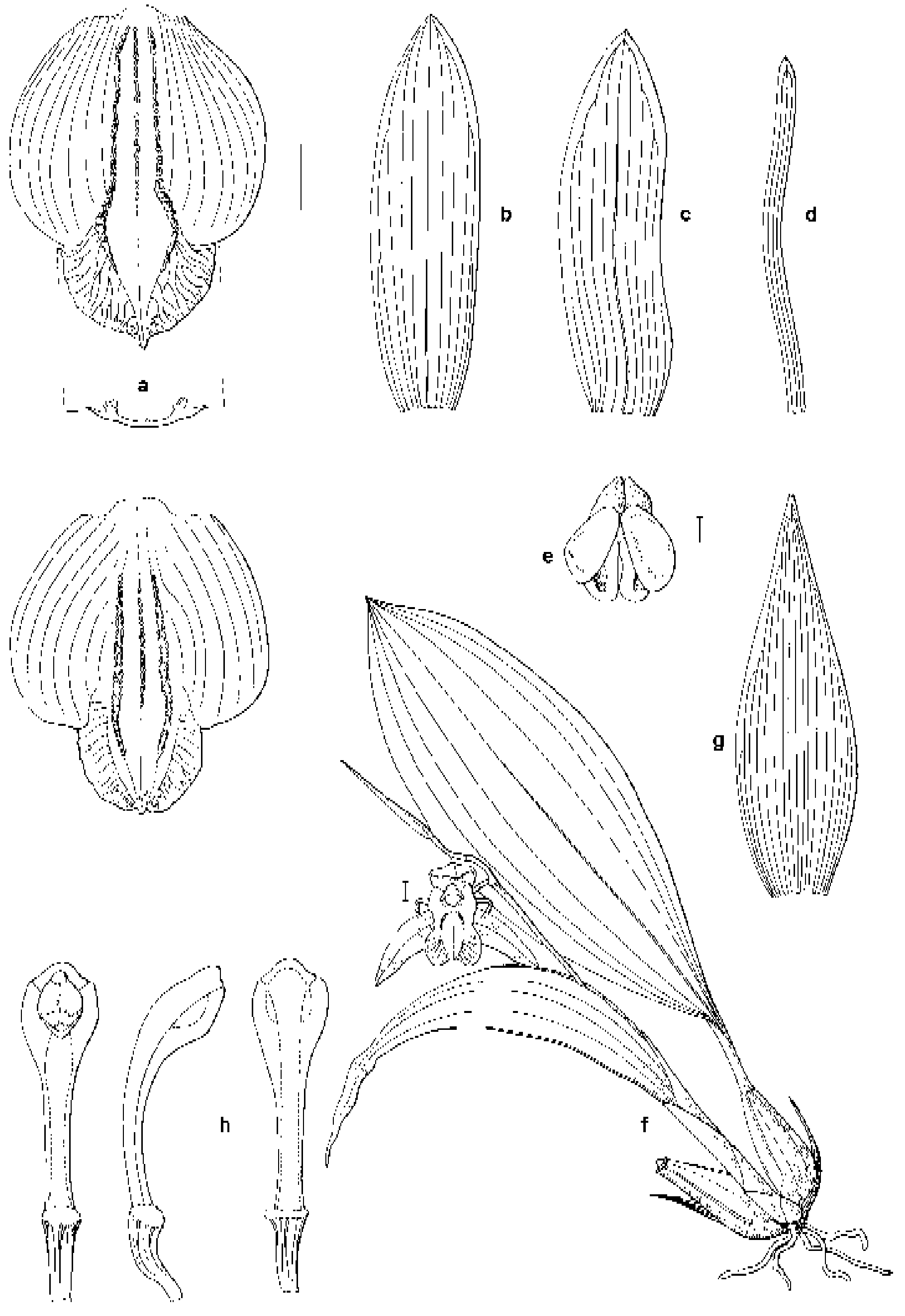
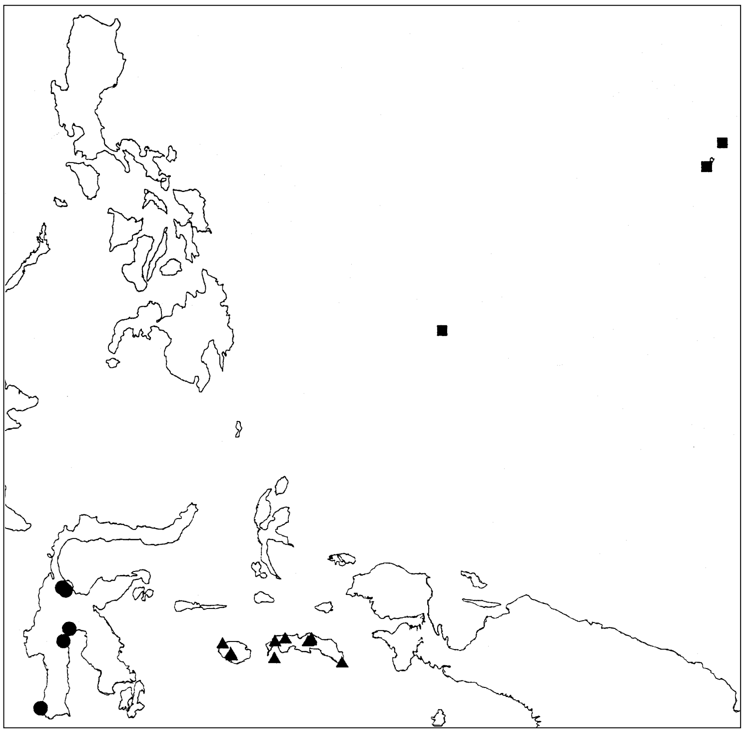


Fig. 4.7. *Coelogyne celebensis* J.J. Sm. a. Variation in lip ornamentation with cross section of claw, from top to bottom: *Leiden cult. (De Vogel) 20202, Leiden cult. (De Vogel) 27369*; b. median sepal; c. lateral sepal; d. petal [*Leiden cult. (De Vogel) 21099*]; e. pollinia; f. habit [*Leiden cult. (De Vogel) 27369*]; g. floral bract [*Leiden cult. (De Vogel) 20202*]; h. column: front, lateral and rear view [*Leiden cult. (De Vogel) 30714*]. — Scale bars: 1 cm (a–d, f–h); 1 mm (e).

midrib eccentric. *Lip* 46–52 by 35–39 mm, nerves 17–19. *Hypochile* when flattened 33–36 by 35–39 mm; base attached over 19–22 mm, not saccate; lateral lobes in front obtuse, extending 5.5–9 mm in front and slightly diverging, front margin at the base slightly irregularly erose to entire, with acute sinus; apex not saccate; keels 3, starting at the basal quarter of the lip and there 0.4–0.6 mm high, all keels widened along the crest, with many slender, tapering, either or not branched, elongate and sometimes plate-like projections 0.5–1 mm high, with papillae but without hairs (Plate 4.1c); the lateral keels up to 1.3 mm high, diverging towards the apex of the hypochile, converging again on the epichile, the median keel only developed in the basal half to two thirds of the hypochile, lower than the lateral ones. *Epichile* convex, when flattened elliptic, 12–24 by 18.6–25.4 mm, with a broad, short claw 0.1–0.5 mm thick; base attached over 14–18 mm; apex retuse, slightly raised, with an acute apex with warts 0.3–0.45 mm high; margin slightly erose, recurved; sides pronounced as lateral lobes, with warts at the base 0.3–0.45 mm high, centre 0.25–0.5 mm thick, margin 0.2–0.3 mm thick; keels 2, ending 9–14 mm from the apex of the epichile, on the claw and plate changing into one or two, irregularly interrupted rows of slender, tapering, either or not branched plate-like projections with papillae but without hairs, sometimes with a narrow longitudinal groove between the rows, the inner row shorter than the outer row. *Column* 36–37 by 9–11 mm; hood with truncate apical margin, irregularly dentate,



Map 4.2. Distribution of *Coelogyne celebensis* J.J. Sm. (l), *C. guamensis* Ames (n), and *C. rumphii* Lindl. (s).

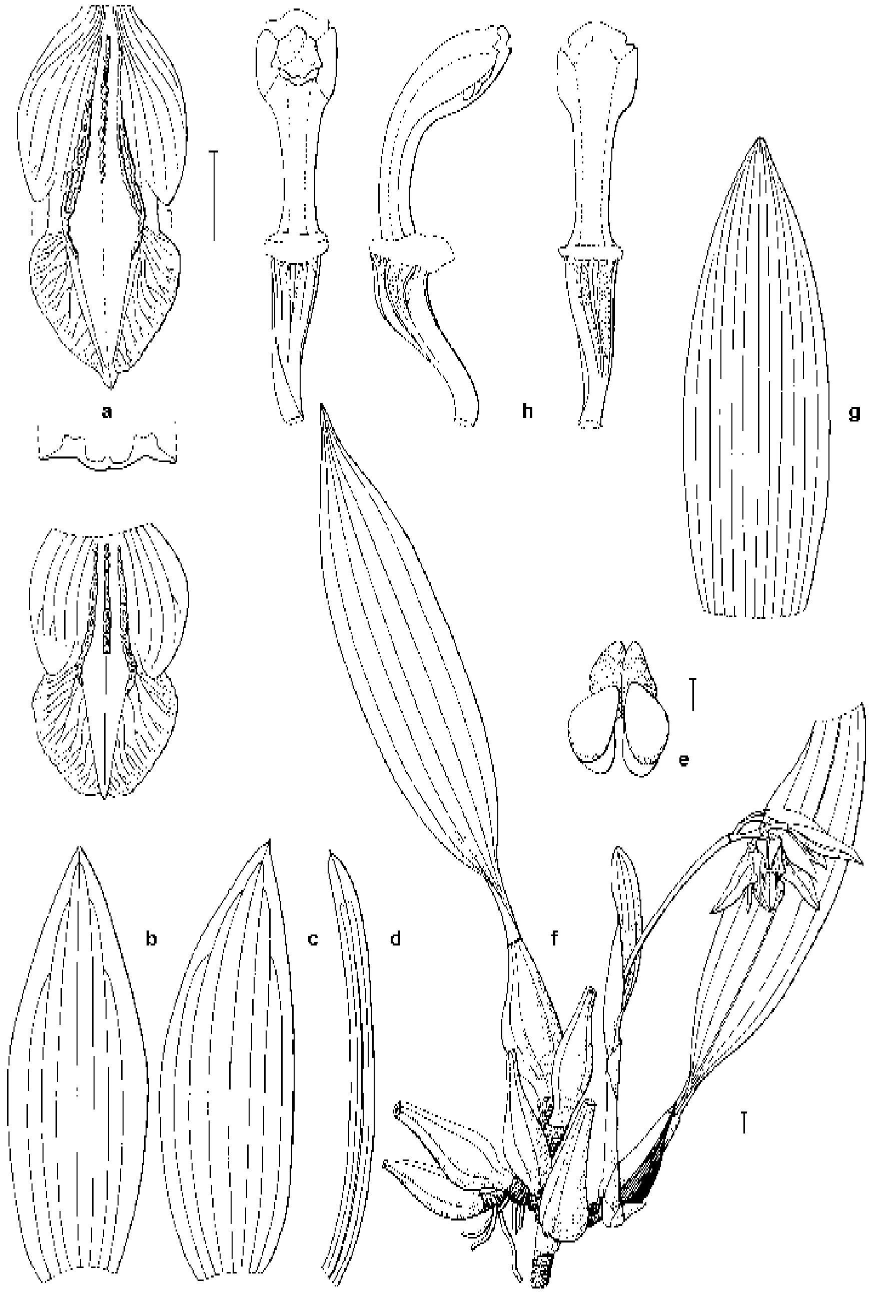


Fig. 4.8. *Coelogyne fragrans* Schltr. a. Variation in lip ornamentation with cross section of claw, from top to bottom: *Leiden cult. (Schuiteman, Mulder & Vogel) 31508*, *Leiden cult. (De Vogel) 25670*; b. median sepal; c. lateral sepal; d. petal [*Leiden cult. (Schuiteman, Mulder & Vogel) 32268*]; e. pollinia; f. habit [*Leiden cult. (Schuiteman, Mulder & Vogel) 31598*]; g. floral bract; h. column: front, lateral and rear view [*Leiden cult. (Schuiteman, Mulder & Vogel) 32268*]. — Scale bars: 1 cm (a–d, f–h); 1 mm (e).

laterally notched where the wings are attached, the middle part slightly rounded, recurved. Anther elongate bell-shaped in outline, 7.5–9 by 6–7 mm, near the place of attachment with a little rounded projecting apex; apex acute, without notch. Pollinia obliquely ellipsoid, 3–4 by 1.7–2.2 mm; caudicle 1.5–3 by 1.5–2 mm. *Stigma* 4–4.4 by 4–5 mm; margin apex with a more or less pronounced notch; rostellum 4–5.8 by 5.5–7 mm, with an acute apex without notch. *Fruit* body 41–43 by 27–28 mm; valvae keels 6.5–8.5 mm high; juga with a pronounced longitudinal ridge 4–5 mm high without incisions.

Distribution — Sulawesi.

Habitat & Ecology — Epiphyte in primary forest. Altitude 0–1000 m. Flowering: February–March (March–July in greenhouse).

Notes — 1. Sepals and petals pale green, translucent. Lip ground colour whitish, at the base, between the keels and at the base of the epichile very dark brown, rest suffused with dark brown, keels dark brown, sometimes with few small white dots. Column pale green grading to orange at the apex, hood margins citron yellow. Anther cream coloured. No smell.

2. The epithet *celebensis* refers to the island Sulawesi, formerly called Celebes, where the type specimen was collected by Elbert.

3. The species is easily recognised by the dark brown lip with elongate, tapering projections on the keels and broad sidelobes with obtuse front margin.

4. Coelogyne fragrans Schltr. — Fig. 4.8, Map 4.1, Plate 4.1b, 4.3b

Coelogyne fragrans Schltr., Feddes Repert. Beih. 1, 1 (1914) 102; 21 (1923) f. 136; Chadim, Orchadian 7, 3 (1982) 60, f. 8–10; 84, f. 1–6; O'Byrne, Lowland Orchids of Papua New Guinea (1994) 76. — Lectotype (here chosen): *Schlechter 18216* (K; iso AMES, G, L), Papua New Guinea, Kaiser-Wilhelmsland. Paratype: *Schlechter 18083* (BO, G, K, L).

Roots 1.8–2.4 mm diam. Rhizome 8–13.4 mm thick. Scale-covered part of the inflorescence-bearing young shoot 9–13.4 cm long. *Pseudobulbs* up to 1.5 cm apart, oblongoid, obtusely 4-angled when fresh, 6.5–10 cm long. *Leaves* one or two per pseudobulb. Petiole 3–5 cm long. Blade lanceolate, 21–38.5 by 3.8–6.8 cm; apex acuminate; main nerves 5–7. *Inflorescence* synanthous with the partially to entirely developed leaves, 2–6-flowered. Peduncle during flowering at the base enclosed by the petiole and scales of the young shoot, 18–38 cm long. Rhachis (sub)erect, zigzag, 2.6–9.5 cm long; internodes 13–20.4 mm long, slightly curved, (slightly) thickened. *Floral bracts* ovate-lanceolate, 33–53 by 8–12 mm, deciduous or persistent; apex acute; nerves 11–13. *Flowers* opening (nearly) simultaneously or in succession. Pedicel 6–8 by 1.5–2.6 mm; ovary 8–14 by 3–4 mm. *Median sepal* oblong, 34–49 by 9–17 mm; apex acuminate; nerves 7–9, the midrib a rounded keel 0.6–1 mm high. *Lateral sepals* oblong, 33–46 by 9–14 mm; apex acuminate; nerves 6 or 7, the midrib a rounded keel 0.7–1 mm high. *Petals* recurved, 31–45.2 by 2–5 mm; apex acuminate; nerves 3. *Lip* 28–45 by 15–22 mm, nerves 13–15, midrib eccentric. *Hypochile* when flattened 15–22 by 15–22 mm; base attached over 9–17 mm, not saccate; lateral lobes in front obtuse, extending 3–6 mm in front and slightly diverging, front margin at the base slightly irregularly erose, with acute sinus; apex slightly saccate; keels 3, not widened along the crest, all keels starting at the base of the lip and there 0.5–1 mm high, diverging towards the apex of the hypochile, converging again on the epichile, the lateral keels up to 2.5 mm high, consisting of two, often interrupted, undulating rows of irregularly rounded warts on each side of the crest 0.5–0.8 mm high, with papillae but without hairs, separated by a longitudinal groove (Plate 4.1b), the median keel lower than the lateral ones and consisting of one, at a few places interrupted row of undulating, irregularly rounded warts with papillae but without hairs. *Epichile* convex, when flattened elliptic, 13–20 by 11–22 mm, with a broad, short claw 0.2–0.25 mm thick; base attached over 10–11 mm; apex retuse, slightly raised, with an acute apex; margin slightly erose, recurved; sides not pronounced as lateral lobes, without warts, centre 0.4–0.5 mm thick, margin 0.25–0.35 mm thick; keels 2 or 3, ending 9–28 mm from the apex of the epichile, on the claw and plate identical with the ornamentations on the hypochile. *Column* 24–26.7 by 7–8.3 mm; hood with more or less truncate apical margin, laterally notched where the wings are attached, the middle part slightly rounded, recurved. Anther broadly bell-shaped in outline, 5.3–6 by 4.5–5 mm, near the place of attachment with a rounded projecting apex; apex with or without notch. Pollinia obliquely ellipsoid, 2.8–3.5 by 1.6–1.8 mm; caudicle 0.6–2.6 by 2.2–2.3 mm. *Stigma* 3.5–5 by 3.3–3.8 mm; margin apex notched; rostellum 2.7–5.2 by 4.2–5 mm, with an acute apex without notch. *Fruit* body 54–60 by 26–38 mm; valvae keels 7–11 mm high; juga with a pronounced longitudinal ridge 3.5–6 mm high without incisions.

Distribution — Irian Jaya, Papua New Guinea.

Habitat & Ecology — Common. Epiphyte in (un)disturbed rain forest on slopes, secondary forest and oak forests, less frequently terrestrial. Altitude 100–2000 m. Flowering: April, August–November (January–September, December in greenhouse).

Notes — 1. Ovary bright green. Sepals and petals light green to golden yellow. Lip greenish white or cream coloured, at the base tinged pale green to orange, on the keels brown, warts on keels brown to light orange, epichile base and lateral margins at the base brownish to orange to yellow, lateral lobes along the margins with brownish to bright orange to dark yellow markings, which continue along the margins of the claw. Front half of the epichile cream coloured to greenish white. Column stalk greenish grading to bright yellowish green on the hood, margins of the hood orange; in front below the stigma with two brown lines. Anther creamy yellow. No smell just after start of anthesis, later very fragrant.

2. The epithet *fragrans* refers to the strong fragrance of the flowers during a limited period of time during anthesis.

3. In some cases, the species is difficult to keep apart from *C. carinata* (see note 3 under *C. carinata*).

5. **Coelogyne guamensis** Ames — Fig. 4.9, Map 4.2

Coelogyne guamensis Ames, Philipp. J. Sci., Bot. 9 (1914) 11; Schltr., Bot. Jahrb. Syst. 56 (1921) 457; Tuyama, J. Jap. Bot. 17 (1941) 505. — Type: *Thompson's collector 195* (holo not found), Guam, Experiment station.

Coelogyne palawensis Tuyama, J. Jap. Bot. 17 (1941) 506. — Type: *Tuyama s. n.*, 15-8-1939 (holo TI, not seen), Carolina Islands, Palau, Baobeltaob, Ngatpang (Gaspan).

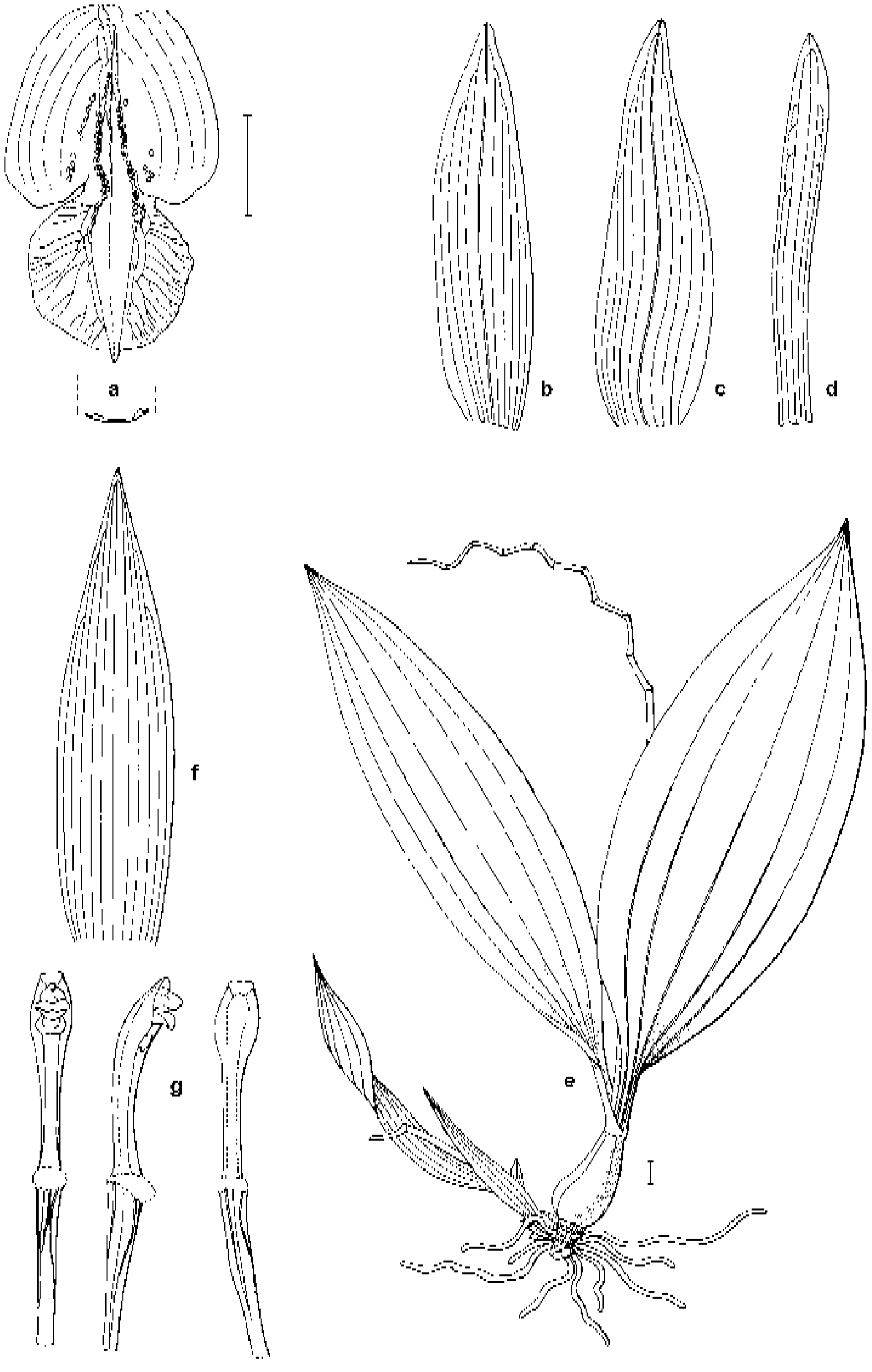


Fig. 4.9. *Coelogyne guamensis* Ames. a. Lip ornamentation with cross section of claw; b. median sepal; c. lateral sepal; d. petal; e. habit; f. floral bract; g. column: front, lateral and rear view (*Rinehart LR 7689*). — Scale bars: 1 cm.

Roots 1.5–2.2 mm diam. Rhizome 6.5–15.5 mm thick. Scale-covered part of the inflorescence-bearing young shoot c. 3.6 cm long. *Pseudobulbs* up to 1 cm apart, oblongoid, not seen when fresh, 5.1–8 cm long. *Leaves* two per pseudobulb. Petiole 2.5–5 cm long. Blade lanceolate, 26–36 by 3.9–9.4 cm; apex acuminate; main nerves (3–)5–7. *Inflorescence* synanthous with the partially to entirely developed leaves, 4–11-flowered. Peduncle during flowering at the base enclosed by the petiole and scales of the young shoot, 8.5–20 cm long. Rhachis curved, zigzag, 1.6–12 cm long; internodes 14–21 mm long, distinctly curved, incrassate. *Floral bracts* lanceolate to ovate-lanceolate, 37–49 by 11–14 mm, deciduous; apex acuminate; nerves 9–11. *Flowers* opening in succession. Pedicel 4.7–7.5 by 1–1.5 mm; ovary 9–14 by 2–4 mm. *Median sepal* ovate-lanceolate, 37–42 by 8–10 mm; apex acuminate; nerves 10–12, the midrib a rounded keel 0.1–0.4 mm high. *Lateral sepals* ovate-lanceolate, 35–41 by 8.5–11 mm; apex acuminate; nerves 9–11, the midrib a rounded keel 0.1–0.5 mm high. *Petals* not seen when fresh, midrib centric, 35–38 by 2–4 mm; apex acuminate; nerves 3–5. *Lip* 28–36 by 15–22 mm, nerves 13–15. *Hypochile* when flattened 15–20 by 15–22 mm; base attached over 4.5–9 mm; lateral lobes in front obtuse, extending 2.5–4 mm in front, not seen when fresh, front margin at the base irregularly erose, with acute sinus; keels 5, starting at the base of the lip and there 0.4–0.5 mm high, all keels slightly widened along the crest, raised, plate-like, decurrent towards the centre of the hypochile, crest slightly undulating, entire, papillose, halfway along the hypochile changing into a slightly elevated row with two pronounced, irregularly shaped transversal ridges, with papillae but without hairs, the three median keels parallel on the base of the hypochile, diverging towards the apex of the hypochile, the outer two median keels converging again on the epichile, up to 1.3 mm high, the most central of these keels only developed on the hypochile, up to 2 mm high, the two lateral keels starting at the base of the hypochile or halfway towards the epichile, only developed on the hypochile, lower than the median keels. *Epichile* slightly convex, when flattened broadly ovate, 14–16 by 13–17 mm, with a broad, short claw 0.1–0.3 mm thick; base attached over 7–10 mm; apex acuminate, slightly raised, with an acute apex without warts; margin slightly erose, recurved; sides pronounced as lateral lobes, without warts, centre 0.1–0.3 mm thick, margin 0.1–0.5 mm thick; keels 3, ending 8–12 mm from the apex of the epichile, on the claw identical with the keels on the apical half of the hypochile, on the blade changing into irregular plate-like projections, decurrent towards the apex of the epichile, crest heavily undulating, interrupted, with papillae but without hairs. *Column* 12–19 by 3–5.5 mm; hood with more or less truncate apical margin, not laterally notched where the wings are attached, the middle part rounded, slightly recurved. Anther broadly bell-shaped in outline, 3.3–4 by 3–4.5 mm, near the place of attachment with a little rounded projecting apex; apex without notch. Pollinia not seen; caudicle not seen. *Stigma* 3–4.5 by 4–5.5 mm; margin apex notched; rostellum 3–5 by 2.5–5.5 mm, with an obtuse apex without notch. *Fruit* body 73–75 by 29–33 mm; valvae keels 7–9 mm high; juga with a pronounced longitudinal ridge 4–4.5 mm high without incisions.

Distribution — Palau Islands (Aimiriik, Coral Island), Mariana Islands (Guam, Rota).

Habitat & Ecology — Epiphyte in damp rain forest. Altitude 425 m. Flowering: July–September (not in cultivation).

Notes — 1. No colours and smell recorded.

2. The epithet *guamensis* refers to the island Guam, where the type collection was made under the direction of J.B. Thompson in 1912.

3. The holotype of *C. palawensis* [*Tuyama s.n.* (15-8-1939), Palau TI] was not studied, but the vegetative and floral characters of the paratype (*Kanehira 1949*, Aimiriik NY) are identical with the studied material of *C. guamensis*. Therefore it is concluded that these species must be synonyms.

4. The dimensions in the description refer to herbarium material only.

5. The species can be recognised by five undulating, plate-like keels with entire margin on the lip.

6. Coelogyne lycastoides F. Muell. & Kraenzl. — Fig. 4.10, Map 4.3, Plate 4.1j, 4.2b

Coelogyne lycastoides F. Muell. & Kraenzl., Oesterr. Bot. Z. 45 (1895) 179; Pfitzer & Kraenzl. in Engl., Pflanzenr. 32 (1907) 32, f. 8F; B.A. Lewis & P.J. Cribb, Orchids of Vanuatu (1989) 59; Kores, Allertonia 5 (1989) 68. — Type: *Betche s.n.*, 24-11-1880 (holo MEL?, not seen), Samoa, Upolu.

Coelogyne whitmeei Schltr., Feddes Repert. Spec. Nov. Regni Veg. 11 (1912) 41. — Type: *Whitmee s.n.* (holo B†; iso K), Samoa.

Roots 2.2–3 mm diam. Rhizome 8–11.5 mm thick. Scale-covered part of the inflorescence-bearing young shoot 11–14 cm long. *Pseudobulbs* up to 1.2 cm apart, oblongoid, obtusely 4-angled when fresh, 61–80 cm long. *Leaves* one per pseudobulb. Petiole 1.5–3 cm long. Blade ovate-lanceolate, 26–43 by 8–11.5 cm; apex acuminate; main nerves 7–9. *Inflorescence* synanthous with the partially to entirely developed leaves, 2–4-flowered. Peduncle during flowering at the base enclosed by the petiole and scales of the young shoot, 24–27 cm long. Rhachis (sub)erect, zigzag, 4–5.5 cm long; internodes 20–27 mm long, slightly to distinctly curved, incrassate. *Floral bracts* ovate-lanceolate to ovate-oblong, 41–61 by 11–26 mm, persistent; apex acute; nerves 11–21. *Flowers* opening (almost) simultaneously. Pedicel 4–5 by 2.2–2.7 mm; ovary 14–24 by 6–7 mm. *Median sepal* ovate-oblong, 42–45 by 15–17 mm; apex acuminate; nerves 9, the midrib a rounded keel 0.45–0.5 mm high. *Lateral sepals* ovate-lanceolate, 42–46 by 13–14.5 mm; apex acuminate; nerves 8, the midrib a rounded keel 0.35–0.5 mm high. *Petals* slightly recurved, midrib eccentric, 42–43 by 3.5–7 mm; apex acuminate; nerves 3. *Lip* 37–39 by 22–29 mm, nerves 15–17. *Hypochile* when flattened 21–22 by 22–29 mm; base attached over 12–14 mm, slightly saccate; lateral lobes in front obtuse, not extending in front, front margin at the base slightly irregularly erose, without sinus; apex not saccate; keels 5–7, not widened along the crest, each consisting of a slightly elevated row of undulating, irregularly shaped, rounded warts 0.5–1.4 mm high, with papillae but without hairs (Plate 4.1j), the median 3 keels parallel at the base of the hypochile and there 0.3–0.35 mm high, diverging towards the apex of the hypochile, converging again on the epichile, the most median one shorter and lower than the lateral ones, the 2–4 lateral keels starting at the middle to the apex of the hypochile, much shorter than the median keels. *Epichile* oblong, when flattened broadly obovate to broadly spathulate, 17–18 by 12–12.5 mm, with a broad, short claw 0.25–0.3 mm thick; base attached over 11–14 mm; apex retuse, slightly raised, with an acute to obtuse apex without warts; margin slightly erose, recurved; sides not pronounced as lateral lobes, without warts, centre 0.25–0.3 mm thick, margin 0.2–

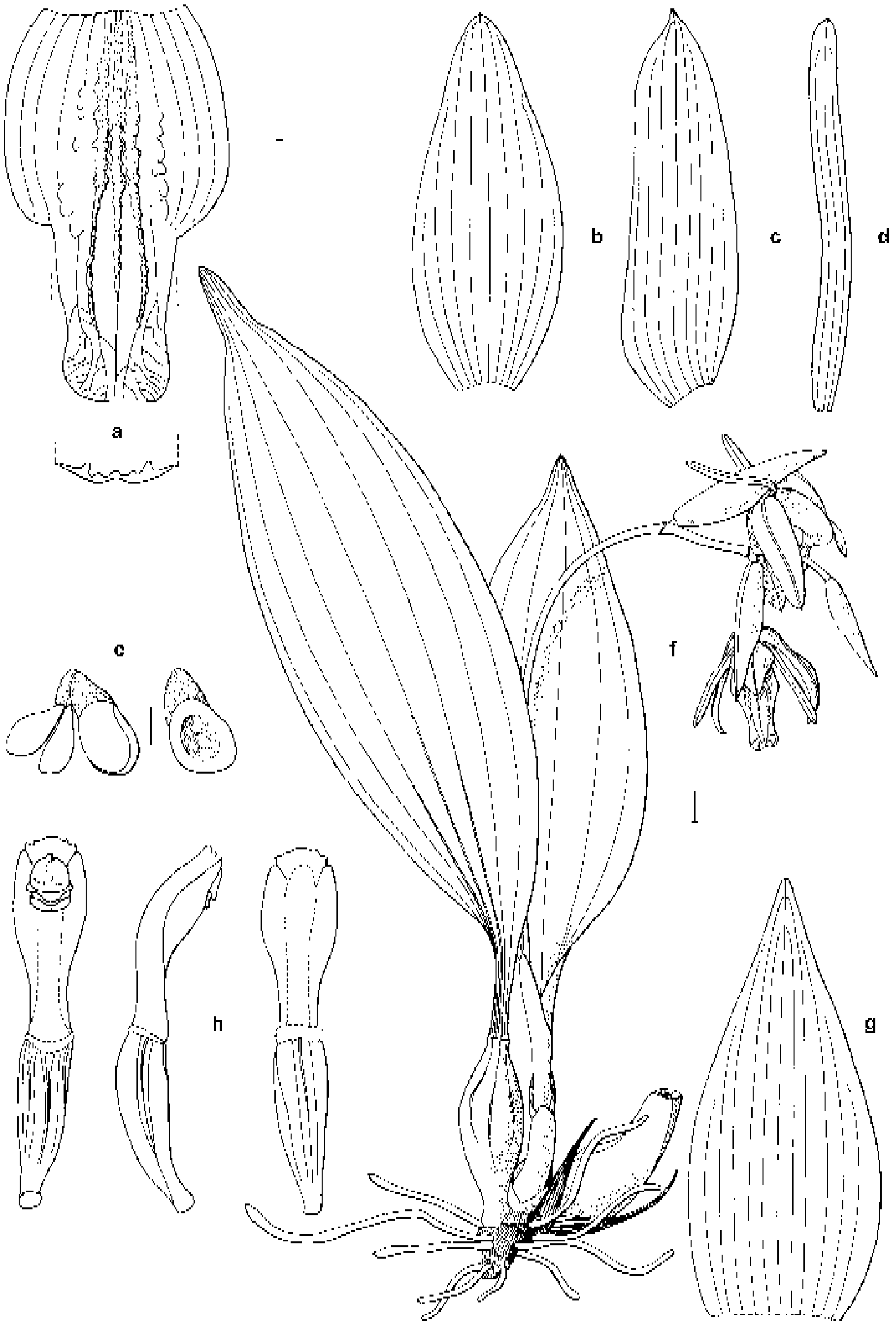
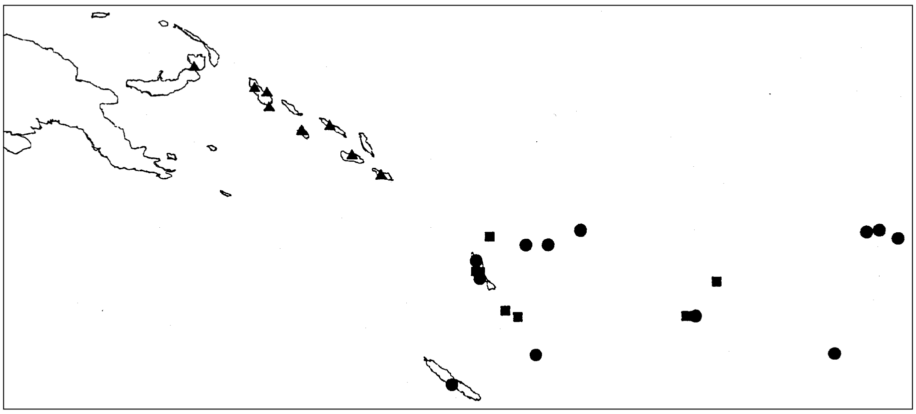


Fig. 4.10. *Coelogyne lycastoides* F. Muell. & Kraenzl. a. Lip ornamentation with cross section of claw; b. median sepal; c. lateral sepal; d. petal [*Leiden cult. (Mulder) 913070*]; e. pollinia; f. habit; g. floral bract [*Leiden cult. (De Vogel) 914325*]; h. column: front, lateral and rear view [*Leiden cult. (Mulder) 913070*]. — Scale bars: 1 cm (a–d, f–h); 1 mm (e).



Map 4.3. Distribution of *Coelogyne lycastoides* F. Muell. & Kraenzl. (l), *C. macdonaldii* F. Muell. & Kraenzl. (n), and *C. susanae* P.J. Cribb & B.A. Lewis (s).

0.25 mm thick; keels 3–5, ending 7.5–9 mm from the apex of the epichile, on the claw identical with the keels on the hypochile, on the claw changing into a row of tightly packed irregularly rounded warts 0.8–1.4 mm high, with papillae but without hairs. *Column* 23–27 by 8–9 mm; hood with more or less truncate apical margin, laterally notched where the wings are attached and above, the middle part rounded, recurved. Anther broadly bell-shaped in outline, 4–5 by 4.5–5 mm, near the place of attachment with a little rounded projecting apex; apex slightly notched. Pollinia obliquely ellipsoid to obliquely orbicular, 2.5–2.8 by 1.5–1.8 mm; caudicle 1.8–2 by 2–4 mm. *Stigma* 2.8–3 by 4–4.5 mm; margin apex notched; rostellum 3–5 by 4–6 mm, with an obtuse apex without notch. *Fruit* body 50–64 by 24–34 mm; valvae keels 6–10 mm high, juga with a pronounced longitudinal ridge 4–5 mm high without incisions.

Distribution — Vanuatu, New Caledonia, Fiji, Tonga, Samoa.

Habitat & Ecology — Epiphyte in primary rain forest and open woodland. Altitude 300–1550 m. Flowering: January–August (August–September in greenhouse).

Notes — 1. Ovary pale green. Sepals and petals very pale green. Lip whitish, for the greater part tinged orange brown, except for the margins and apical half of the midlobe; keels orange brown. Column whitish green. Anther pale yellow. No smell to slightly fragrant.

2. The epithet *lycastoides* refers to the morphological similarity with species within the genus *Lycaste*.

3. The species may be confused with *C. macdonaldii*, but can be recognised by the one-leafed pseudobulbs and nearly confluent rows of undulating, irregularly rounded warts on the lip.

7. Coelogyne macdonaldii F. Muell. & Kraenzl. — Fig. 4.11, Map 4.3, Plate 4.1k, 4.2c

Coelogyne macdonaldii F. Muell. & Kraenzl., Oesterr. Bot. Z. 44 (1894) 209 [‘M’Donaldi’]; Pfitzer & Kraenzl. in Engl., Pflanzenr. 32 (1907) 31 [‘M’Donaldi’]; B.A. Lewis & P.J. Cribb, Orchids of Vanuatu (1989) 60; Kores, Allertonia 5 (1989) 68. — Type: *Melbourne cult. (MacDonald) s.n.* (holo MEL?, not seen), (said to come from) the New Hebrides.

Coelogyne lamellata Rolfe, Kew Bull. (1895) 36; 4 (1900) 103; Pfitzer & Kraenzl. in Engl., Pflanzenr. 32 (1907) 28, f. 7F. — Type: *Sander & Co. cult. s.n.*, ?-8-1895 (holo K), New Hebrides.

Roots 2.5–3 mm diam. Rhizome 7–9.5 mm thick. Scale-covered part of the inflorescence-bearing young shoot 8–15 cm long. *Pseudobulbs* up to 1.8 cm apart, oblongoid, obtusely 4-angled when fresh, 5–7.5 cm long. *Leaves* two per pseudobulb. Petiole 1.6–2.5 cm long. Blade ovate-lanceolate, 20–29.8 by 5.1–11.5 cm; apex acuminate; main nerves 5–7. *Inflorescence* synanthous with the partially to entirely developed leaves, 3–5-flowered. Peduncle during flowering at the base enclosed by the petiole and scales of the young shoot, 11.5–16.5 cm long. Rhachis (sub)erect, zigzag, 2.7–5.6 cm long; internodes 10.5–20 mm long, slightly to distinctly curved, incrassate. *Floral bracts* ovate-oblong, 51–70 by 21–29 mm, persistent; apex acuminate; nerves 11–13. *Flowers* opening (almost) simultaneously. Pedicel 9–10 by 2.2–2.7 mm; ovary 16–25 by 5.5–7 mm. *Median sepal* ovate-oblong, 42–52 by 15.5–22 mm; apex obtuse; nerves 9, the midrib a rounded keel 0.4–0.5 mm high. *Lateral sepals* ovate-oblong, 40–50 by 15–16 mm; apex obtuse; nerves 9 or 10, the midrib a rounded keel 0.5–0.9 mm high. *Petals* slightly recurved, 41–48 by 4.1–4.7 mm; apex acute; nerves 3–5, midrib centric. *Lip* 35–45 by 25–28 mm, nerves 15–17. *Hypochile* when flattened 20–22 by 25–28 mm; base attached over 7–10 mm, not saccate; lateral lobes in front obtuse, extending 2.8–3 mm in front and slightly converging, front margin at the base irregularly erose, with acute sinus; apex not saccate; keels 9–13, consisting of longitudinal rows of irregularly shaped ridges 0.7–2.1 mm high, with papillae but without hairs (Plate 4.1k), not widened along the crest, the most median 4–7 keels parallel at the base of the hypochile and there 0.7–1 mm high, diverging towards the apex of the hypochile and converging again on the epichile, the lateral 4–6 keels only developed on the hypochile and sometimes on the basal half of the epichile, lower than the median keels. *Epichile* convex, when flattened obovate to elliptic to ovate, 15–18 by 11–15 mm, with a broad, short claw 0.2–0.9 mm thick; base broadly attached over 11–13 mm; apex rounded to retuse, slightly raised, with an acuminate to acute apex without warts; margin slightly erose, recurved; sides more or less pronounced as lateral lobes, without warts, centre 0.25–0.4 mm thick, margin 0.1–0.2 mm thick; keels 5–7, ending 7–10 mm from the apex of the epichile, on the claw and plate identical with the keels on the hypochile. *Column* 19–23 by 7.6–8 mm; hood with more or less truncate apical margin, laterally notched where the wings are attached, the middle part rounded, recurved. Anther broadly bell-shaped in outline, 4.9–5 by 5–5.5 mm, near the place of attachment with a little slightly elongate projecting apex; apex with small notch. Pollinia obliquely ellipsoid to obliquely orbicular, 2.5–3 by 1.7–2 mm; caudicle 3–3.5 by 3–4 mm. *Stigma* 3–4 by 4–5 mm; margin apex notched; rostellum 3–4 by 5–6 mm, with an obtuse apex without notch. *Fruit* body 62–76 by 21.5–32 mm; valvae keels 7–11 mm high; juga with a pronounced longitudinal ridge 5–8 mm high with 9–12 incisions up to 6.3 mm deep.

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Plate 4.2. – a. *Coelogyne beccarii* Rchb.f. [*Leiden cult. (Schuiteman, Mulder & Vogel) 32230*, Papua New Guinea]. Photograph C.G. Koops. – b. *C. lycastoides* F. Muell. & Kraenzl. [*Leiden cult. (Mulder) 914325*, Fiji]. Photograph C.G. Koops. – c. *C. macdonaldii* F. Muell. & Kraenzl. [*Leiden cult. (Cribb & Morrisson) 25836*, Vanuatu]. Photograph C.G. Koops. – d. *C. susanae* P.J. Cribb & B.A. Lewis (Bougainville). Photograph J.B. Comber.

a. *Coelogyne beccarii*

b. *Coelogyne lycastoides*

c. *Coelogyne macdonaldii*

d. *Coelogyne susanae*

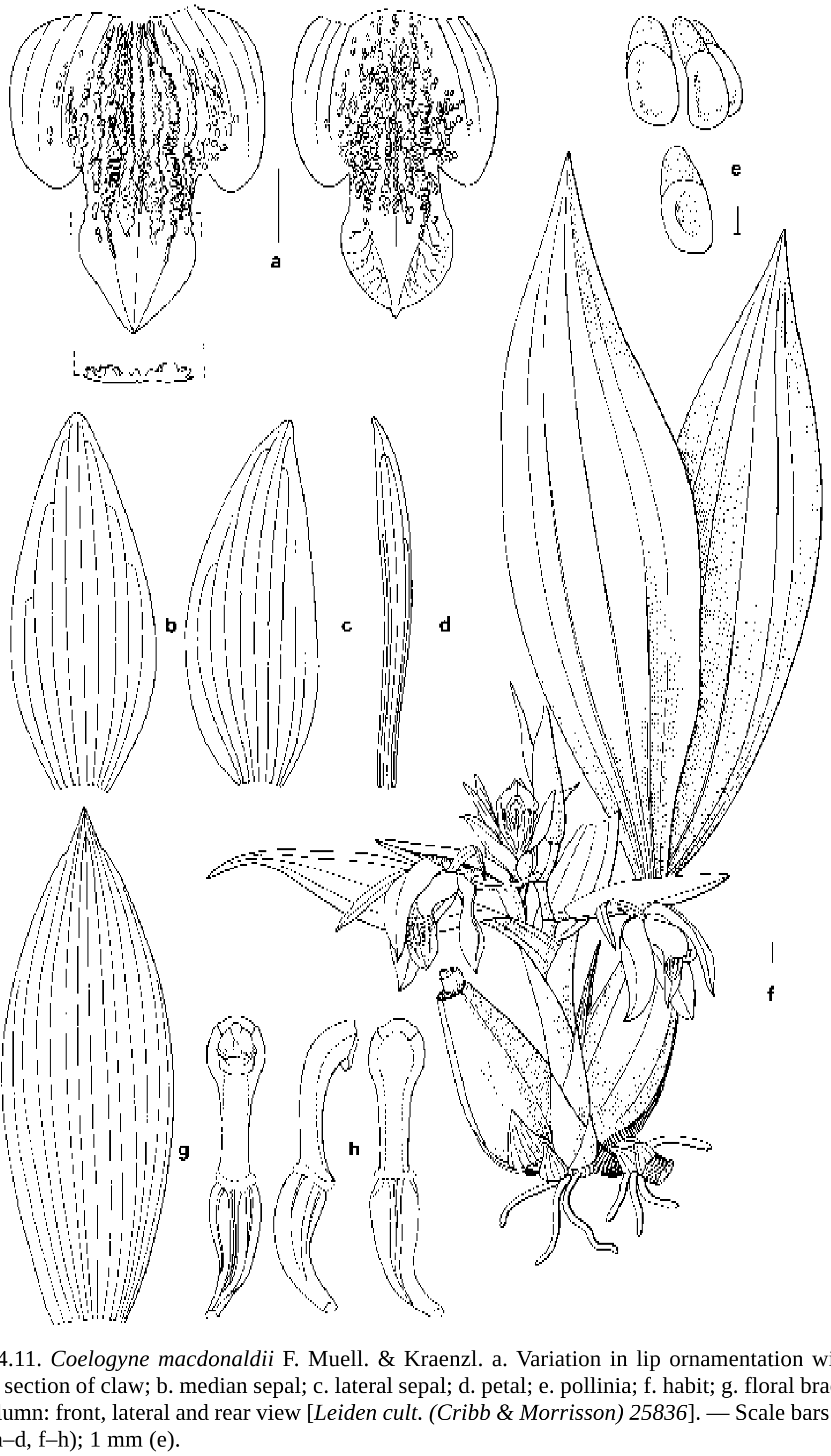

Fig. 4.11. *Coelogyne macdonaldii* F. Muell. & Kraenzl. a. Variation in lip ornamentation with cross section of claw; b. median sepal; c. lateral sepal; d. petal; e. pollinia; f. habit; g. floral bract; h. column: front, lateral and rear view [*Leiden cult. (Cribb & Morrisson) 25836*]. — Scale bars: 1 cm (a–d, f–h); 1 mm (e).

Distribution — Banks Islands (Vanua Lava), Vanuatu (Espirito Santo, Ambae, Pentecost, Efate, Erromango), Fiji.

Habitat & Ecology — Epiphyte in rain forest. Altitude 300–1100 m. Flowering: September–March (July–November in greenhouse).

Notes — 1. Sepals and petals very pale green to whitish green. Lip greenish white, inside light orange brown with lighter spots, the low warts cream, darker brown at the base of the midlobe, outside of the lip the brown shimmering through. Column greenish white, anther cream to pale brown. Fragrant.

2. The epithet *macdonaldii* refers to rev. M. McDonald, who collected the type specimen, probably somewhere on the New Hebrides as McDonalds' collections principally come from these islands [Index Herbariorum 2 (1976) 4: 480].

3. The species may be confused with *C. lycastoides* (see note 3 under *C. lycastoides*).

8. Coelogyne rumphii Lindl. — Fig. 4.12, Map 4.2, Plate 4.1f, 4.3d

Coelogyne rumphii Lindl., Fol. Orchid. 1, 14 (1854) nr. 36; Miq., Fl. Ned. Ind. 3 (1859) 668; Rchb. f., Ann. Bot. Syst. 6 (1861) 234; J.J. Sm., Orch. Ambon (1905) 16; Pfitzer & Kraenzl. in Engl., Pflanzenr. 32 (1907) 28; J.J. Sm., Teysmannia 31 (1920) 254. — *Angraecum nervosum* Rumph., Herb. Amboin. 6 (1750) 106, t. 48. — *Pleione rumphii* (Lindl.) Kuntze, Rev. Gen. Pl. 2 (1891) 680. — Type: Rumphius, Herb. Amboin. (1750) t. 48.

Coelogyne psittacina Rchb. f., Xenia Orchid. 2 (1868) 141, t. 153. — *Pleione psittacina* (Rchb. f.) Kuntze, Rev. Gen. Pl. 2 (1891) 680. — Type: *Doleschall 90* (holo W), Ambon.

Coelogyne psittacina Rchb. f. var. *huttonii* Rchb. f., Gard. Chron. 32 (1870) 1053. — Type: *Hutton s. n.* (holo W), Moluccas.

Roots 1.7–2.1 mm diam. Rhizome 6.6–10.4 mm thick. Scale-covered part of the inflorescence-bearing young shoot 7.3–18.7 cm long. *Pseudobulbs* up to 1.5 cm apart, oblongoid, obtusely 4-angled when fresh, 5.4–13.4 cm long. *Leaves* one per pseudobulb. Petiole 2.5–3.8 cm long. Blade lanceolate, 28–59 by 8–12.9 cm; apex acuminate; main nerves 7. *Inflorescence* synanthous with the partially to entirely developed leaf, 2–6-flowered. Peduncle during flowering at the base enclosed by the petiole and scales of the young shoot, 24–51 cm long. Rhachis (sub)erect, zigzag, 1.9–7.5 cm long; internodes 16–19 mm long, slightly curved, hardly thickened. *Floral bracts* ovate-lanceolate to lanceolate, 53–65.7 by 10.7–15 mm, deciduous; apex cuspidate; nerves 11–13. *Flowers* opening in succession. Pedicel 6.5–8.2 by 2–2.2 mm; ovary 9–14.4 by 3.3–4.5 mm. *Median sepal* oblong, 39.1–50.7 by 15–17.5 mm; apex acuminate; nerves 9–11, the midrib a rounded keel 0.8–1 mm high. *Lateral sepals* oblong, 37.6–47.3 by 11.8–14.3 mm; apex acuminate; nerves 9, the midrib a rounded keel 0.7–0.8 mm high. *Petals* slightly to extremely recurved, 38–46 by 3–4 mm; apex acute; nerves 3, midrib centric. *Lip* 31.8–42 by 20–22.4 mm, nerves 13–15. *Hypochile* when flattened 18–22.4 by 20–22.4 mm; base attached over 13.7–14 mm, not saccate; lateral lobes in front obtuse, extending 4–5.3 mm in front and slightly diverging, front margin

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Plate 4.3. – a. *Coelogyne carinata* Rolfe [*Leiden cult. (De Vogel) 30714*, Sulawesi]. Photograph C.G. Koops. – b. *C. fragrans* Schltr. [*Leiden cult. (Schuiteman, Mulder & Vogel) 31598*, Papua New Guinea]. Photograph C.G. Koops. – c. *C. celebensis* J.J. Sm. [*Leiden cult. (De Vogel) 27369*, Sulawesi]. Photograph B. Kieft. – d. *C. rumphii* Lindl. [*Leiden cult. (De Vogel) 24505*, Buru]. Photograph A. Vogel.

a. *Coelogyne carinata*

b. *Coelogyne fragrans*

c. *Coelogyne celebensis*

d. *Coelogyne rumphii*

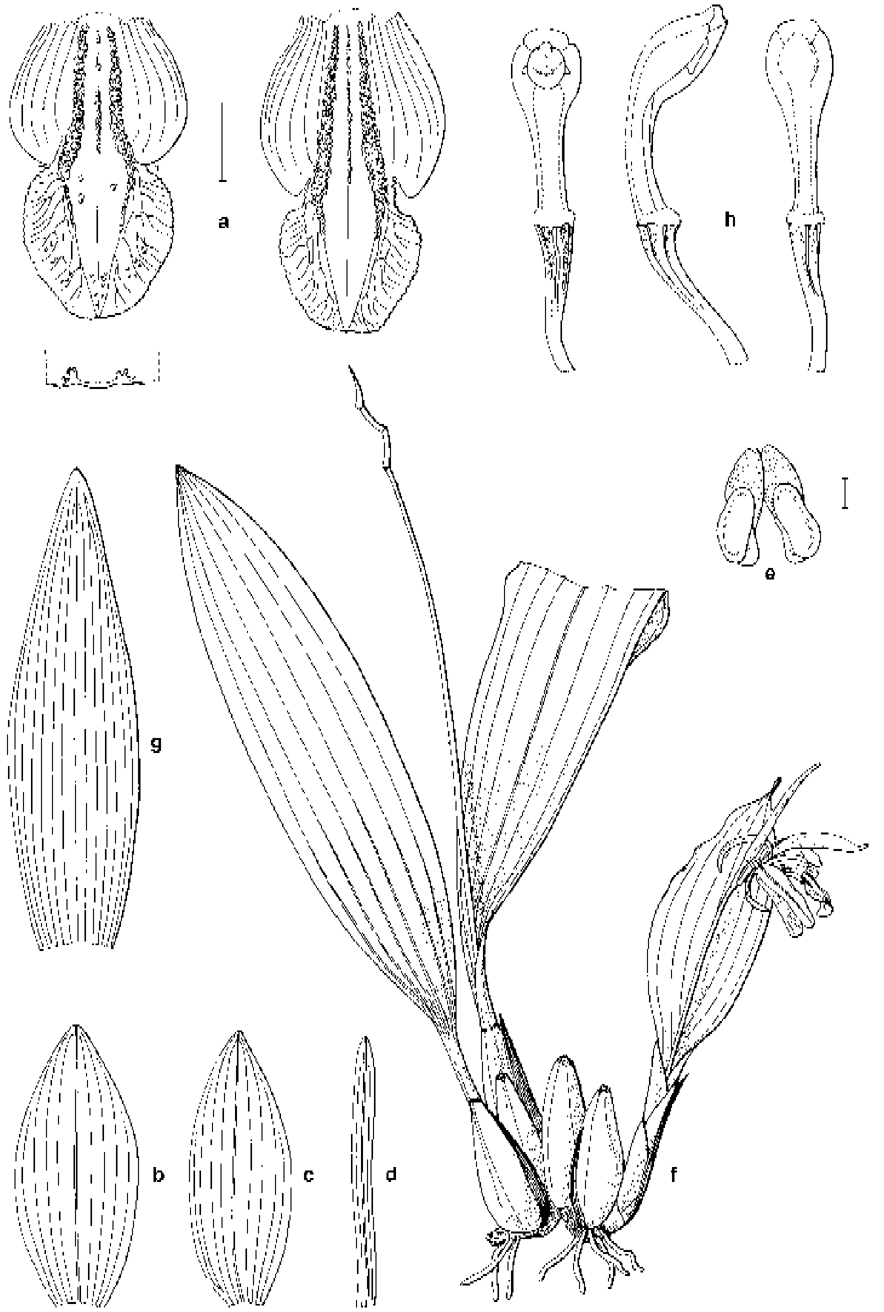

Fig. 4.12. *Coelogyne rumphii* Lindl. a. Variation in lip ornamentation with cross section of claw, from left to right: *Dickson MD 129*, *Leiden cult. (De Vogel) 21524*; b. median sepal; c. lateral sepal; d. petal [*Leiden cult. (De Vogel) 21537*]; e. pollinia; f. habit [*Leiden cult. (De Vogel) 21524*]; g. floral bract [*Leiden cult. (De Vogel) 24504*]; h. column: front, lateral and rear view [*Leiden cult. (De Vogel) 21537*]. — Scale bars: 1 cm (a–d, f–h); 1 mm (e).

at the base irregularly erose, with acute sinus; apex slightly saccate; keels 3, starting at the base of the lip and there 0.8–0.9 mm high, the lateral keels parallel at the basal half of the hypochile, diverging towards the apex of the hypochile, converging again on the epichile, up to 1.5 mm high, widened along the crest, with up to 5 rows of slender, tapering, undulating plate-like projections 1.1–1.4 mm high, with papillae but without hairs (Plate 4.1f), the median keel only developed on the hypochile (sometimes also on a small part of the epichile), lower than the lateral ones and consisting of up to 2 rows of slender, tapering plate-like projections with papillae but without hairs. *Epichile* convex, when flattened (transversely) elliptic to obrhomboid, 14–16.3 by 16.2–18 mm, with a broad, short claw 0.25–0.4 mm thick; base attached over 9.3–12.3 mm; apex weakly retuse, raised, with an acute apex with few warts 0–0.5 mm high; margin erose, recurved; sides pronounced as lateral lobes, with radiating rows of low warts 0.4–0.6 mm high, centre 0.25–0.5 mm thick, margin 0.15–0.3 mm thick; keels 2, ending 9.5–15 mm from the apex of the epichile, identical with the keels on the hypochile. *Column* 23.7–28.6 by 7.3–9.4 mm; hood irregularly dentate, its apical margin slightly rounded to more or less truncate, laterally notched where the wings are attached, the middle part rounded, slightly recurved. Anther broadly bell-shaped in outline, 5–6 by 4.9–5.4 mm, near the place of attachment with a little rounded projecting apex; apex without notch. Pollinia obliquely ellipsoid, 2.7–3.5 by 1.6–2.2 mm; caudicle 1–2 by 1.5–3 mm. *Stigma* 3.3–4.5 by 3.4–3.5 mm; margin apex notched; rostellum 3.1–5 by 4.4–4.9 mm, with an acute apex without notch. *Fruit* body 68.9–84 by 27.6–36.5 mm; valvae keels 8–9 mm high; juga with a pronounced longitudinal ridge 4–5.1 mm high with up to 3 incisions c. 0.2 mm deep.

Distribution — Moluccas: Buru, Ambon, Ceram.

Habitat & Ecology — Epiphyte on trees in riverine forest. Altitude 100–1100 m. Flowering: August–November (January–July in greenhouse).

Notes — 1. Ovary bright green. Sepals and petals greenish yellow to yellowish cream. Lip cream coloured to whitish, at the base orange yellow, lateral lobes tinged red to orange brown, inside with red brown lines, junction of epichile and hypochile and the projections on the keels red brown, apices of papillae on the lateral keels and the entire central keel red brown, epichile at the base with a transverse W-shaped light brown band, back orange. Column cream coloured to light green, with orange margin, front with red brown minute spots, hood bright yellow. Anther light yellow to cream coloured, with brown margins. Slightly fragrant.

2. The epithet *rumphii* refers to G.E. Rumpf (Rumphius), who described and depicted the species in his Herbarium Amboinense in 1750.

3. The species is easily recognised by the five rows of slender, tapering, undulating plate-like projections on the keels (Fig. 4.12a).

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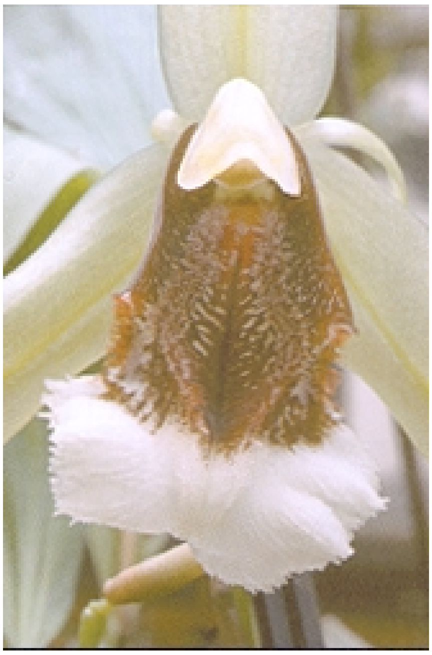
Plate 4.4. – a. *Coelogyne salmonicolor* Rchb.f. [*Leiden cult. (De Vogel) 28002*, Sumatra]. Photograph B. Kieft. – b. *C. septemcostata* J.J. Sm. [*Leiden cult. (Van Balgooy) 960143*, Peninsular Malaysia]. Photograph A. Vogel. – c. *C. speciosa* (Blume) Lindl. subsp. *speciosa* [*Leiden cult. (De Vogel) 911353*, Java]. Photograph C.G. Koops. – d. *C. speciosa* subsp. *incarnata* Gravendeel [*Leiden cult. (De Vogel & Vermeulen) 25441*, Sumatra]. Photograph C.G. Koops.

a. *Coelogyne salmonicolor*

b. *Coelogyne septemcostata*



c. *Coelogyne speciosa* subsp. *speciosa*

d. *Coelogyne speciosa* subsp. *incarnata*

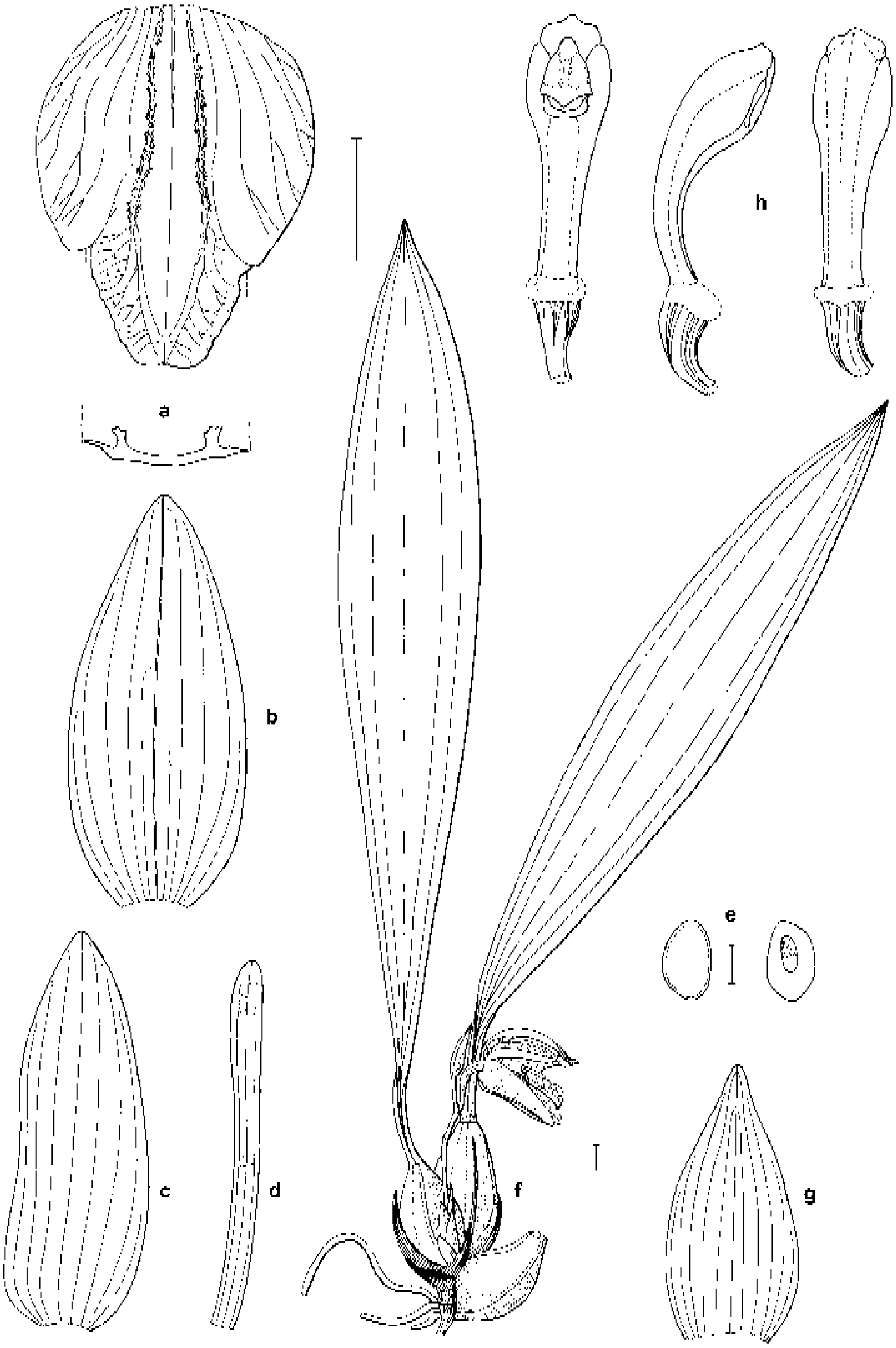


Fig. 4.13. *Coelogyne salmonicolor* Rchb.f. a. Lip ornamentation with cross section of claw; b. median sepal; c. lateral sepal; d. petal; e. pollinia; f. habit; g. floral bract; h. column: front, lateral and rear view [*Leiden cult. (De Vogel) 28002*]. — Scale bars: 1 cm (a–d, f–h); 1 mm (e).

9. Coelogyne salmonicolor Rchb.f. — Fig. 4.13, Map 4.5, Plate 4.1d, 4.4a

Coelogyne salmonicolor Rchb.f. in Gard. Chron. 2, 20 (1883) 328; Rolfe, Kew Bull. 4 (1900) 104; Pfitzer & Kraenzl. in Engl., Pflanzenr. 32 (1907) 29; Latif, Bunga Anggerik (1953) 98. — *Coelogyne speciosa* (Blume) Lindl. var. *salmonicolor* Schltr., Orchideen (1915) 146; J.J. Sm., Bull. Jard. Bot. Buitenzorg III, 8 (1927) 353; Feddes Repert. Beih. 32 (1933) 168. — Type: *Veitch 410 (Curtis)* (holo W), Sunda Islands.

Coelogyne bella Schltr. in Engl., Bot. Jahrb. Syst. 104 (1911) 5. — Type: *Schlechter 15921* (holo B†), Sumatra.

Coelogyne salmonicolor Rchb.f. var. *virescentibus* J.J. Sm. ex Dakkus, Orch. Ned. Ind. 3 (1935) 89. — Type: not designated.

Roots 1.3–1.8 mm diam. Rhizome 4.9–5.5 mm thick. Scale-covered part of the inflorescence-bearing young shoot 3.5–5 cm long. *Pseudobulbs* up to 1 cm apart, ovoid, distinctly 4-ridged when fresh, 2.5–4.2 cm long. *Leaves* one per pseudobulb. Petiole 2.1–3.2 cm long. Blade lanceolate, 21–27 by 3.9–4.4 cm; apex acuminate; main nerves 5. *Inflorescence* synanthous with the partially to entirely developed leaves, 2–4-flowered. Peduncle during flowering at the base enclosed by the petiole and scales of the young shoot, 2.2–3.8 cm long. Rhachis (sub)erect, zigzag, 2–3.7 cm long; internodes 9–13 mm long, slightly to distinctly curved, hardly thickened. *Floral bracts* ovate-oblong, 20–26 by 8–11 mm, persistent; apex acuminate; nerves 11–13. *Flowers* opening (almost) simultaneously. Pedicel 3–4 by 1–1.2 mm; ovary 5–5.5 by 2–2.5 mm. *Median sepal* ovate-oblong, 28–33 by 10–14 mm; apex obtuse; nerves 9–11, the midrib a rounded keel 0.5–0.55 mm high. *Lateral sepals* ovate-oblong, 31–32 by 10–12 mm; apex obtuse; nerves 8, the midrib a rounded keel 0.4–0.5 mm high. *Petals* slightly recurved, 31–32 by 2.3–2.8 mm; apex obtuse; nerves 3, midrib centric. *Lip* 27–34 by 19–22 mm, nerves 13–15. *Hypochile* when flattened 19–20 by 19–22 mm; base attached over 8–9 mm, slightly saccate; lateral lobes in front obtuse, extending 5–5.5 mm in front and slightly diverging, front margin at the base slightly irregularly erose, with acute sinus; apex slightly saccate; keels 2–4, starting at the base of the lip and there 0.25–0.5 mm high, all keels widened along the crest, with two slightly elevated rows of irregularly shaped, tapering projections 0.5–0.6 mm high on each side of the crest, with a longitudinal groove with hairs 0.1–0.2 mm long implanted on the rims, with papillae (Plate 4.1d), the two lateral keels parallel on the base of the hypochile, diverging towards the apex of the hypochile, converging again on the epichile, the median keels (if present) developed on the basal two thirds of the hypochile, lower than the lateral ones. *Epichile* convex, when flattened obovate to orbicular, 9.5–10 by 12.5–13 mm, with a broad, short claw 0.25–0.5 mm thick; base broadly attached over 9–9.5 mm; apex retuse, slightly raised, with an obtuse apex with few warts 0.5–0.6 mm high; the margin slightly erose, recurved; sides not pronounced as lateral lobes, with warts 0.4–0.5 mm high, centre 0.25–0.45 mm thick, margin 0.2–0.4 mm thick; keels 2, ending 6–6.5 mm from the apex of the epichile, on the

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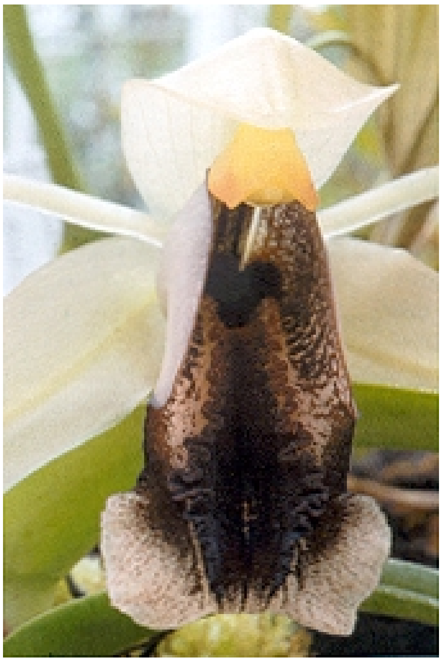
Plate 4.5. – a. *Coelogyne dichroantha* Gagnep. (*Eberhardt s.n.*, Vietnam). Photograph B. Kieft. – b. *C. xyrekes* Ridl. [*Leiden cult. (Roelfsema, Vogel & Van Balgooy) 960160*, Peninsular Malaysia]. Photograph C.G. Koops. – c. *C. tiomanensis* M.R. Hend. (Pulau Tioman). Photograph J.B. Comber. – d. *C. tommii* Gravendeel & O'Byrne [*Leiden cult. (De Vogel) 21524*, Singapore Botanical Gardens]. Photograph C.G. Koops.

a. *Coelogyne dichroantha*



b. *Coelogyne xyrekes*

c. *Coelogyne tiomanensis*

d. *Coelogyne tommii*

claw identical with the keels on the hypochile, on the plate changing into one row of tightly packed irregularly waving plate-like projections with papillae and hairs. *Column* 18–21 by 6–6.3 mm; hood irregularly dentate, its apical margin more or less obtuse, laterally notched where the wings are attached and sometimes with a small additional notch above, the middle part rounded, slightly recurved. Anther oblong bell-shaped in outline, 4.5–5 by 3.5–3.6 mm, near the place of attachment with a little elongate projecting apex; apex not to slightly notched. Pollinia obliquely ellipsoid, 2.1–2.2 by 1.5–1.8 mm; caudicle 1.5–2 by 2–3.5 mm. *Stigma* 2.5–3 by 3–3.5 mm; margin apex notched; rostellum 2.9–3.5 by 3.5–4 mm, with an acute apex without notch. *Fruit* body 51–53 by 21.5–24 mm; valvae keels plate-like, 6–6.5 mm high; juga with a pronounced longitudinal ridge 4–4.1 mm high without incisions.

Distribution — Sumatra.

Habitat & Ecology — Epiphyte in montane rain forest. Altitude 900–1500 m. Flowering: February, March, June, August, September, December (April in greenhouse).

Notes — 1. Sepals and petals pale salmon or creamy white with a greenish tint. Lip pale salmon or creamy white with a pale salmon flush on the midlobe, sidelobes with light orange-brownish reticulate lines, keels and central median streak on the lip similarly coloured, the very base of the lip more orange coloured. Column cream or creamy yellow coloured, anther cream or yellow brown coloured tinged slightly yellow. No smell.

2. The epithet *salmonicolor* refers to the salmon colour of the flowers.

3. The species is easily recognised by the pale pink flowers with 2–4 keels with small hairs on the lip. It can be kept apart from *C. speciosa* subsp. *incarnata* by the longitudinally grooved keels.

10. Coelogyne septemcostata J.J. Sm. — Fig. 4.14, Map 4.5, Plate 4.1e, 4.4b

Coelogyne septemcostata J.J. Sm., Icon. Bogor. 2 (1903) 23, t. 106A; Pfitzer & Kraenzl. in Engl., Pflanzenr. 32 (1907) 31; Seidenf. & J.J. Wood, Orchids of Penins. Malaysia and Singapore (1992) 205, f. 86 E–F. — Type: *Nieuwenhuis s.n.* (holo BO?, not found), Borneo.

Coelogyne membranifolia Carr, Gard. Bull. Straits Settlem. 7 (1932) 2, pl. 1; Holttum, Orchids of Malaya 3 (1964) 243. — Type: *Carr s.n.* (holo SING), Malay Peninsula, Pahang, Tembeling.

Roots 1.9–2.3 mm diam. Rhizome 5.6–10.5 mm thick. Scale-covered part of the inflorescence-bearing young shoot 4.8–8 cm long. *Pseudobulbs* up to 0.7 cm apart, oblongoid, obtusely 4-angled when fresh, 4.3–9 cm long. *Leaves* one per pseudobulb. Petiole 2.2–4.7 cm long, with lateral notches at the apex. Blade oblong, 23–42 by 5.8–12.5 cm; apex acuminate; main nerves 5–7. *Inflorescence* synanthous with the partially to entirely developed leaf, 2–4(–22)-flowered. Peduncle during flowering at the base enclosed by the petiole and scales of the young shoot, 8.8–39 cm long. Rhachis (sub)erect to curved, zigzag, 2–32 cm long; internodes 17–23 mm long, distinctly curved, hardly thickened. *Floral bracts* ovate-lanceolate, 31–40 by 7–10 mm, deciduous; apex acuminate; nerves 9–11. *Flowers* opening in succession, finely papillose. Pedicel 5–7 by 1.5–2.3 mm; ovary 5.3–9.5 by 3–5.5 mm. *Median sepal* ovate-oblong, 34–48 by 16–23 mm; apex mucronate; nerves 11–13, the midrib a rounded keel 0.5–1 mm high. *Lateral sepals* oblong, 34–46 by 15–19 mm; apex mucronate; nerves

9–11, the midrib a rounded keel 0.6–1 mm high. *Petals* slightly recurved, 36–46 by 2–3 mm; apex mucronate; nerves 3, midrib eccentric. *Lip* 34–43 by 36–44 mm, nerves 19–21. *Hypochile* when flattened 29–33 by 36–44 mm; base attached over 17–22 mm, not saccate; lateral lobes in front obtuse, extending 7–12 mm in front and slightly convergent, front margin at the base slightly irregularly erose to entire, with acute sinus; apex slightly saccate; keels 5–7(–8), starting at the base of the lip and there 0.5–1 mm high, all keels more or less widened along the crest, with a longitudinal groove, at both margins drawn out in many hairlike projections 0.7–1.5 cm long, with papillae but without hairs (Plate 4.1e); all keels parallel at the base of the hypochile, the 2–5 lateral keels only developed on the basal half to three quarters of the hypochile, up to 3 mm high, the 3 median keels diverging towards the apex of the hypochile, converging again on the epichile, lower than the lateral keels and with shorter projections at the basal half of the hypochile. *Epichile* convex, when flattened elliptic, 5–8 by 13–19 mm, with a broad, short claw 0.25–1.1 mm thick; base broadly attached over 14–16 mm; apex retuse, slightly raised, with an acute apex with warts 0.25–0.4 mm high; margin slightly erose, recurved; sides pronounced as lateral lobes, with warts at the base 0.5–0.8 mm high, centre 0.3–1 mm thick, margin 0.2–0.3 mm thick; keels 2, ending 6–11 mm from the apex of the epichile, on the claw and plate changing into an uninterrupted, undulating row of plate-like projections 0.1–0.6 mm high with papillae but without hairs. *Column* 27–34 by 9–11 mm; hood irregularly dentate to entire, its apical margin more or less obtuse, laterally notched or with 2 small cuneate projections where the wings are attached, the middle part rounded, slightly recurved. Anther broadly bell-shaped in outline, 5.2–7 by 4.5–6.5 mm, near the place of attachment with a little rounded projecting apex; apex slightly notched to entire. Pollinia obliquely ellipsoid, 3–4 by 1.5–2 mm; caudicle 1–3 by 1–2 mm. *Stigma* 4–5 by 4–6 mm; margin apex slightly notched; rostellum 4–6 by 5–8 mm, with a truncate to obtuse to acute apex without notch. *Fruit* body 53–68 by 29–35 mm; valvae keels plate-like, 7–9 mm high; juga with a pronounced longitudinal ridge 4–6.5 mm high without incisions.

Distribution — Thailand, Peninsular Malaysia, Sarawak, Brunei, Sabah, Kalimantan.

Habitat & Ecology — Epiphyte, rarely terrestrial in shady rain forest or mixed forest on a variety of soil types. Altitude 50–2278 m. Flowering: February–July (July–August in greenhouse).

Notes — 1. Ovary pale green. Sepals and petals green to very pale green. Lip whitish to medium cream, lateral lobes orange to dull orange brown, very dark brown on the margin in the sinus; keels orange to orange brown, more dull brown in front, projections on the keels orange; epichile creamy white, at the base with a transverse brown band. Column stalk cream coloured, in front at the base tinged orange to orange brown. Anther light yellow. No smell to slightly fragrant.

2. The epithet *septemcostata* refers to the number of keels on the lip of the type specimen. However, the number of keels of the specimens studied varies between 5 and 8.

3. The species is easily recognised by the 5–8 keels on the lip with long hairs at their margins and strongly curved rhachis.

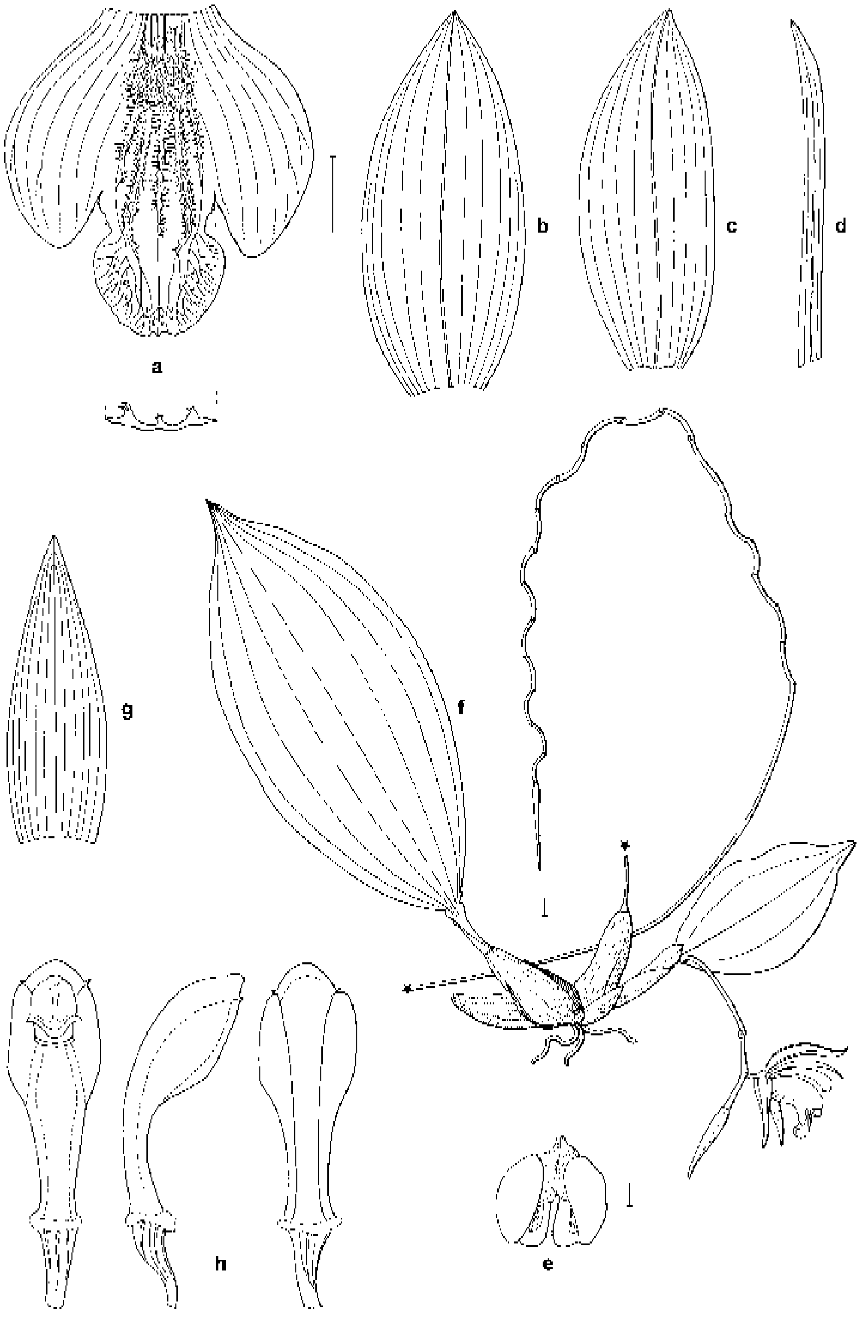


Fig. 4.14. *Coelogyne septemcostata* J.J. Sm. a. Lip ornamentation with cross section of claw [*Leiden cult. (Nooteboom) 23184*]; b. median sepal; c. lateral sepal; d. petal; e. pollinia; f. habit [*Leiden cult. (Van Balgooy) 960143*]; g. floral bract [*Leiden cult. (Nooteboom) 23187*]; h. column: front, lateral and rear view [*Leiden cult. (Van Balgooy) 960143*]. — Scale bars: 1 cm (a–d, f–h); 1 mm (e).

11. **Coelogyne speciosa** (Blume) Lindl.

Literature: see under the subspecies.

Pseudobulbs ovoid, obtusely 4-angled when fresh. *Leaves* one or two per pseudobulb. Blade obovate-lanceolate to linear-lanceolate to lanceolate; apex acuminate or cuspidate; main nerves 3–5. *Inflorescence* synanthous with the partially to entirely developed leaves. Peduncle during flowering at the base enclosed by the petiole and scales of the young shoot. Rhachis (sub)erect, zigzag, internodes slightly to distinctly curved, hardly thickened. *Floral bracts* ovate-oblong to oblong, deciduous; apex acute. *Flowers* opening in succession. *Median sepal* oblong or lanceolate; apex emarginate to acuminate. *Lateral sepals* oblong or ovate-lanceolate; apex emarginate to acuminate. *Petals* slightly to extremely recurved, 52–56.7 by 2.5–3.3 mm; apex emarginate to acute to acuminate; nerves 1–3; midrib centric. *Hypochile* base not saccate; lateral lobes rounded to obtuse to acute, slightly diverging in front; front margin at the base slightly to extremely irregularly erose, with broadly rounded to acute sinus; apex slightly saccate; keels 2 or 3, starting at the base of the lip, all keels widened along the crest, with up to 5 rows of slender, tapering, either or not branched, elongate and sometimes plate-like projections, with papillae and stellately arranged multicellulate hairs at their apices, the lateral keels parallel at the basal half of the hypochile, diverging towards the apex of the hypochile, converging again on the epichile, the median keel only developed in the basal one to three quarters of the hypochile, lower than the lateral ones. *Epichile* convex, when flattened (semi-)orbicular to transversely elliptic to obrhomboid, with a broad, short claw; apex retuse to emarginate, raised, with an acute apex with warts; margin more or less erose or fringed, recurved; sides more or less pronounced as lateral lobes, with radiating rows of warts; keels 2, on the (basal half of the) claw identical with the keels on the hypochile, on the apical half of the claw or plate changing into a row of successive undulating plate-like projections, which are not widened along the crest, with shorter hairs, in front continuing into rows of low warts. *Column* hood with irregularly dentate or truncate apical margin, laterally notched where the wings are attached, the middle part rounded, slightly recurved. Anther broadly bell-shaped in outline, near the place of attachment with a rounded or elongate projecting apex; apex without notch. Pollinia obliquely ellipsoid. *Stigma* margin apex with a more or less pronounced notch; rostellum with a broadly rounded or obtuse apex without notch. *Fruit* with juga with a pronounced longitudinal ridge with or without incisions.

Notes — 1. Three different subspecies can be recognised, based on the size of the sepals, petals and lip, the length of the projections of the margin of the lip and the colour of the flowers. The rank of subspecies is chosen because the infraspecific taxa of *C. speciosa* seem to occupy distinct distribution areas: *C. speciosa* subsp. *fimbriata* on the mountain range between Mt Bandahara and Mt Kerintji in Sumatra, *C. speciosa* subsp. *incarnata* on the mountain range between Mt Mamas and Mt Barisan in Sumatra and on the mountain range between Mt Gedé and Mt Halimun in Java and *C. speciosa* subsp. *speciosa* on Mt Gedé, Mt Muria, Mt Papandajan, Mt Raung, Mt Salak, Mt Semeru, Mt Tengger and Mt Ungarang in Java and throughout Flores. It must be stressed, however, that many of the studied collections lack colour descriptions and/or indications of localities. Therefore, the assumption of distinct geographic areas is only based on a few collections and may be rejected when more collections are made.

2. The species is easily recognised by the ornamentation of the keels of the lip: five rows of tapering, elongate or plate-like projections, with stellately arranged multicellulate hairs at their apices.

KEY TO THE SUBSPECIES

1a. Petals and sepals yellowish green; lateral sepals shorter than 50 mm 2
b. Petals and sepals salmon coloured; lateral sepals longer than 56 mm ....
.... **c.** subsp. **incarnata**
2a. Margin of midlobe of lip irregularly erose. — Java and Flores ....
.... **a.** subsp. **speciosa**
b. Margin of midlobe of lip fimbriate, with projections up to 3.5 mm long. — Sumatra
.... **b.** subsp. **fimbriata**

a. subsp. **speciosa** — Fig. 4.15a, Map 4.4, Plate 4.1g, 4.4c

Coelogyne speciosa (Blume) Lindl., Gen. Sp. Orchid. Pl. (1830) 39; Fol. Orchid. (1854) 11; Bot. Mag. 81 (1855) t. 4889; Rchb. f., Ann. Bot. Syst. 6 (1861) 231; Cogn. & Gooss., Dict. Icon. Orch. (1903) t. 3; J.J. Sm., Orch. Java (1905) 138; Pfitzer & Kraenzl. in Engl., Pflanzenr. 32 (1907) 29; Schltr., Orchideen (1915) 145; Koord., Fl. Tjibodas (1919) 42; J.J. Sm., Teysmannia 31 (1920) 253; Bremek., Trop. Natuur 11 (1922) 181, f. 2; Dakkus, Orch. Ned. Ind. 2 (1931) 73; C.F. Sander, F.K. Sander & L.L. Sander, Sander's Orch. Guide (1927) 128; J.J. Sm., Feddes Repert. Beih. 32 (1933) 168; Dakkus, Orch. Ned. Ind. 3 (1935) 90; Backer & Bakh. f., Fl. Java 3, 12 (1952) 127; Latif, Bunga Anggerik (1953) 98; Backer & Bakh. f., Fl. Java 3 (1968) 280; Bechtel in P.J. Cribb & Launert, Orch. Atl. (1980) 105, f. 5, photo p. 185; J.B. Comber, Orchids of Java (1990) 111. — *Chelonanthera speciosa* Blume, Bijdr. (1825) 384, t. 52. — *Pleione speciosa* (Blume) Kuntze, Rev. Gen. Pl. 2 (1891) 680. — Type: *Blume s.n.* (?-1-1822) (holo W), Java, Mt Salak.

Coelogyne speciosa (Blume) Lindl. var. *albicans* H.J. Veitch, Man. Orchid. Pl. (1890) 50, pl. 6; Cogn. & Gooss., Dict. Icon. Orch. (1903) t. 3. — Lectotype (here chosen): H.J. Veitch, Man. Orchid. Pl. (1890) 50, pl. 6.

Coelogyne speciosa (Blume) Lindl. var. *alba* Hort., Gard. Chron. 3, 37 (1905) 205; J.J. Sm., Teysmannia 6 (1920) 254; Dakkus, Orch. Ned. Ind. 2 (1931) 73; 3 (1935) 91. — Type: not designated.

Coelogyne speciosa (Blume) Lindl. var. *rubiginosa* Hort., Orch. Rev. 30 (1922) 37. — Type: not designated.

Roots 1.5–2 mm diam. Rhizome 4–7 mm thick. Scale-covered part of the inflorescence-bearing young shoot 5.2–8.2 cm long. *Pseudobulbs* up to 0.8 cm apart, 4.4–7 cm long. *Leaves* one or two per pseudobulb. Petiole 2.5–4 cm long. Blade lanceolate, 22.5–35 by 3.7–8.4 cm. *Inflorescence* 3–8-flowered. Peduncle 14–20 cm long. Rhachis 4–7.5 cm long; internodes 13–19 mm long. *Floral bracts* ovate-oblong, 23–39 by 6–18 mm; nerves 11–15. Pedicel 4.8–8 by 1–2.5 mm; ovary 5–13 by 2.5–5.7 mm. *Median sepal* oblong, 49.6–55 by 18.3–20.6 mm; apex emarginate; nerves 9–11, the midrib a rounded keel 0.7–1 mm high. *Lateral sepals* oblong, 47.5–50.5 by 14.6–17 mm; apex emarginate; nerves 8–10, the midrib a rounded keel 0.5–1 mm high. *Petals* 52–56.7 by 2.5–3.3 mm; apex emarginate to acute. *Lip* when flattened 44.3–53 by 33.1–42.7 mm, nerves 11–13. *Hypochile* when flattened 28.2–47.2 by 33.1–42.7 mm;

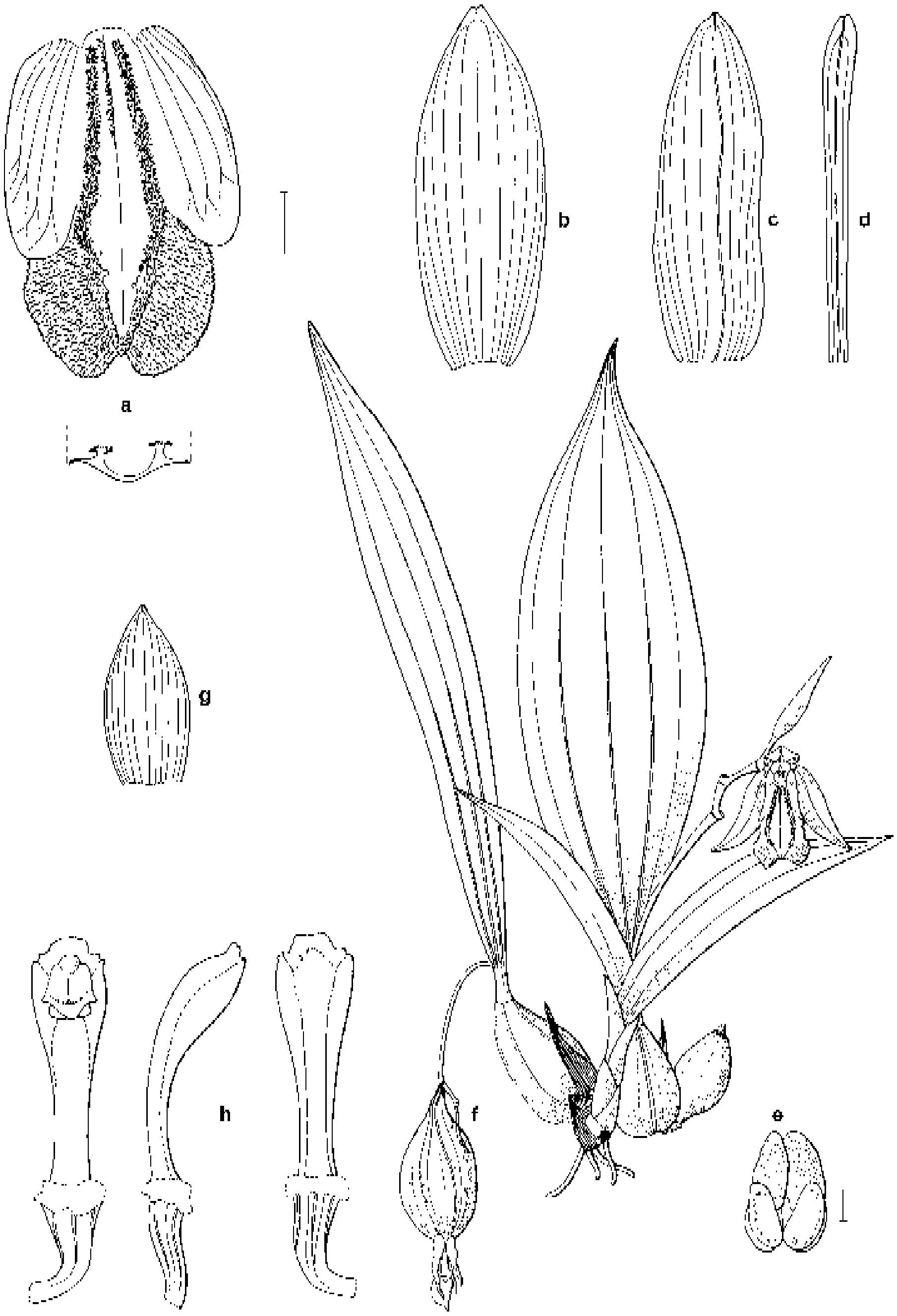


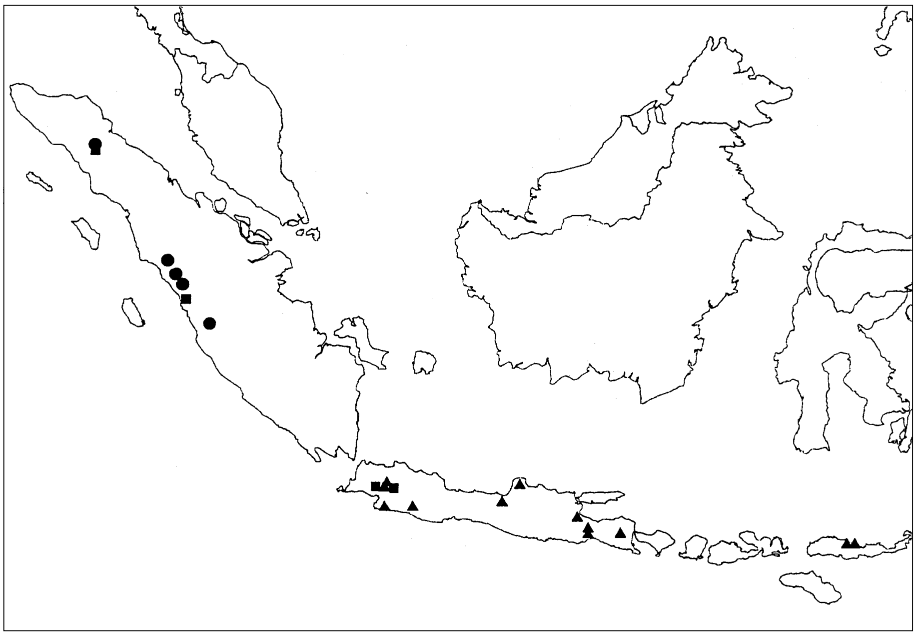
Fig. 4.15a. *Coelogyne speciosa* (Blume) Lindl. subsp. *speciosa*. a. Lip ornamentation with cross section of claw; b. median sepal; c. lateral sepal; d. petal; e. pollinia; f. habit; g. floral bract; h. column: front, lateral and rear view [*Leiden cult. (De Vogel) 911339*]. — Scale bars: 1 cm (a–d, f–h); 1 mm (e).

base attached over 12.2–16.3 mm; lateral lobes in front rounded to obtuse, extending 2–6 mm in front, front margin at the base irregularly erose, with broadly rounded to acute sinus; keels 3, at the base of the lip 0.5–1 mm high, the lateral keels up to 1.5 mm high, projections 1.6–2.1 mm high, hairs 0.25–0.3 mm long (Plate 4.1g). *Epichile* when flattened semi-orbicular to transversely elliptic, 16.8–19.5 by 27–30.2 mm, with a broad, short claw 0.25–0.8 mm thick; base attached over 17–23 mm; apex retuse to emarginate, apex with warts 1–1.7 mm high; margin more or less erose; sides pronounced as lateral lobes, with radiating rows of warts 0.2–0.8 mm high, centre 0.6–1 mm thick, margin 0.25–0.3 mm thick; keels ending 9–12 mm from the apex of the epichile. *Column* 29–37 by 6.6–10.2 mm; hood with irregularly dentate apical margin. Anther broadly bell-shaped in outline, 6.3–8.5 by 5.6–7.4 mm, near the place of attachment with a rounded projecting apex. Pollinia 2.5–3.7 by 1.3–2.2 mm; caudicle 2.5–3.5 by 2.5–3 mm. *Stigma* 2.8–4.8 by 4–5.7 mm; margin apex with a more or less pronounced notch; rostellum 4–5.7 by 5–7.1 mm, with a broadly rounded apex. *Fruit* body 62–65 by 27–27.5 mm; valvae keels 8.5–9 mm high; longitudinal ridge of juga 3.5–4 mm high with up to 4 incisions up to 2.5 mm deep.

Distribution — Java, Lesser Sunda Islands (Flores).

Habitat & Ecology — Epiphyte on forest trees, rarely terrestrial. Common. Altitude 760–2000 m. Flowering: February, April–July, October–December (whole year round in greenhouse).

Notes — 1. Ovary light green. Sepals and petals light green to yellowish green, transparent. Lip white to cream with dense dark red to orange brown markings inside,



Map 4.4. Distribution of *Coelogyne speciosa* (Blume) Lindl.: subsp. *fimbriata* (J.J. Sm.) Gravendeel (l), subsp. *incarnata* Gravendeel (n), and subsp. *speciosa* (s).

shimmering through on the outside, midlobe creamy white with orange to brown lines on the base. Column light green, front of stalk tinged brownish, its apex pale yellowish, wings cream coloured. Anther pale yellow, pollinia bright yellow. Stigma pale yellow, rostellum white. No smell to slightly fragrant.

2. The epithet *speciosa* (which is Latin for beautiful) refers to the showy flowers.

3. The type specimen of *C. speciosa* subsp. *speciosa* is described by Blume as having white yellow sepals, and lip white grey outside and yellow inside.

b. subsp. **fimbriata** (J.J. Sm.) Gravendeel, *stat. nov.* — Fig. 4.15b, Map 4.4, Plate 4.1h

Coelogyne speciosa (Blume) Lindl. var. *fimbriata* J.J. Sm., Bull. Dép. Agric. Indes Néerl. 5 (1907) 1; Schltr., Bot. Jahrb. Syst. 104 (1911) 6; J.J. Sm., Teysmannia 31 (1920) 254; Dakkus, Orch. Ned. Ind. 2 (1931) 73; J.J. Sm., Feddes Repert. Beih. 32 (1933) 168; Dakkus, Orch. Ned. Ind. 3 (1935) 91; Latif, Bunga Anggerik (1953), col. pl. 21. — Type: *Storm van 's Gravesande s.n.* (holo BO?, not found), Sumatra, Padang Pandjang.

Roots 1.7–3 mm diam. Rhizome 7.5–9 mm thick. Scale-covered part of the inflorescence-bearing young shoot 5.2–10.3 cm long. *Pseudobulbs* up to 0.7 cm apart, not seen when fresh, 3.2–7.2 cm long. *Leaves* one per pseudobulb. Petiole 4.5–10.5 cm long. Blade obovate-lanceolate to linear-lanceolate, 26–43.5 by 4.5–8 cm; apex acuminate to cuspidate; main nerves 5. *Inflorescence* 2–4(–20)-flowered. Peduncle 8–27 cm long. Rhachis 2–37 cm long; internodes 14–22 mm long. *Floral bracts* ovate-oblong, 35–42.5 by 14–16 mm; nerves 11–13. Pedicel 3–3.5 by 3.5–4 mm; ovary 6–6.5 by 3.5–4 mm. *Median sepal* lanceolate, 47–50 by 15–19 mm; apex acuminate; nerves 9–11, the midrib a rounded keel 0.5–0.7 mm high. *Lateral sepals* ovate-lanceolate, 43–48 by 12–15 mm; apex acuminate; nerves 8 or 9, the midrib a rounded keel 0.7–1 mm high. *Petals* 44–49 by 2.5–3.5 mm; apex acuminate. *Lip* when flattened 33–43 by 27–35 mm, nerves 13–15. *Hypochile* when flattened 23–30 by 27–35 mm; base attached over 10–18 mm; lateral lobes in front acute to rounded, extending 2.5–4 mm in front, front margin at the base slightly to extremely irregularly erose, with rounded to acute sinus; keels 2 or 3, at the base of the lip 0.5–1.5 mm high, the lateral keels up to 1.5 mm high, with projections 2–4 mm high on the basal part of the hypochile, 1.5–2 mm high on the apical part of the hypochile, with hairs 0.15–0.2 mm long, projections of median keel 1–1.5 mm high, with papillae but without hairs (Plate 4.1h). *Epichile* when flattened orbicular to obrhomboid, 8–15 by 15–22 mm, claw (if present) broad and short, 0.6–0.65 mm thick; base attached over 7–20 mm; apex (slightly) retuse; apex with few warts 0.4–1 mm high; margin fringed with elongate projections 0.5–3.5 mm long, with papillae but without hairs; sides more or less pronounced as lateral lobes, with few, irregularly placed warts 0.4–1 mm high, centre 0.5–0.6 mm thick, margin 0.2–0.5 mm thick; keels ending 3.5–9 mm from the apex of the epichile. *Column* 28–32 by 5.5–8 mm; hood with more or less truncate

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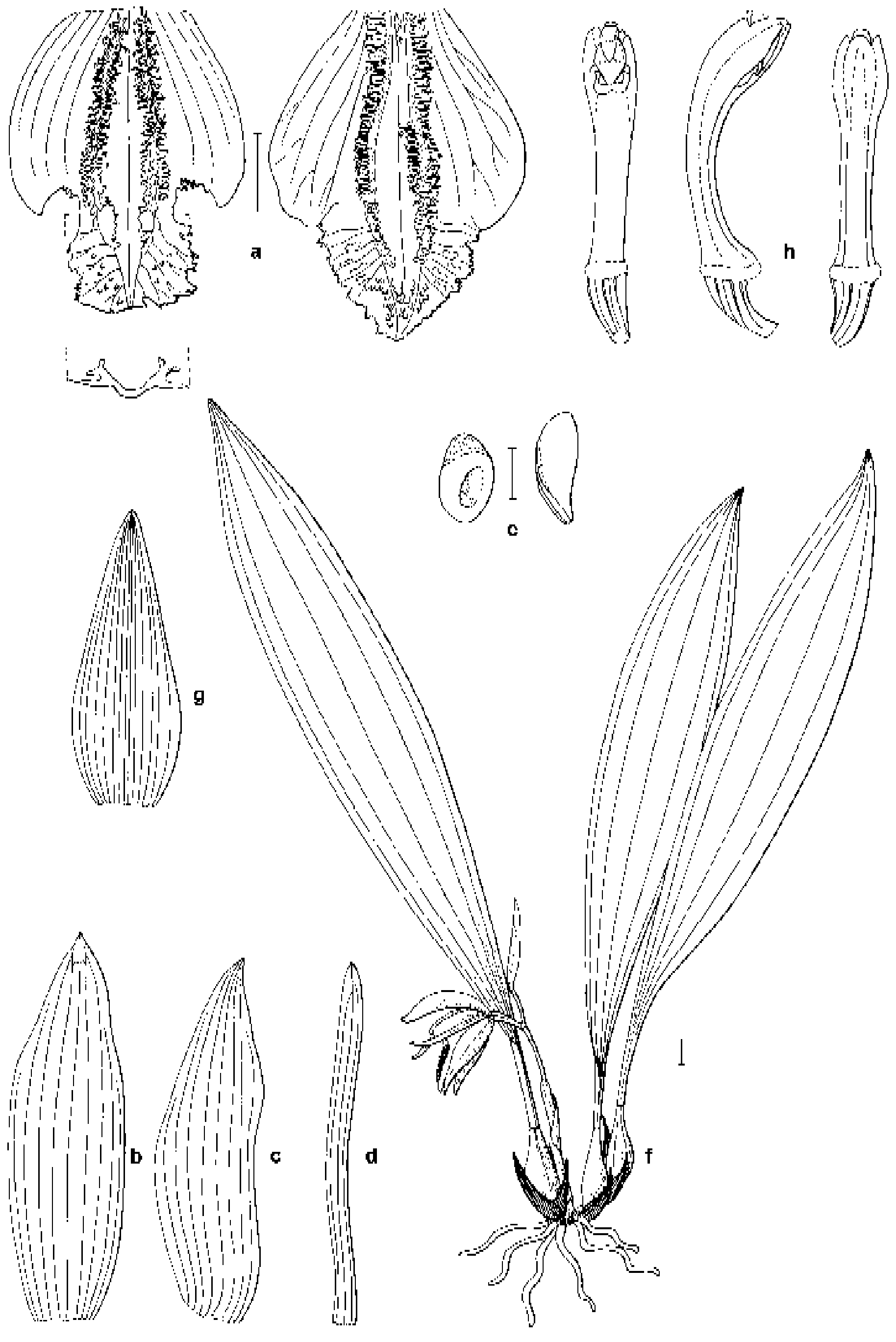
Fig. 4.15b. *Coelogyne speciosa* (Blume) Lindl. subsp. *fimbriata* (J.J. Sm.) Gravendeel. a. Lip ornamentation with cross section of claw, from left to right: *Bogor cult. 992-XI-311*, *De Wilde & De Wilde-Duyfjes 15579*; b. median sepal; c. lateral sepal; d. petal; e. pollinia (*Bogor cult. 992-XI-311*); f. habit (*Bünnemeijer 1094*); g. floral bract; h. column: front, lateral and rear view (*Bogor cult. 992-XI-311*). — Scale bars: 1 cm (a–d, f–h); 1 mm (e).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apical margin. Anther elongate bell-shaped in outline, 6.3–6.7 by 4–5.5 mm, near the place of attachment with an elongate projecting apex. Pollinia 1.7–3.2 by 1–1.5 mm; caudicle c. 2.5 by c. 1.5 mm. *Stigma* 2.5–4 by 3.5–4.5 mm; margin apex without notch; rostellum 4.5–5 by 4–5.25 mm, with an obtuse apex. *Fruit* body c. 54 by c. 36 mm; valvae keels 7–8.5 mm high; juga with a pronounced longitudinal ridge 3.5–4 mm high without incisions.

Distribution — Sumatra.

Habitat & Ecology — Epiphyte in rain forest. Altitude 800–1100 m. Flowering: January, March, May, June (November in greenhouse).

Notes — 1. Ovary not documented. Sepals and petals ochrish yellow. Lip cream coloured, with a reticulate pattern of brown lines inside on the lateral lobes which shimmers through on the outside, inside median orange, keels at the base of the lip orange, to the front brown. Column yellowish, in front with few brown markings. No smell.

2. The epithet *fimbriata* refers to the fringed margins of the epichile.

c. subsp. **incarnata** Gravendeel, *subsp. nov.* — Fig. 4.15c, Map 4.4, Plate 4.1i, 4.4d

> Subspecies nova, quoad pseudobulbis, foliis fructibusque ad *C. speciosam* subsp. *speciosam* accedit, sed ab ea praecipue sepalis petalisque majoribus, labello multo longiore et floribus incarnatis differt. — Typus: *De Wilde & De Wilde-Duyfjes 15767* (holo L; iso K), Sumatra, Mt Mamas.

Coelogyne speciosa auct. non (Blume) Lindl.: Lindl., Bot. Reg. 33 (1847) t. 23. — Type: *Veitch cult. (Lobb) s.n.* (holo K), Java.

Coelogyne speciosa (Blume) Lindl. var. *major* C.F. Sander, F.K. Sander & L.L. Sander, Sander's Orch. Guide (1927) 128. — Type: not designated.

Roots 1.5–2.5 mm diam. Rhizome 5–8 mm thick. Scale-covered part of the inflorescence-bearing young shoot 6–10.7 cm long. *Pseudobulbs* up to 1 cm apart, 4.7–7.3 cm long. *Leaves* one or two per pseudobulb. Petiole 3–5.2 cm long. Blade lanceolate, 19–38 by 3.4–6 cm. *Inflorescence* 2–3(–11)-flowered. Peduncle 9.5–17.5 cm long. Rhachis 1.4–3.5 cm long; internodes 14–24 mm long. *Floral bracts* ovate-oblong to oblong, 22–52 by 8–35 mm; nerves 11–13. Pedicel 4–7 by 2–2.5 mm; ovary 10–18 by 4.2–6 mm. *Median sepal* oblong, 54.5–72 by 20–24 mm; apex emarginate; nerves 9, the midrib a rounded keel 0.7–1 mm high. *Lateral sepals* oblong, 56.8–68 by 17.5–20 mm; apex emarginate; nerves 8 or 9, the midrib a rounded keel 0.75–1.5 mm high. *Petals* 53.7–68 by 2.3–4 mm; apex emarginate to acute. *Lip* when flattened 45.9–61 by 40–45 mm, nerves 13–15. *Hypochile* when flattened 33–38 by 40–45 mm; base attached over 12–20 mm; lateral lobes in front rounded to obtuse, extending 2.3–5 mm in front; front margin at the base irregularly erose, with broadly rounded to acute sinus; keels 3, at the base of the lip 0.5–1.1 mm high, the lateral keels up to 1.1

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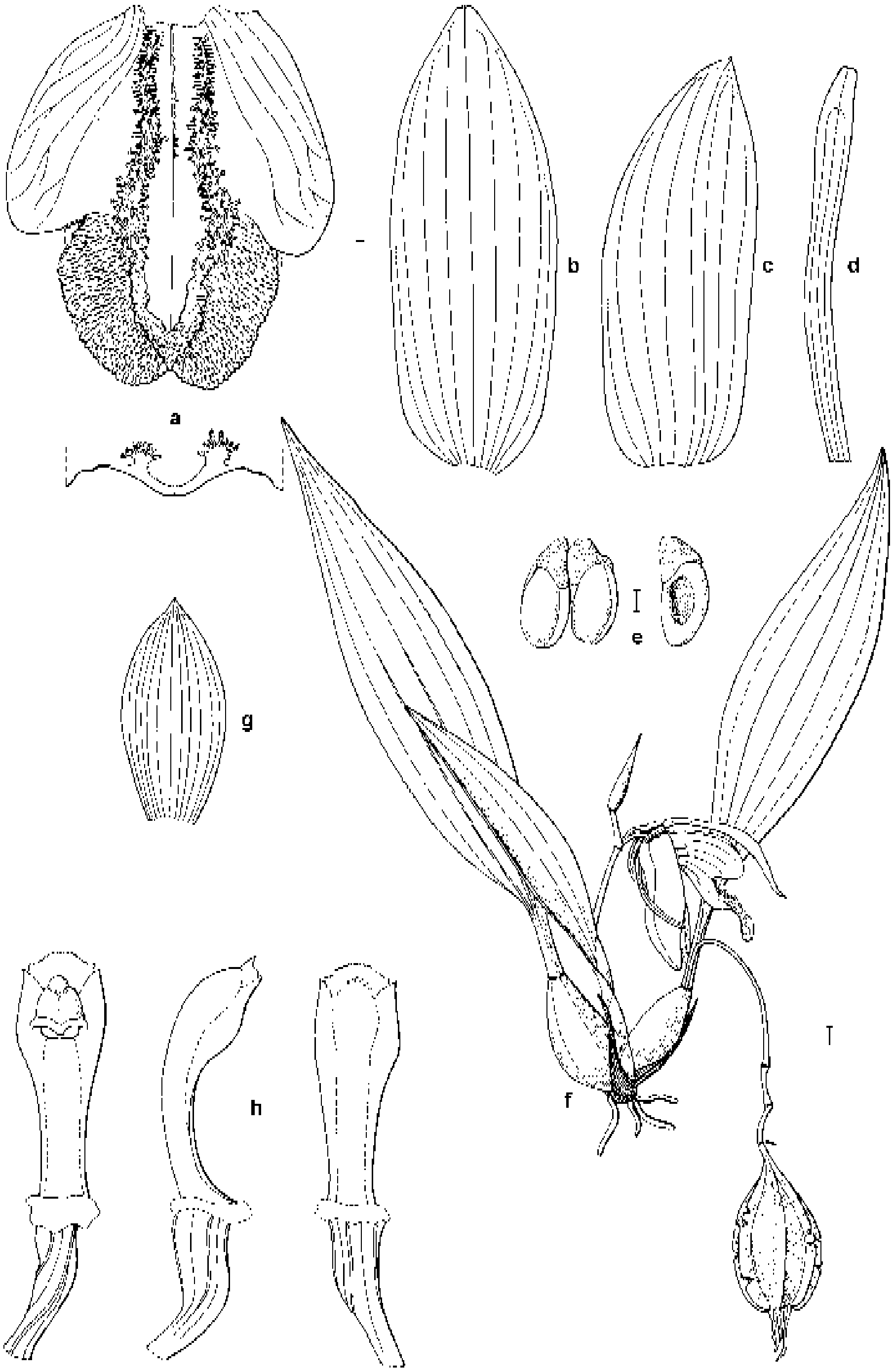
Fig. 4.15c. *Coelogyne speciosa* (Blume) Lindl. subsp. *incarnata* Gravendeel. a. Lip ornamentation with cross section of claw; b. median sepal; c. lateral sepal; d. petal; e. pollinia [*Leiden cult. (De Vogel) 940790*]; f. habit [*Leiden cult. (Roelfsema, Vogel & Van Balgooy) 960608*]; g. floral bract; h. column: front, lateral and rear view [*Leiden cult. (De Vogel) 940790*]. — Scale bars: 1 cm (a–d, f–h); 1 mm (e).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mm high, projections 1–4 mm high, hairs 0.3–0.5 mm long (Plate 4.1i). *Epichile* when flattened semi-orbicular to transversely elliptic, 17–24 by 23.3–31 mm, with a broad, short claw 0.4–1 mm thick; base attached over 17.2–22.2 mm; apex retuse to emarginate; apex with warts 0.8–2 mm high; margin more or less erose; sides pronounced as lateral lobes, with radiating rows of warts 0.5–1.5 high, centre 0.8–1.5 mm thick, margin 0.3–0.6 mm thick; keels ending 1–11 mm from the apex of the epichile. *Column* 32.7–43 by 9–13 mm; hood with irregularly dentate apical margin. Anther broadly bell-shaped in outline, 6.6–8 by 5.5–7.7 mm, near the place of attachment with a rounded projecting apex. Pollinia 2.5–3.5 by 1.3–1.5 mm; caudicle 2.7–3.5 by 2.5–2.8 mm. *Stigma* 1.5–5 by 4.5–6.3 mm, with a more or less pronounced notched margin; rostellum 4.1–7.5 by 5.5–7.5 mm, with a broadly rounded apex. *Fruit* body 54–71 by 28–33.5 mm; valvae keels 8–9.5 mm high; pronounced longitudinal ridge of juga 3.5–4 mm high with up to 9 incisions up to 4 mm deep.

Distribution — Sumatra, Java.

Habitat & Ecology — Epiphyte on forest trees in montane forest, old deserted coffee and tea plantations and pole tree forest. Altitude 900–1500 m. Flowering: March, October (April, July–December in greenhouse).

Notes — 1. Ovary olive green tinged salmon. Sepals and petals greenish cream tinged salmon to salmon to brownish salmon. Lip outside salmon with a brownish tinge, hypochile deep brown to red brown with lighter spots, at the base yellowish; lateral lobes brown to red brown with creamy white spots, lateral keels red brown, median keel yellow, projections on keels creamy white; epichile white to creamy white with at the base some brown markings; margins of the claw red brown. Column white to greenish cream, front of stalk tinged brown to red brown. Anther pale yellow, pollinia bright yellow. Stigma pale yellow, rostellum white with dark brown margin. No smell to slightly fragrant.

2. The epithet *incarnata* refers to the flesh-coloured flowers.

3. Horticulturists often use the epithet *salmonicolor* for *C. speciosa* subsp. *incarnata*. To prevent further confusion with the distinct species *C. salmonicolor* Rchb. f. (synonym *C. speciosa* Lindl. var. *salmonicolor* Schltr.), the epithet *incarnata* is chosen.

4. The dimensions in the description refer to herbarium material only.

12. Coelogyne susanae P.J. Cribb & B.A. Lewis — Fig. 4.16, Map 4.3, Plate 4.1l, 4.2d

Coelogyne susanae P.J. Cribb & B.A. Lewis, Kew Bull. 46 (1991) 317; Orchids of the Solomon Islands and Bougainville (1991) 90, f. 18. — Type: *Wickison 40* (holo K), Solomon Islands.

Roots 2–3 mm diam. Rhizome 9.5–15 mm thick. Scale-covered part of the inflorescence-bearing young shoot 10–11.5 cm long. *Pseudobulbs* up to 2 cm apart, oblongoid, obtusely 4-angled when fresh, 6.8–17 cm long. *Leaves* two per pseudobulb, stiff herbaceous. Petiole 3–7 cm long. Blade linear-lanceolate, 32–45 by 6.5–8.7 cm; apex acuminate to cuspidate; main nerves 5–7. *Inflorescence* synanthous with the partially

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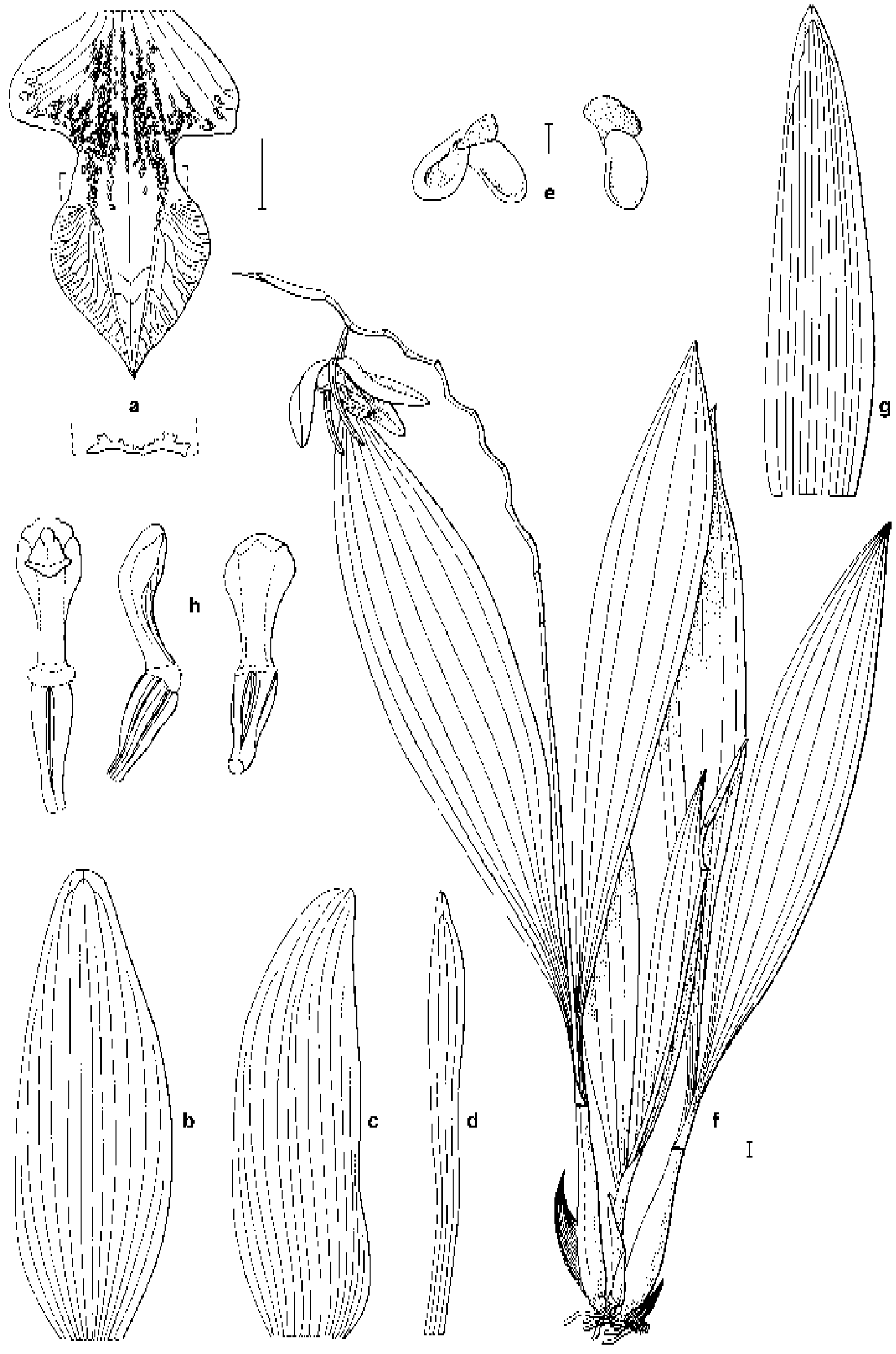
Fig. 4.16. *Coelogyne susanae* P.J. Cribb & B.A. Lewis. a. Lip ornamentation with cross section of claw (*Cruttwell 3185*); b. median sepal; c. lateral sepal; d. petal; e. pollinia (*Cribb 1922*); f. habit (*Craven 206*); g. floral bract [*NGF (Millar) 38405*]; h. column: front, lateral and rear view (*Hunt 2205*). — Scale bars: 1 cm (a–d, f–h); 1 mm (e).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to entirely developed leaves, 2–18-flowered. Peduncle during flowering at the base enclosed by the petiole and scales of the young shoot, 7–41.5 cm long. Rhachis (sub)erect, zigzag, 2.5–32 cm long; internodes 14–32 mm long, distinctly curved, incrassate, each with a swollen base bearing a flower. *Floral bracts* ovate-lanceolate, 41–67 by 14–15 mm, deciduous; apex acute; nerves 11–13. *Flowers* opening in succession. Pedicel 5–9 by 2.5–3.2 mm; ovary 14–28 by 5–7.5 mm. *Median sepal* ovate-oblong, 50–67 by 17–23 mm; apex obtuse; nerves 13–15, the midrib a rounded keel 0.5–0.8 mm high. *Lateral sepals* ovate-lanceolate, 56–62 by 16–19.5 mm; apex acute; nerves 13–17, the midrib a rounded keel 0.5–0.8 mm high. *Petals* slightly recurved, 50–67 by 3.5–5 mm; apex acuminate; nerves 3, midrib centric. *Lip* 40–55 by 31–36 mm, nerves 15–19. *Hypochile* when flattened 18–23 by 31–36 mm; base attached over 16–27 mm, not saccate; lateral lobes in front obtuse, extending 1–4 mm in front, front margin at the base slightly irregularly erose, with obtuse sinus; apex not saccate; keels 11–13, each consisting of a row of irregularly shaped, elongate warts 1–2 mm high with papillae but without hairs on the basal quarter of the hypochile and a slightly elevated row with irregularly shaped horizontal ridges 1.2–2 mm high with papillae but without hairs on the apical parts of the hypochile, not widened along the crest, the 5 median keels parallel at the base of the hypochile and there 0.5–1 mm high, diverging on the apical half of the epichile, converging again on the basal half of the epichile, the 3 most median keels developed on the hypochile and the basal half of the epichile, the 6–8 lateral keels only developed on the apical half of the hypochile, lower than the median keels (Plate 4.11). *Epichile* convex, when flattened elliptic to ovate to orbicular, 21–37 by 19–21 mm, with a broad, relatively long claw 0.2–0.7 mm in cross section; base broadly attached over 12–15.5 mm; apex retuse, slightly raised, with an acute apex with warts 0.3–0.5 mm high; margin slightly erose, recurved; sides not to slightly pronounced as lateral lobes, with a few warts 0.8–1 mm high, centre 0.4–0.9 mm in cross section, margin 0.2–0.25 mm in cross section; keels 7–9, the 2 longest ones ending 12–15 mm from the apex of the epichile, on the claw identical with the keels on the hypochile, on the plate changing into a row of irregularly shaped, elongate warts with papillae but without hairs. *Column* 22.5–23.5 by 8–10.5 mm; hood with truncate apical margin, laterally notched where the wings are attached and above, the middle part rounded, recurved. Anther oblong bell-shaped in outline, 5.5–6 by 5.9–6 mm, near the place of attachment with a little elongate projecting apex; apex without notch. Pollinia obliquely ellipsoid, 2.5–3.2 by 1.5–1.7 mm; caudicle flattened, broadly triangular in outline, 1.5–1.8 by 1.5–3.5 mm. *Stigma* 4–6 by 6–7 mm; margin apex notched; rostellum 3.8–6 by 6–7 mm, with an obtuse apex with or without notch. *Fruit* not seen.

Distribution — New Britain, Bougainville, Shortland Islands, Solomon Islands (Kolombangara, New Georgia, Guadalcanal, San Cristobal).

Habitat & Ecology — Epiphyte in rain forest, rarely terrestrial. Altitude 25–1250 m. Flowering: April–January (not in cultivation).

Notes — 1. Sepals and petals pale yellow green to creamy green with an orange or red brown lip and a white or pale yellow apex. Column whitish, brown on ventral surface. Fragrant.

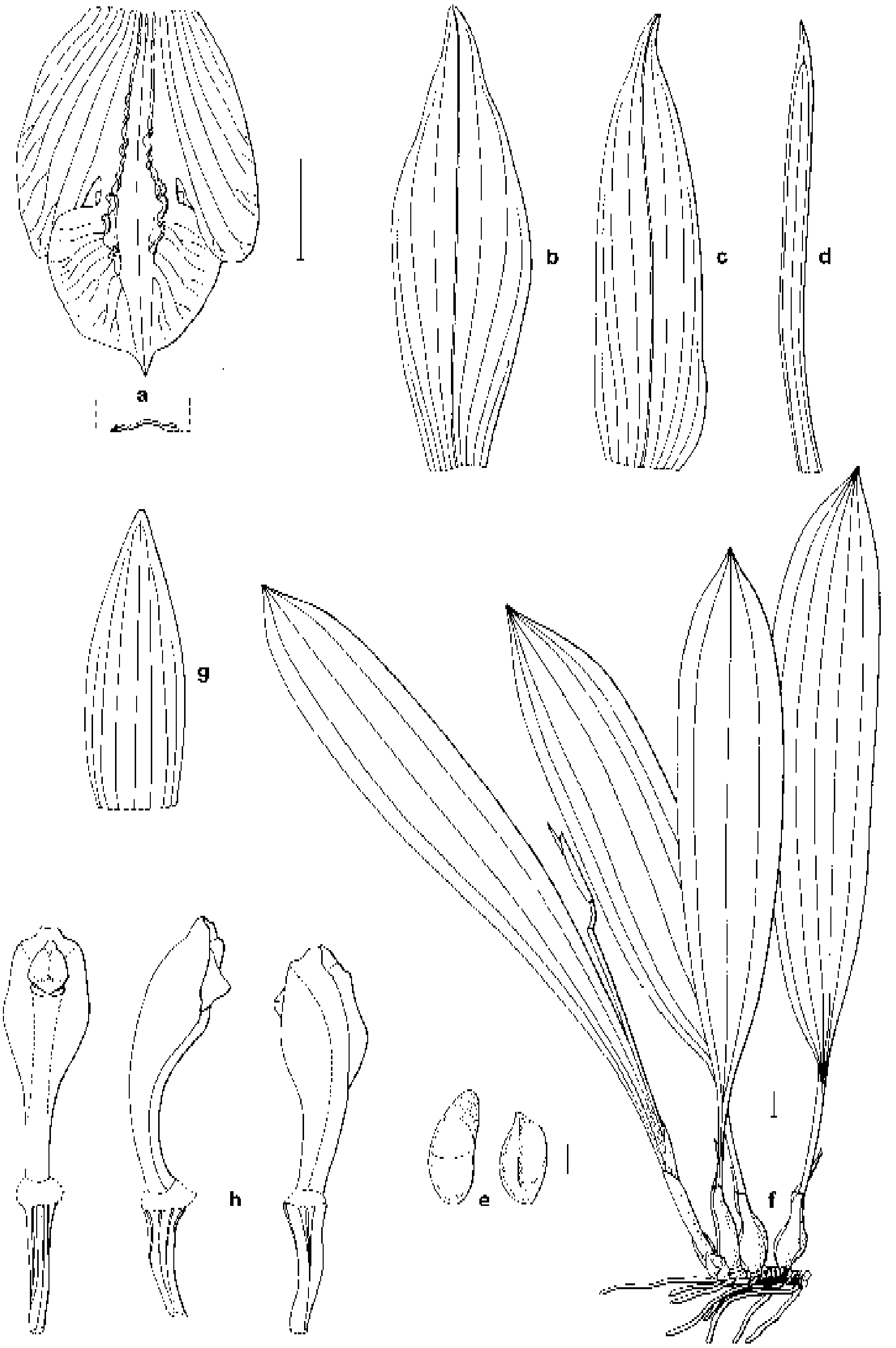
2. The epithet *susanae* refers to Sue Wickison, who collected the type specimen in New Georgia.

3. The species can be distinguished from *C. macdonaldii* by the obtuse sinus of the hypochile, orange/red brown keels and much larger flowers.

13. Coelogyne tiomanensis M.R. Hend. — Fig. 4.17, Map 4.5, Plate 4.5c

Coelogyne tiomanensis M.R. Hend., Gard. Bull. Straits Settlem. 5 (1930) 80; Holttum, Orchids of Malaya 3 (1964) 243; Seidenf. & J.J. Wood, Orchids of Penins. Malaysia and Singapore (1992) 205, f. 86c–d, pl. 12A. — Type: *SF (Henderson) 18397* (holo SING?, not found), Tioman Island, Mt Rokam.

Roots 1.7–2.7 mm diam., very long and tough. Rhizome 5–7.5 mm thick. Scale-covered part of the inflorescence-bearing young shoot 6.8–11 cm long. *Pseudobulbs* up to 3 cm apart, ovoid, flattened bilaterally, obtusely 4-angled when fresh, 2.2–5 cm long. *Leaves* one per pseudobulb. Petiole 3–6 cm long. Blade lanceolate, 21–32 by 3.2–6.5 cm; apex acuminate to cuspidate; main nerves 3–5. *Inflorescence* synanthous with the partially to entirely developed leaves, 2–10-flowered. Peduncle during flowering at the base enclosed by the petiole and scales of the young shoot, 11.5–20 cm long. Rhachis (sub)erect, zigzag, 1.1–10 cm long; internodes 9–15 mm long, slightly curved, hardly thickened. *Floral bracts* ovate-oblong, 23–30 by 8.5–11 mm, deciduous; apex acuminate; nerves 7–9. *Flowers* opening in succession, finely papillose. Pedicel c. 5 by 1–1.1 mm; ovary c. 6 by 1.1–1.5 mm. *Median sepal* lanceolate, 31–47 by 8–12 mm; apex acuminate; nerves 9, the midrib a rounded keel 0.2–0.7 mm high. *Lateral sepals* ovate-lanceolate, 24–43 by 6–11 mm; apex cuspidate; nerves 8 or 9, the midrib a rounded keel 0.2–0.6 mm high. *Petals* slightly recurved, 30–42 by 1.5–1.9 mm; apex cuspidate; nerves 3, midrib centric. *Lip* 24–37 by 16–22 mm, nerves 15–17. *Hypochile* when flattened 18–26 by 16–22 mm; base broadly attached over 5–12 mm; lateral lobes in front rounded, extending 3–9 mm in front and diverging, front margin at the base entire, with acute sinus; keels 2 or 3, starting at the base of the lip and there 0.2–1 mm high, all keels widened along the crest, plate-like, undulating, 1–2 mm high, with papillae but without hairs, the lateral keels parallel on the base of the hypochile, diverging towards the apex of the hypochile, converging again on the epichile, the median keel (if present) only developed in the upper quarter of the hypochile, lower than the lateral ones. *Epichile* convex, when flattened obrhomboid to obovate, 6–11 by 11–15 mm, with a broad, short claw 0.2–0.4 mm thick; base attached over 6–8 mm; apex acuminate, slightly raised, with an acute apex without warts; margin entire, recurved; sides pronounced as lateral lobes, without warts, centre 0.25–0.3 mm thick, margin 0.1–0.25 mm thick; keels 2, ending 4–9 mm from the apex of the epichile, on the claw identical with the keels on the hypochile, on the plate changing into a row of waving irregularly plate-like projections 1–2 mm high, with papillae but without hairs. *Column* 18–27 by 8–12 mm; hood with truncate apical margin, laterally notched where the wings are attached and with an additional notch above, the middle part rounded, slightly recurved. Anther broadly bell-shaped in outline, 3.5–6 by 3.5–5 mm, near the place of attachment with a little rounded projecting apex; apex without notch. Pollinia obliquely ellipsoid, 3–3.5 by 1.4–1.5 mm; caudicle 2.5–2.6 by 1.5–1.6 mm. *Stigma* 2.5–4 by 1.5–5 mm; margin apex slightly notched; rostellum 2.5–5 by 2–5 mm, with an obtuse apex without notch. *Fruit* body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36–38 by c. 14 mm; valvae keels 3–3.5 mm high; juga with a pronounced longitudinal ridge 2.5–3 mm high without incisions.

Distribution — Peninsular Malaysia (Tioman Island).

Habitat & Ecology — Epiphyte and lithophyte in mossy, montane dwarf forest. Altitude 600–1040 m. Flowering: May, August (not in cultivation).

Notes — 1. Sepals yellow to pale salmon, petals pale greenish to pale salmon. Lip side lobes white with brown veins; centre dark brown; edges light brown; side lobes paler with brown veins. Column greenish with two faint brown streaks below; hood reddish brown to orange. No smell.

2. The epithet *tiomanensis* refers to the island Tioman, where the type specimen was collected by Murray Ross Henderson.

3. The species is easily recognised by the dark brown lip and undulating, plate-like keels (Fig. 4.17a).

14. Coelogyne tommii Gravendeel & O'Byrne, *spec. nov.* — Fig. 4.18, Plate 4.1o, 4.5d

Herba epiphytica. Pseudobulbi monophylli, oblongi vel ovoidei, in vivo obtuso-angulati, 4.1–7.3 cm longi. Folia lanceolata, 20.5–25 cm longa, 4.3–5.2 cm lata, nervis 5. Inflorescentia erecta, proterantha, pauciflora (floribus 4 vel 5). Rhachis (sub)erecta, internodiis 17–18 mm longis. Florum bracteae ovate-oblongae, 24–26 mm longae, 12–14 mm latae, caducae, nervis 11–13. Flores fere simultanei expandent. Sepalum dorsale lanceolatum, 40–41 mm longum, 13–13.5 mm latum, nervis 9. Sepala lateralia obliqua, ovato-lanceolata, 37–39 mm longa, 10–11 mm lata, nervis 8 vel 9. Petala paulo recurvata, linearia, 36–38 mm longa, 3–3.5 mm lata, nervis 3 vel 5. Labellum immobile, cymbiforme, 3-lobatum, ubi applanatum panduratum, 33–35 mm longum, 24–26 mm latum, nervis 13 vel 15. Hypochile ubi applanatum 19–22 mm longum, 24–26 mm latum; lobi laterales erecti, antice acuti, 2.5–3 mm longi et aliquantum divergentes, sinu acuto; carinae 3 e basi labelli, 0.5–0.7 mm altae, alato-erectae, lamelliformes, crista irregulariter crenulata 1.5–2.5 mm alta, papillis 0.1–0.15 mm altis, in dimidio hypochilii mutata in projecturis prominentibus 1–1.2 mm altis, contractis, ramosis vel simplicibus, marginibus irregulariter crenulatis, papillis 0.1–0.15 mm altis, carinae medianae parallelae in hypochilii parte basali, distaliter paulo divergentes, epichilii in parte convergentes, carina intermedia exterioribus humilior et brevior. Epichile convexum, ubi applanatum obrhomboideum vel orbiculare, 13–14 mm longum, 18–18.5 mm latum; apex acutus verrucis 0.3–0.4 mm altis; margo irregulariter denticulata, recurvata, lateraliter lobata verrucis 0.25–0.3 mm altis; carinae 3–5, duae exteriores quam adsunt in epichilii parte quarta apicali evolutae, 10.5–11 mm infra epichilii apicem terminantes, duae medianae in epichilii dimidio apicali evolutae, 6–7.5 mm infra epichilii apicem terminantes, carina mediana quam adest in epichilii parte quarta basali, 12–13 mm infra epichilii apicem terminantes. — Typus: *Sing cult. s.n.* (holo K; iso L), unknown locality.

Coelogyne tomiensis O'Byrne, Malayan Orchid Rev. 29 (1995) 33, nom. invalid.

Roots 1.5–1.6 mm diam. Rhizome 8–8.5 mm thick. Scale-covered part of the inflorescence-bearing young shoot c. 4.9 cm long. *Pseudobulbs* up to 1.2 cm apart, oblongoid

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Fig. 4.17. *Coelogyne tiomanensis* M.R. Hend. a. Lip ornamentation with cross section of claw; b. median sepal; c. lateral sepal; d. petal; e. pollinia; f. habit (*Dunleavy 101*); g. floral bract [*SF (Henderson) 21668*]; h. column: front, lateral and rear view (*Dunleavy 101*). — Scale bars: 1 cm (a–d, f–h); 1 mm (e).

to ovoid, obtusely 4-angled when fresh, 4.1–7.3 cm long. *Leaves* one per pseudobulb. Petiole 2.5–3.5 cm long. Blade lanceolate, 20.5–25 by 4.3–5.2 cm; apex acuminate; main nerves 5. *Inflorescence* proteranthous, 4–5-flowered. Peduncle during flowering at the base enclosed by the scales of the young shoot, c. 6 cm long. Rhachis (sub)erect, zigzag, c. 3.8 cm long; internodes 17–18 mm long, slightly curved, hardly thickened. *Floral bracts* ovate-oblong, 24–26 by 12–14 mm, deciduous; apex acute; nerves 11–13. *Flowers* opening (almost) simultaneously. Pedicel 7–8 by 2.3–2.7 mm; ovary 10–11 by 3–4.5 mm. *Median sepal* lanceolate, 40–41 by 13–13.5 mm; apex retuse to acute; nerves 9, the midrib a rounded keel 0.7–0.75 mm high. *Lateral sepals* ovate-lanceolate, 37–39 by 10–11 mm; apex acute; nerves 8 or 9, the midrib a rounded keel 0.65–0.9 mm high. *Petals* slightly recurved, 36–38 by 3–3.5 mm; apex acute; nerves 3–5, midrib centric. *Lip* 33–35 by 24–26 mm, nerves 13–15. *Hypochile* when flattened 19–22 by 24–26 mm; base broadly attached over 8–10 mm, slightly saccate; lateral lobes in front rounded, extending 2.5–3 mm in front and slightly diverging, front margin at the base irregularly erose, with acute sinus; apex not saccate; keels 3, starting at the base of the lip and there 0.5–0.7 mm high, all keels widened along the crest, on the basal part of the hypochile raised, plate-like, with undulating and heavily fringed margin 1.5–2.5 mm high, with papillae 0.1–0.15 mm long, but without hairs, halfway along the hypochile changing into slender, tapering, either or not branched, irregularly shaped projections with undulating, irregular margin 1–1.2 mm high, with papillae 0.1–0.15 mm long, but without hairs, the three median keels parallel on the basal part of the hypochile, slightly diverging towards the apical part of the hypochile, converging again on the epichile, the most median keel lower than the lateral ones (Plate 4.1o). *Epichile* convex, when flattened obrhomboid to orbicular, 13–14 by 18–18.5 mm, with a broad, short claw 0.8–1.6 mm thick; base attached over 11–12 mm; apex acute, slightly raised, with an acute apex with warts 0.3–0.4 mm high; margin slightly erose, recurved; sides pronounced as lateral lobes, with warts 0.25–0.3 mm high, centre 0.3–0.35 mm thick, margin 0.15–0.2 mm thick; keels 3–5, on the claw and plate identical with the keels on the basal half of the hypochile, the outer two keels (if present) developed on the apical quarter of the epichile, ending 10.5–11 mm from the apex of the epichile, the median two keels developed on the apical half of the epichile, ending 6–7.5 mm from the apex of the epichile, the most median keel (if present on the epichile) developed on the basal quarter of the epichile, ending 12–13 mm from the apex of the epichile. *Column* 22–27 by 7.5–8 mm; hood with more or less truncate apical margin, irregularly dentate, laterally notched where the wings are attached, the middle part rounded, slightly recurved. Anther broadly bell-shaped in outline, 3.5–5.5 by 2.5–5 mm, near the place of attachment with a little rounded projecting apex; apex slightly notched. Pollinia obliquely ellipsoid, 2–2.5 by 1.2–1.5 mm; caudicle 1–1.5 by 1.5–1.6 mm. *Stigma* 2.5–3 by 3–3.5 mm; margin apex slightly notched; rostellum 3–4.5 by 3.5–4 mm, with an obtuse apex without notch. *Fruit* not seen.

Distribution — Unknown.

Habitat & Ecology — Flowering: April, October–December in greenhouse.

Notes — 1. Ovary yellowish green. Sepals and petals light green to creamy yellow, transparent. Lip light brown to rusty brown inside with red brown veins shimmering

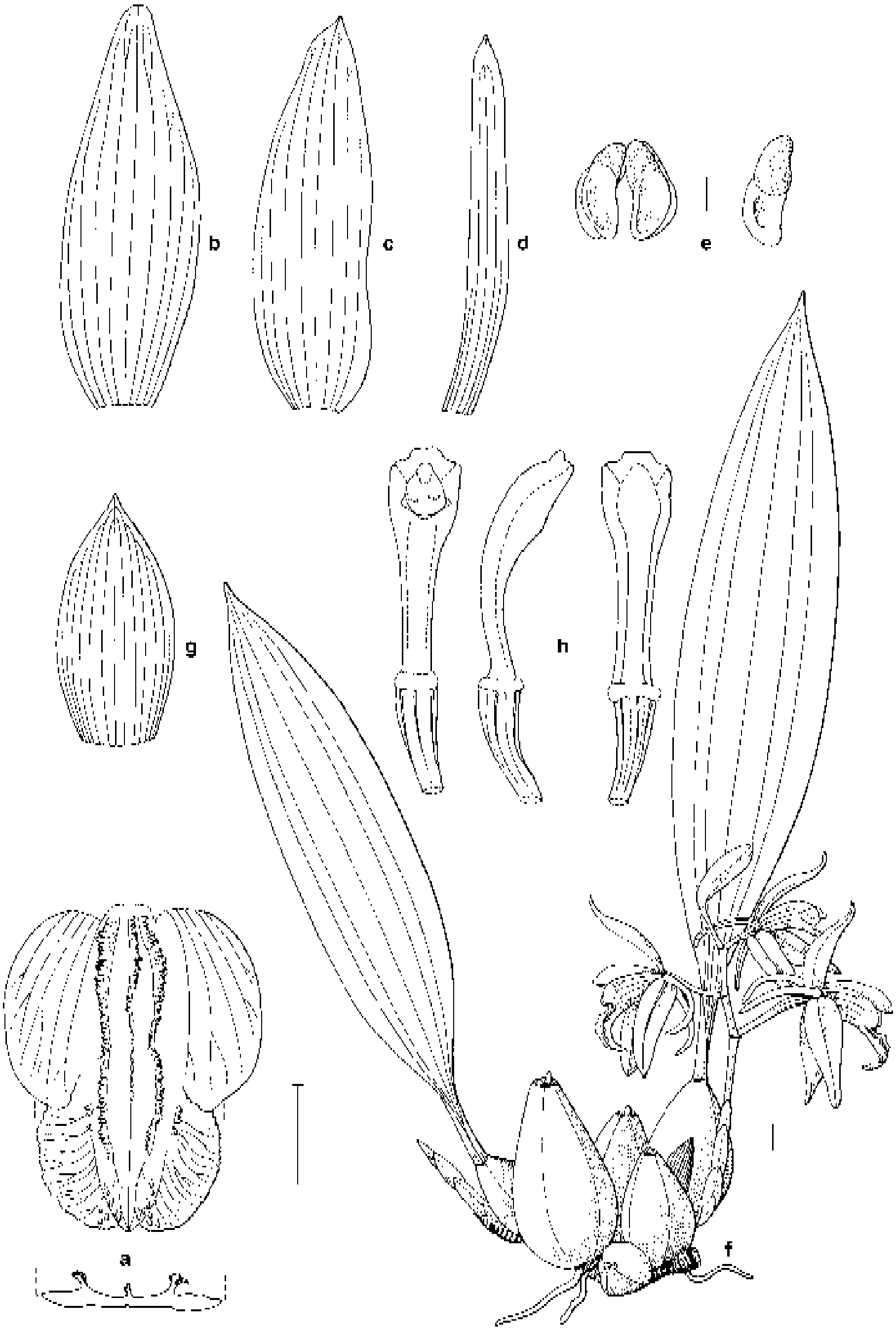
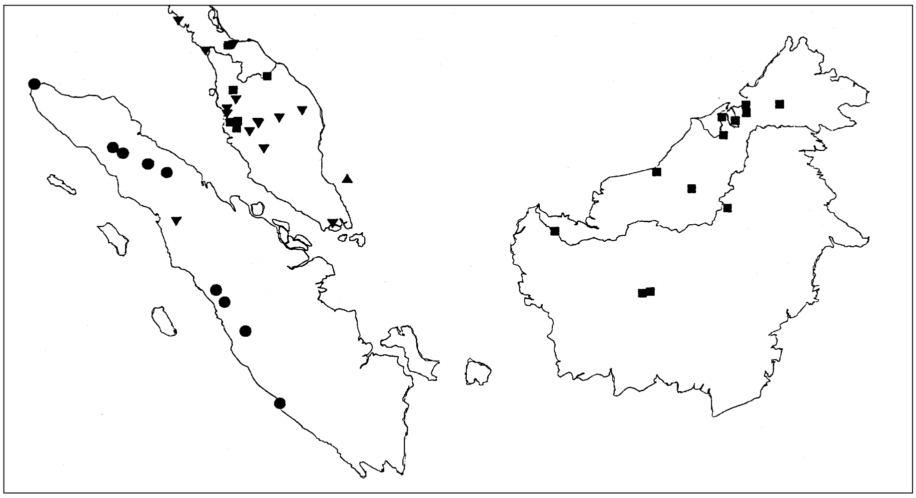


Fig. 4.18. *Coelogyne tommii* Gravendeel & O'Byrne. a. Lip ornamentation with cross section of claw; b. median sepal; c. lateral sepal; d. petal; e. pollinia; f. habit; g. floral bract; h. column: front, lateral and rear view [*Leiden cult. (Kebun Raya Bogor) 21526*]. — Scale bars: 1 cm (a–d, f–h); 1 mm (e).



Map 4.5. Distribution of *Coelogyne salmonicolor* Rchb. f. (l), *C. septemcostata* J. J. Sm. (n), *C. tiomanensis* M.R. Hend. (s), and *C. xyrekes* Lindl. (t).

through on the outside, midlobe light brown with creamy white apex, with 5 brown keels. Column creamy yellow to light green, front of stalk with 3 brown lines, its apex white, wings cream coloured. Anther and stigma pale yellow, pollinia bright yellow, rostellum light brown. Fragrant.

2. The former epithet *tomiensis* is changed to *tommii*, the proper orthographic form to commemorate Mr. Tommy Sng, who grew the plant from which the type collection was made in his garden in Singapore.

3. It is concluded that this species is not conspecific with *C. dichroantha* Gagnep. because the pseudobulbs have two leaves (instead of one) and the lip is completely rusty brown (instead of brown and cream) with 4 or 5 keels instead of only 3 as depicted in Eberhardt's picture of *C. dichroantha*.

4. The species is easily recognized by the proteranthous inflorescence and (nearly) simultaneously opening flowers with plate-like keels.

15. Coelogyne xyrekes Ridl. — Fig. 4.19, Map 4.5, Plate 4.1m, 4.5b

Coelogyne xyrekes Ridl., J. Fed. Malay States Mus. 6 (1915) 181; Fl. Malay Penins. 4 (1924) 134; Seidenf. & Smitinand, Orch. Thail. (1959) 109; Holttum, Orchids of Malaya 3 (1964) 243; Seidenf., Dansk Bot. Ark. 29, 4 (1975) 11, f. 2; Seidenf. & J. J. Wood, Orchids of Penins. Malaysia and Singapore (1992) 203, f. 86a–b. — Type: *Ridley 16282* (holo SING; iso K), Malay Peninsula, Pahang, Mt Tahan.

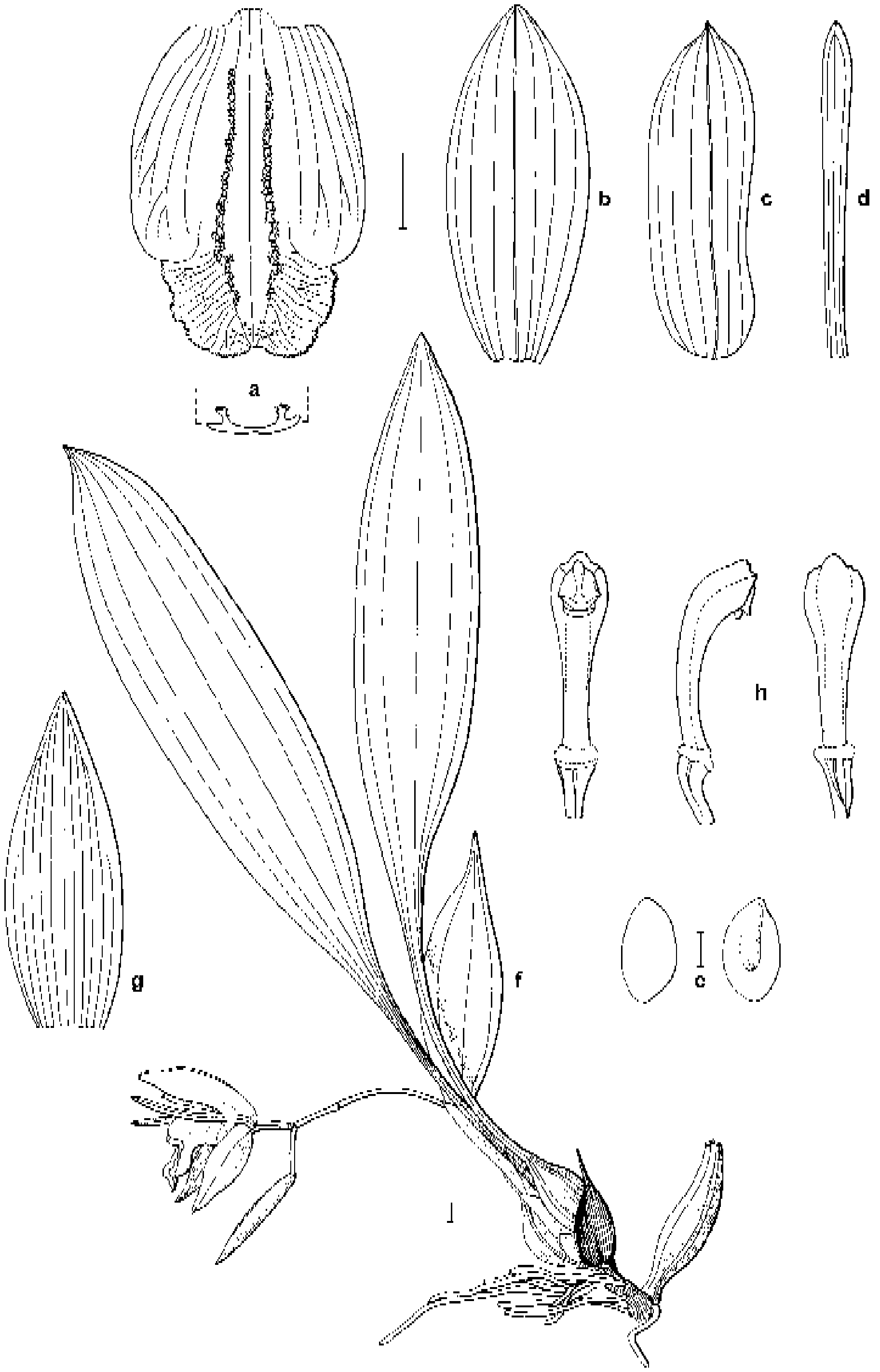
Coelogyne xanthoglossa Ridl., J. Fed. Malay States Mus. 6 (1915) 180; Fl. Malay Penins. 4 (1924) 134; Holttum, Orchids of Malaya 3 (1964) 243; Seidenf. & J.J. Wood, Orchids of Penins. Malaysia and Singapore (1992) 205. — Type: *Ridley s.n.* (holo K), Malay Peninsula, Pahang, Mt Tahan.

Roots 1.5–2.1 mm diam. Rhizome 5–8 mm thick. Scale-covered part of the inflorescence-bearing young shoot 6.5–9 cm long. *Pseudobulbs* up to 1.5 cm apart, oblongoid, not seen when fresh, distinctly 4-ridged when dried, 4–5.5 cm long. *Leaves* one per pseudobulb. Petiole 3.5–9 cm long. Blade obovate-lanceolate, 20.5–36.5 by 4.1–9.2 cm; apex acuminate; main nerves 5. *Inflorescence* synanthous with the partially to entirely developed leaves, 2–4-flowered. Peduncle during flowering at the base enclosed by the petiole and scales of the young shoot, 7–15 cm long. Rhachis (sub)erect, zigzag, 1.8–5.8 cm long; internodes 16–22.5 mm long, slightly curved, hardly thickened. *Floral bracts* ovate-oblong, 29–56.5 by 9–18 mm, deciduous; apex acute; nerves 9–11. *Flowers* opening in succession. Pedicel 4.5–8 by 1.3–1.5 mm; ovary 6–11 by 2.5–4 mm. *Median sepal* ovate-oblong, 43–56 by 16–23.5 mm; apex acute; nerves 7–13, the midrib a rounded keel 0.9–1 mm high. *Lateral sepals* obovate-lanceolate, 41–59 by 14–16 mm; apex acute; nerves 6–10, the midrib a rounded keel 0.7–1.3 mm high. *Petals* slightly recurved, 42–55 by 2.3–3.5 mm; apex acute; nerves 3, midrib centric. *Lip* 36–49 by 29–44 mm, nerves 15–17. *Hypochile* when flattened 30–36 by 29–40 mm; base attached over 7–24 mm, slightly saccate; lateral lobes in front rounded, extending 3.5–5.5 mm in front and slightly diverging, front margin at the base irregularly erose, with acute sinus; apex slightly saccate; keels 2, starting at the base of the lip and there 0.5–1 mm high, widened along the crest, plate-like, undulating, cm long. Blade lanceolate, 15–18 by c. 4 cm; apex acute; main nerves 7. *Inflorescence* synanthous, 3-flowered. Peduncle during flowering at the base enclosed by the scales of the young shoot, c. 3.8 cm long. Rhachis curved, zigzag, c. 1.8 cm long; internodes c. 14 mm long, slightly curved, thickened. *Floral bracts* ovate-lanceolate, c. 25 mm long, persistent; apex acute; nerves not seen. *Flowers* opening in succession. Pedicel c. 10 by 1.5 mm; ovary not seen. *Median sepal* oblong, 2.5 by 1 cm; apex acute; nerves not seen. *Lateral sepals* falcate, 2.2 by 0.7 cm; apex acute; nerves not seen. *Petals* slightly recurved, 22–24 by 1 mm; apex acute; nerves not seen, midrib centric. *Lip* c. 18 by 13 mm, nerves not seen. *Hypochile* not seen when flattened; base not seen; lateral lobes in front acute, extending c. 1 mm in front and slightly diverging, front margin entire, with acute sinus; keels 3, plate-like with an interrupted margin, all keels starting at the base of the lip, continuing on the epichile, the median keel shorter than the lateral keels. *Epichile* convex, when flattened not seen, with a broad, short claw; apex subacute with an acute apex; margin entire, recurved; sides not pronounced as lateral lobes; keels 3, ending 8–11 mm from the apex of the epichile, on the claw and plate identical with the keels on the hypochile. *Column* hood with acute apical margin. Anther not seen. Pollinia not seen. *Stigma* not seen. *Fruit* not seen.

Distribution — Thailand, Peninsular Malaysia, Sumatra.

Habitat & Ecology — Epiphyte in (montane) rain forest. Altitude 700–1900 m. Flowering: February–December (February–March in greenhouse).

Notes — 1. Sepals and petals brownish salmon tinged olive on the outside, transparent. Lip pale salmon, heavily reticulated with dark brown inside, keels blackish brown, outside greyish salmon. Column cream coloured tinged salmon, anther greenish yellow. Ovary and pedicel olive brown. No smell. 2. The epithet *xyrekes* (which is Greek for smooth, clean-shaven) refers to the absence of long hairs on the keels, in contrast with *C. speciosa* (according to Ridley a closely related species), which has keels with relatively long hairs. 3. The vegetative parts and the keels of the (immature) flower of the type specimen of *C. xanthoglossa* match very well with *C. xyrekes*. Therefore it is concluded that these names must be synonyms. 4. The species is easily recognized by the purple colour of the young leaves and undulating, plate-like keels on the lip with long papillae (Fig. 15a).


a
b
c
d
f
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INSUFFICIENTLY KNOWN SPECIES

16. Coelogyne dichroantha Gagnep. — Plate 4.5a

Coelogyne dichroantha Gagnep., Bull. Mus. Hist. Nat. (Paris) 2, 22, 4 (1950) 506; Notul. Syst. (Paris) 14, 2 (1951) 122; Seidenf., Contr. Orch. Fl. of Cambodia, Laos and Vietnam (1975) 32; Aver., Prelim. List of Vietn. Orchids 1 (1988) 89; Vasc. Plants Syn. Vietn. Flora 1 (1990) 55; Seidenf., Opera Bot. (1992) 114, pl. 7A. — Type: An unnumbered watercolour by Eberhardt (holo P).

Roots 1–1.8 mm diam. Rhizome 5–6 mm thick. Scale-covered part of the inflorescence-bearing young shoot c. 3.7 mm long. *Pseudobulbs* up to 1.2 cm apart, oblongoid, obtusely 4-angled when fresh, c. 5 cm long. *Leaves* two per pseudobulb. Petiole c. 1.5 cm long. Blade lanceolate, 15–18 by c. 4 cm; apex acute; main nerves 7. *Inflorescence* synanthous, 3-flowered. Peduncle during flowering at the base enclosed by the scales of the young shoot, c. 3.8 cm long. Rhachis curved, zigzag, c. 1.8 cm long; internodes c. 14 mm long, slightly curved, thickened. *Floral bracts* ovate-lanceolate, c. 25 mm long, persistent; apex acute; nerves not seen. *Flowers* opening in succession. Pedicel c. 10 by 1.5 mm; ovary not seen. *Median sepal* oblong, 2.5 by 1 cm; apex acute; nerves not seen. *Lateral sepals* falcate, 2.2 by 0.7 cm; apex acute; nerves not seen. *Petals* slightly recurved, 22–24 by 1 mm; apex acute; nerves not seen, midrib centric. *Lip* c. 18 by 13 mm, nerves not seen. *Hypochile* not seen when flattened; base not seen; lateral lobes in front acute, extending c. 1 mm in front and slightly diverging, front margin entire, with acute sinus; keels 3, plate-like with an interrupted margin, all keels starting at the base of the lip, continuing on the epichile, the median keel shorter than the lateral keels. *Epichile* convex, when flattened not seen, with a broad, short claw; apex subacute with an acute apex; margin entire, recurved; sides not pronounced as lateral lobes; keels 3, ending 8–11 mm from the apex of the epichile, on the claw and plate identical with the keels on the hypochile. *Column* hood with acute apical margin. Anther not seen. Pollinia not seen. *Stigma* not seen. *Fruit* not seen.

Distribution — Vietnam.

Habitat & Ecology — Unknown.

Notes — 1. Sepals and petals light green. Lip light green outside, white inside, with yellowish purple margin and yellowish keels.

2. The epithet *dichroantha* refers to the two colours (yellowish green and brown) of the flowers.

3. The description above is based on the type collection (a watercolour) and the type description. Sterile bracts at the base of the peduncle or rhachis are lacking and the plant has few, large flowers, which suggests its position in sect. *Speciosae*. The exact details of the keels are not clearly visible on the aquarelle, however, hence it is doubtful whether the species really belongs to this section.

♦

Fig. 4.19. *Coelogyne xyrekes* Ridl. a. Lip ornamentation with cross section of claw; b. median sepal; c. lateral sepal; d. petal; e. pollinia [*Leiden cult. (De Vogel) 28024*]; f. habit [*SF (Henderson) 17701, (Sinclair & Kiah) 38722*]; g. floral bract (*Hislop* ?-7-1952); h. column: front, lateral and rear view [*Leiden cult. (De Vogel) 28024*]. — Scale bars: 1 cm (a–d, f–h); 1 mm (e).

EXCLUDED SPECIES

17. *Coelogyne eberhardtii* Gagnep., Bull. Mus. Hist. Nat. (Paris) 2, 2, 1 (1930) 423; Fl. Indo-Chine 6 (1934) 311, f. 27; Notul. Syst. (Paris) 14, 2 (1951) 122; Seidenf., Contr. Orch. Fl. of Cambodia, Laos and Vietnam (1975) 32, f. 6; Aver., Prelimin. List of Vietn. Orchids 1 (1988) 90; Vasc. Plants Syn. Vietn. Flora 1 (1990) 55; Seidenf., Orchids of Indochina (1992) 109, pl. 7A. — Type: *Eberhardt 1887* (holo P), Vietnam, Langbian.

Note — The molecular phylogeny of *Coelogyne* constructed in chapter 2 indicates that *C. eberhardtii* is clearly separated from the species of sect. *Speciosae* sampled. Hysteranthous inflorescences, yellowish white coloured flowers and shining green pseudobulbs are not present in sect. *Speciosae*, hence it is concluded that this species does not belong to this section. According to the molecular phylogeny constructed in chapter 2, *C. eberhardtii* is closer related to *C. miniata* (subgenus *Hologyne*), *C. barbata* (sect. *Elatae*) and *C. cristata* (sect. *Coelogyne*), which also have hysteranthous inflorescences, yellowish white coloured flowers and/or shining green pseudobulbs.

18. *Coelogyne lawrenceana* Rolfe, Gard. Chron. 1 (1905) 227; Bot. Mag. 4, 3 (1907) 8164; Ridl., J. Nat. Hist. Soc. Siam 4, 3 (1921) 117; Gagnep., Fl. Indo-Chine (1934) 314; Notul. Syst. (Paris) 14, 2 (1951) 123; Guillaumin, Bull. Mus. Hist. Nat. (Paris) 2, 28, 5 (1956) 488; Seidenf., Contr. Orch. Fl. of Cambodia, Laos and Vietnam (1975) 33; Aver., Prelimin. List of Vietn. Orchids 1 (1988) 91; Vasc. Plants Syn. Vietn. Flora 1 (1990) 56. — Type: *Micholitz s.n.* (holo not found), Vietnam, Annam.

Coelogyne fleuryi Gagnep., Bull. Mus. Hist. Nat. (Paris) 2, 2, 1 (1930) 424; Fl. Indo-Chine (1934) 314. — Syntypes: *Poilane 5975* (NY, P), *Chevallier 30900* (P), Vietnam, Annam.

Note — Hysteranthous inflorescences, yellowish white coloured flowers and shining green, smooth pseudobulbs are not present in other species of sect. *Speciosae*, hence it is concluded that this species does not belong to this section. We assume *C. lawrenceana* to be closely related to *C. eberhardtii*, and therefore exclude this species from sect. *Speciosae*, too.

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IDENTIFICATION LIST

Dates are used if the number of the collection is unknown. If only the year is known, it is placed between brackets.

A series (Cuadra) 1429: 10; (Kadir) 2059: 10 — Aarhus cult. 32839: 10 — Afriastini 2007: 3; 2455: 15 — d'Alleizette ?/6/1909: 18 — Amsterdam cult. (De Vogel) 794597 A: 2; 794597 B: 2; 794617 B: 2; 794643: 2; 794942: 2; 795175: 3; 795178: 3; 795178 B: 3; 795180 A: 3; 795286 A: 3; 795540: 3 — Anderson 322: 5 — Averyanow 0/135 LE (colour photo): 17.

Barcock 400: 15 — Barnes ?/10/1900: 15 — Batten Pooll (1939): 15; ?/11/1939: 15 — Beauverd cult. 29/9/1903: 1; 30/8/1911: 1 — Beccari 1869: 10; 10329: 1 — Bergman 534: 4; 589: 4 — Berlin cult. (Schwerdtfeger) 18270: 3; 25094: 3 — Blume ?/1/1822: 11a — Boden Kloss 3/8/1912: 1; 7/11/1913: 1; ?/4/1918: 18 — Bogor cult. 34: 8; 35: 10; 36: 11b; 40: 9; 42: 8; 43: 8; 44: 10; 45: 10; B 57: 8; 62: 9; 65: 11b; 78: 10; 108: 11b; (Rachmat) 124: 2; 145: 11b; 154: 1; 155: 1; 156: 1; (Jacobson) C 220: 9; 992-XI-311: 11b — Bowden (via Anonymous 3) 20/7/1976: 7 — Brass 3397: 12; 5211: 2; 5241: 4; 13225: 2; 24914: 1; 24915: 2; 32057: 4 — Bregulla 11: 7; 116: 7 — Bruges 1914: 11a — BSIP series (Dennis) 4637: 2 — Bünnemeijer 1094: 11b; 3327: 11b; 9048: 9 — Buysman 22: 11a.

Cabalion 451: 6 — Canberra cult. (Taylor) 437: 4 — Carr 77: 15; 2109: 9; 10160: 1; 10212: 4 — Castle-Smith 13: 10 — Chadim K 3: 1; 156: 4 — Cheesman 82: 4; 1414: 1 — Chevalier 30900: 18 — Church, Mahyar & Afriastini 1974: 10 — Clayton cult. (1996): 8 — Clemens 1278: 1; 1654: 1 — Clements 5942: 1; 6440 A: 2; 6440 B: 1; 6486: 4; 6658: 1; 6669: 2; 6845: 2 — Comber 1465: 11a — Coode 6487: 10 — Cox 211: 6 — Craven 206: 12 — Cribb 1922: 12 — Cribb & Wheatley 48: 7 — Cruttwell 110: 4; 3185: 12.

De la Rue 15/9/1936: 7 — De Vogel 5781: 2; 7735: 11c — De Wilde & De Wilde-Duyfjes 13016: 15; 13391: 15; 14709: 15; 15579: 11b; 15767: 11c; 19056: 9 — Degener 14761: 7 — Dennis 3/10/1983: 12; ?/8/1987: 1 — Dickson 18: 2; MD 104: 8; MD 129: 8; 181: 8; MD 237: 8 — Docters van Leeuwen 10460: 1; 10779: 1 — Doleschall 90: 8; II 142: 8 — Dolman 28206: 15 — Dransfield 889: 15 — Dunleavy 101: 13.

Eberhardt 1887: 17 — Everett (1893): 10.

Fleischer ?/11/1910: 11c — Forbes 24: 2; 388: 2 — Franck 1194: 15.

Gjellerup 1084: 1 — Glasnevin cult. ?/10/1904: 1; 9/10/1954: 8 — Grimes 1063: 3; 1198: 3 — Gulliver cult. (1893): 1.

Haegens et al. 524: 10 — Hansen 367: 10 — Haywood ?/8/1896: 1 — Henderson 11131: 15; 25097: 10 — Himson 4/7/1956: 4 — Hislop ?/7/1952: 15 — Hoock ?/11/1974: 6 — Hoogland & Pullen 6180: 4; 6222: 4 — Hunt 2202: 2; 2205: 12; 2250: 12 — Hutton 31/12/1864: 8.

Im Thurn 310: 7.

Jacobson cult. (Groeneveldt) 224: 9; 262: 9 — Jacquet 627: 18 — Johansson 141: 3.

Kalkman 4425: 4 — Kanehira 110: 5; 1949: 5 — Kaudern 133: 2 — Kerr 536: 15; 572: 15; 710: 15; 798: 15; ?/4/1928: 15; 28/4/1930: 15 — Kew cult. A 190: 8; (Seimund) 334-14: 15; 19748: 4; 46147: 1 — Keysser 3: 4 — King's collector 6348: 15 — Koorders 31766 B: 11a — Kornassi 48: 8 — Kostermans 6315: 11a — Krebb 26/3/1930: 15.

LAE series (Foreman & Vinas) 60084: 4; (Croft) 65600: 2 — Lahaie 974: 8 — Lamb 491/85: 10; ?/4/1981: 10 — Larsen & Larsen 32839: 10 — Larsen et al. 42440: 10 — Latif 202: 11b — Lecoufle 29/5/1974: 4 — Leiden cult. (De Vogel) 5563: 3; 19930: 11a; 19959: 3; 20202: 3; 20216: 3; 21099: 3; 21524: 8; (Kebun Raya Bogor) 21526: 14; (De Vogel) 21536: 11a; 21537: 8; (Woods) 21654: 4; 22054: 4; 22059: 1; (De Vogel) 22088: 2; (Woods) 22089: 4; 22093: 4; 22098: 4; 22099: 4; 22101: 4; 22278: 2; (Reeve) 22284: 1; (De Vogel) 22911: 11a; (Nooteboom) 23171: 10; 23184: 10; 23187: 10; (De Vogel) 24393: 9; 24504: 8; 24505: 8; 25246: 11c; 25248: 11c; 25343: 11c; (De Vogel & Vermeulen) 25441: 11c; (De Vogel) 25670: 4; (Cribb & Morrisson) 25836: 7; (De Vogel) 27088: 11a; 27369: 3; 28002: 9; 28024: 15; 30707: 4; 30714: 2; 30720: 4; 30725: 2; (Schuiteman, Mulder & Vogel) 31464: 4; 31508: 4; 31578: 4; 31598: 4; 31874: 4; 31883: 1; 31892: 4; 31899: 4; 31909: 4; 32078: 1; 32214: 1; 32226: 1; 32230: 1; 32268: 4; 32273: 4; 32284: 1; 32313: 4; 32320: 4; 32389: 4; (De Vogel) 911339: 11a; 911353: 11a; (Mulder) 913070: 6; 913112: 6; (De Vogel) 913188: 10; 913265: 10; 914325: 6; 940790: 11c; 950057: 3;

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O’Byrne Sum 010.C: 9; C.X.010: 14 — Orolfo 6289: 10.

Pierrière cult. 21/8/1901: 1; 2/10/1913: 1 — Poilane 5975: 18; 22036: 18 — Polak 978: 1 — Powell 254: 6 — Pridgeon 4/6/1978: 2 — Pulle 242: 1.

Rahmat Si Boeea 10225: 9; 10455: 15; 10490: 15; 10619: 15; 11034: 15 — Raulerson 13243: 5 — Raynal 15988: 7 — Rees & Reeve 356: 1 — Reeve 668: 2; 818: 2; 821: 4; 1609: 4; 5187: 1; 5376: 1; 5691: 1 — Ridley 5198: 15; 13840: 15; 16282: 15; 138200: 15; ?/3/1889: 15; (1891): 10; ?/8/1891: 10; (1904): 15; ?/7/1911: 15; ?/3/1915: 10 — Rinehart LR 7689: 5 — Robinson 7: 8 — Robinson & Kloss 18/5/1914: 11b; 11/6/1914: 11b — Rothschild cult. 21/8/1916: 1 — RSNH series (Green) 1131: 6; 1345: 7; (Hallé) 6420: 6; (Raynal) 16323: 7 — Rutten 48: 8; 311: 8; W 1562: 8; 1793: 8.

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Van Balgooy 4674: 8 — Van Royen 11476: 4 — Van Steenis 9930: 9 — Van Vuuren 124: 2 — Veillon 2430: 7; 2685: 6 — Veitch (Curtis) 410: 9; cult. ?/11/1886: 11c; cult. ?/9/1889: 11c.

Webb (1838): 8 — Wheatley 77: 6; 108: 7; 410: 7 — Whistler W 1400: 6; W 2612: 6; 11/1/1994: 6 — Whitmee ?/3/1878: 6 — Wickison 40: 12 — Wigams cult. ?/8/1899: 1 — Woods 136: 4 — Wray Jr. 955: 15; ?/3/1892: 10.

Ziesing 262: 6 — Zollinger 2940: 11a.

INDEX

Accepted species are in roman type, new species and combinations in **bold** and synonyms, excluded and insufficiently known species in *italics*. Numbers refer to the species number as used in this revision.

REVISION OF COELOGYNE SECTION FULIGINOSAE (ORCHIDACEAE)

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SUMMARY

Section *Fuliginosae* Pfitzer & Kraenzl. of the genus *Coelogyne* Lindl. is revised. With the help of a pollen study, principal component and cluster analyses with morphological characters and a survey of some additional data, two species are recognised (*C. fimbriata* and *C. triplicatula*), including one dubious variety (*C. fimbriata* var. *acuminata*). Eleven names are reduced to synonymy. Three species formerly included in sect. *Fuliginosae* by several authors are excluded (*C. micrantha, C. treutleri* and *C. schilleriana*).

Key words: *Coelogyne* sect. *Fuliginosae*, orchids, phenetics, pollinia, systematics.

INTRODUCTION

Coelogyne Lindl. is an orchid genus with approximately 200 species, distributed throughout southeast Asia. Pfitzer & Kraenzlin (1907d) subdivided the genus into fourteen sections, among which sect. *Fuliginosae*. Nearly all later authors maintained this section, except for Smith (1933a) and Comber (1990), who included sect. *Fuliginosae* and *Speciosae* in sect. *Longifoliae*. The species of sect. *Fuliginosae* are characterised by a scape with scales inserted on its base, small and shiny 2-leaved pseudobulbs, a low number of relatively small flowers per inflorescence which open in succession, and a lip with a fimbriate margin. The lip bears a short median keel on the base of the hypochile and two long lateral keels covering both hypochile and epichile. The species of sect. *Speciosae* are characterised by flowers with a lip longer than 32 mm and the absence of sterile bracts at the base of the peduncle and scape (Gravendeel & De Vogel, 1999). The species of sect. *Longifoliae* are characterised by a long, creeping rhizome, long leaves and small flowers (Pfitzer & Kraenzlin, 1907d). In our view, sect. *Fuliginosae*, *Speciosae* and *Longifoliae* are characterised by clear morphological differences and should be considered different sections. Phylogenetic analyses of *Coelogyne* based on molecular data also indicate that species of these sections remain well separated. Moreover, no species of other sections seem to be nested within sect. *Fuliginosae* (Gravendeel et al., in prep.).

Pfitzer & Kraenzlin (1907d) included *C. fimbriata* Lindl., *C. fuliginosa* Lindl. ex Hook.f., *C. longeciliata* Teijsm. & Binn., *C. micrantha* Lindl., *C. pilosissima* Planch., *C. ovalis* Lindl., *C. treutleri* Hook.f. and *C. triplicatula* Rchb.f. in sect. *Fuliginosae*. Handel-Mazzetti (1936) added *C. xerophyta* Hand.-Mazz. Butzin (1974) included *C. schilleriana* Rchb.f. and *C. chrysotropis* Schltr. Seidenfaden (1975) suggested that

C. pallens Ridl., *C. leungiana* S.Y. Hu and *C. laotica* Gagnep. (as synonyms of *C. fimbriata*) should be added. Barretto (1990) contributed *C. primulina* Barretto, and Chowdhery & Pal (1997) included *C. arunachalensis* H.J. Chowdhery & G.D. Pal.

Coelogyne chrysotropis Schltr., *C. padangensis* J.J. Sm. and *C. pallens* Ridl. were included in sect. *Longifoliae* by Smith (1933a). We consider these species to be close allies of *C. fimbriata*, and therefore place them in sect. *Fuliginosae.*

Pradhan (1979) placed *C. treutleri* and *C. micrantha* in sect. *Micranthae* because of the smooth margin of the lip and the presence of three or more equal-sized keels on the lip. We agree with this opinion.

In our view, *C. schilleriana* does not belong to sect. *Fuliginosae* because the pseudobulbs and lip of this species differ markedly in shape from those of the species presently recognised in sect. *Fuliginosae*. The colour pattern of the lip is deviating, too. Perhaps this species is better placed in a section of its own.

The species in sect. *Fuliginosae* as they were circumscribed up to now have always caused confusion, as indicated by the disagreement in identifications present on herbarium sheets and by the assignment of specimens to different species by different authors in publications. They are distinguished mainly by the size and colour of their flowers (e.g. Bechtel et al., 1980; Das & Jain, 1980) and the shape of the lip (e.g. Seidenfaden & Wood, 1992). However, these characters are very variable and intermediates often cause confusion. In order to find characters to discriminate the different species of sect. *Fuliginosae* the following methods were used:

1) A pollen study to investigate if characters for species discrimination can be found in the morphology of pollinia, caudicles, pollen grains and tetrads. Pollen studies were chosen because they are known for their systematic potential in Orchidaceae (Chesselet & Linder, 1993; Freudenstein & Rasmussen, 1997).
2) Principal component and cluster analyses to explore the variation in macromorphological characters and to find terminal units in the species of the section. Phenetic methods were chosen because of their proven suitability to resolve difficult species complexes in other orchid groups (Johnson & Linder, 1995; Weldy et al., 1996).
3) A survey of data on flowering period, flower colour, habitat, elevation and geographical distributions of the specimens studied to trace possible correlations with clusters found in the phenetic analyses. These data have proven their usefulness for species discrimination in orchids, too (Johnson & Linder, 1995).

MATERIALS AND METHODS

Pollen analysis

A case study of variation in shape and size of pollinaria was done with specimens formerly identified as *C. fimbriata, C. fuliginosa* and *C. ovalis*. Pollinaria of other species of sect. *Fuliginosae* were not available for this study. The pollinaria were taken from four living specimens and kept on silica gel. Two pollinaria per specimen were studied. Preparation of the pollinaria for investigation with the scanning electron microscope (SEM) was done according to Toscano de Brito (1996). The pollinaria were not treated by acetolysis (Erdtman, 1960) to prevent the elastoviscin of the caudicle from dissolving and the pollen from collapsing and distorting. The pollinaria were placed in a 32% ammonia solution for 6 hours. After washing in distilled water, they were dehydrated in a series of 70%, 80%, 90% and 100% alcohol and subsequently critical-point-dried. Afterwards the pollinaria were gold-coated using a BAL-TEC SCD 005 Sputter Coater and examined with a JEOL JSM-5300 scanning microscope (15 kV, 15−48 mm).

Phenetic analysis

Characters were scored from dried specimens formerly identified as *C. fimbriata, C. fuliginosa, C. ovalis, C. padangensis, C. pallens* and *C. triplicatula*. Dried flowers were rehydrated before measurements were taken. Characters were scored from herbarium collections only because flowers from living and spirit collections tended to be consistently larger and thus would influence the analyses. Collections were obtained from the following herbaria: AMES, B, BM, BO, BR, CAL, G, IBSC, K, KYO, L, NY, SING and W. Other species of sect. *Fuliginosae* were not measured, because the type collections were lost or could not be traced.

Principal component analyses were performed with 29 characters (24 metric and 5 binary; see Table 5.1), scored from 34 collections. All data were standardised by log-transformation before calculating the correlation matrix and then analysed by an ordination of the principal components using SPSS (version 8.0).

Table 5.1. Variation of the morphological characters of the principal component analysis examined for 34 specimens of *Coelogyne* sect. *Fuliginosae* in the two main clusters of Fig. 5.2.

Character	cluster 1	cluster 2
Inflorescence number of sterile bracts	1–6	1 or 2
Leaf blade length	33–190 mm	64–114 mm
Leaf blade width	10–44 mm	14–38 mm
Median sepal length	13–40 mm	27–31 mm
Median sepal width	4–13 mm	9–17 mm
Median sepal number of nerves	5–13	9–11
Lateral sepal length	14–37 mm	26–32 mm
Lateral sepal width	4–12 mm	9–11 mm
Lateral sepal number of nerves	5–9	5–9
Petal length	13–33 mm	25–34 mm
Petal width	1–3 mm	1–3 mm
Petal number of nerves	1–3	1–3
Lip length	12–36 mm	25–29 mm
Lip width	12–25 mm	19–29 mm
Lip length sinus	1–8 mm	4–9 mm
Keels shape	plate-like	bar-shaped
Hypochile length	9–23 mm	15–21 mm
Hypochile height lateral keels	0.4–1.6 mm	0.7–1 mm
Hypochile height median keel	0.3–1.8 mm	1–1.3 mm
Hypochile length median keel	1.5–10 mm	4–8 mm
Epichile length	6–17 mm	13–17 mm
Epichile width	6–17 mm	11–18 mm
Epichile height lateral keels	0.5–2.5 mm	0.8–1.3 mm
Epichile distance median keel to apex	1–9 mm	2–4 mm
Epichile length projections on margin	0.5–1.3 mm	0.1–0.3 mm
Claw length	4–12 mm	7–11 mm
Claw thickness	0.5–3 mm	2–3 mm
Column length	10–26 mm	19–21 mm
Column width	3–7 mm	5–6 mm

Cluster analyses were performed with six characters: the three characters with the highest loadings on the first Principal Component (PC1) axis (lateral sepal length, lip length, median sepal length), the character with the highest loading on the second Principal Component (PC2) axis (height of lateral keels on hypochile) and the two characters with the highest loading on the third Principal Component (PC3) axis (length of projections on epichile margin and shape of keels on epichile). These characters are similar to the main key characters that Pfitzer & Kraenzlin (1907d) used for distinguishing the species of sect. *Fuliginosae*: size of the floral parts, length of the projections on the epichile margin and shape of the keels on the lip. Because only these six characters needed to be scored for the cluster analyses, 111 (partly incomplete) collections could be used instead of only 34 (fully intact) collections. The loading of a character is the amount of variation in morphometric space that this particular character explains. Characters with high loadings are more likely to separate groups than characters with lower loadings (Sneath & Sokal, 1973).

Dendrograms were made using the group average, squared Euclidian distance. For the combinations of the characters with the highest loadings, scatterplots were made to study the distribution of the collections in morphometric space. Cluster analyses were done with STATGRAPHICS *Plus* (version 2.1).

Additional data analysis

Data on flowering period, flower colour, habitat and elevation were collected from herbarium labels and photographs. The COOR database (© Peter van Welzen, L) and the program KORT (© Bertel Hansen, C) were used for tracing part of the geographical coordinates of the collections studied and making a distribution map. All data were superimposed on the dendrogram produced by the cluster analyses to trace possible correlations.

SPECIES DELIMITATION

Distinct species are recognised when at least two morphological characters indicate differences (Van Steenis, 1957). The development of two new morphological character (state)s is used here for the recognition of morphological species.

RESULTS

Pollen analysis

The pollinaria of the four taxa studied consisted of four very sturdy pollinia connected by prominent and massive caudicles (Plate 5.1). The pollen grains were united in tetrads, which is in accordance with Schill & Pfeiffer (1977). The morphology of the tetrads was variable, both in the arrangement and shape of the pollen grains. Variation in tetrad morphology was high both among pollinia of different specimens and within one pollinium. The pollen grains on the surface of a pollinium were slightly more angular than those in the centre. Pollenkit kept the tetrads together but tended to dissolve during preparation. The exine ornamentation of the pollen was psilate, which was also noted by Sharma (1967). Apertures were absent, which was also observed by Zavada (1990).

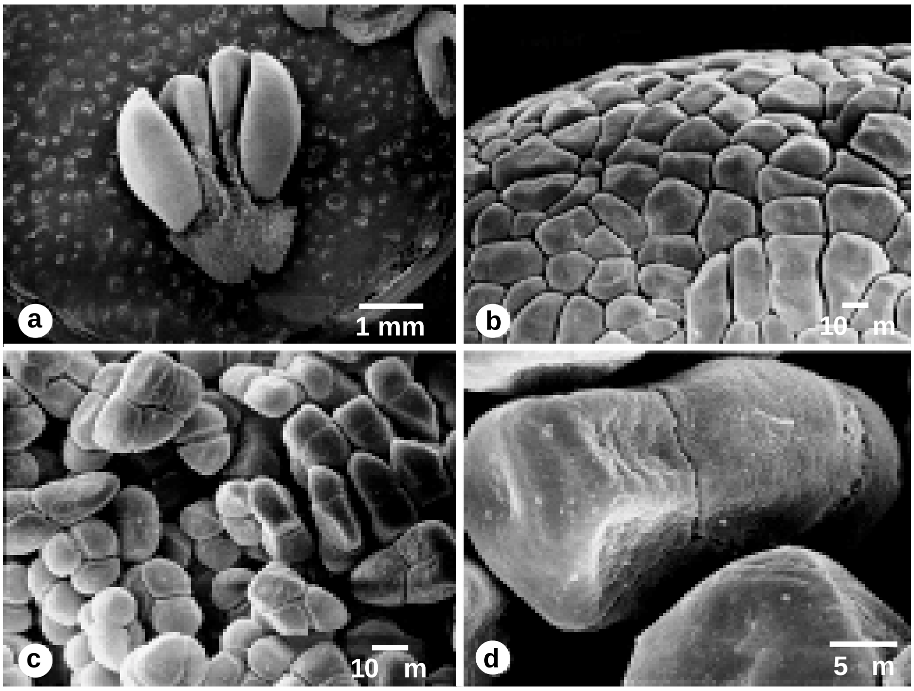


Plate 5.1. *Coelogyne fimbriata* Lindl. a. Pollinia, connected by caudicle (*Leiden cult. 22704*); b. pollinia surface (*Leiden cult. 30759*); c. tetrads (*Leiden cult. 22704*); d. pollen grains (*Leiden cult. 30759*).

Phenetic analysis

Ordination based on a principal components analysis revealed two discrete clusters of specimens (Fig. 5.1). The smallest cluster can be characterised by specimens of *C. triplicatula*. The largest cluster can be characterised by specimens of all other taxa studied in sect. *Fuliginosae*. The first three components explained 44%, 13% and 8% of the total variance in the data. Loading on the first component was contributed mainly by the following characters: lateral sepal length (96%), lip length (95%), median sepal length (93%), median sepal width (92%) and petal length (91%). Loading on the second component was contributed mainly by height of the lateral keels on the hypochile (68%), height of the median keel on the hypochile (67%) and length of the lateral lobes of the lip (66%). Loading on the third component was contributed mainly by length of the projections on the epichile margin (68%) and shape of the keels on the epichile (67%).

Five characters were scored in binary mode: keel shape (either bar-shaped or plate-like), number of sterile bracts on the inflorescence and number of nerves on lateral sepal, median sepal and petal. These characters were fundamentally different from the others, which were all morphometric. To test whether the purely morphometric characters could distinguish *C. triplicatula* from all other specimens studied, we reran the ordinations omitting all binary characters. To test excessive weighting of flower

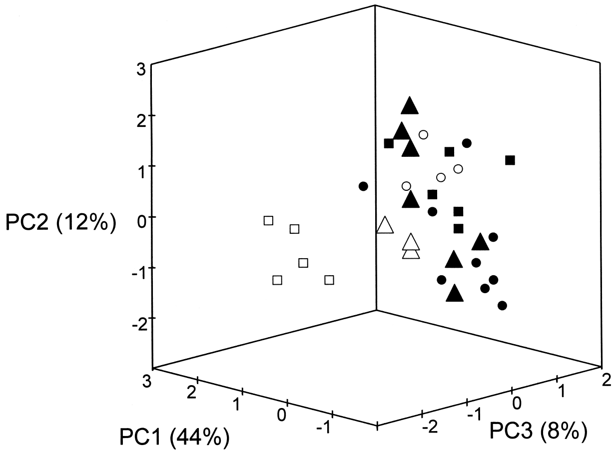


Fig. 5.1. Scatter diagram from ordination of the first three principal components based on 29 morphological characters (Table 5.1) of 34 *Coelogyne* sect. *Fuliginosae* specimens. Component 1 (PC1) separates specimens with long lips and sepals (left) from specimens with short lips and sepals (right). Component 2 (PC2) separates specimens with low lateral keels on the hypochile (above) from specimens with high keels (below). Component 3 (PC3) separates specimens with bar-shaped keels on the epichile and short projections on the epichile margin (front) from specimens with plate-like keels and long projections (background) [specimens previously assigned to *C. fimbriata* (●); *C. fuliginosa* (△); *C. ovalis* (▲); *C. padangensis* (○); *C. pallens* (■) and *C. triplicatula* (○)].

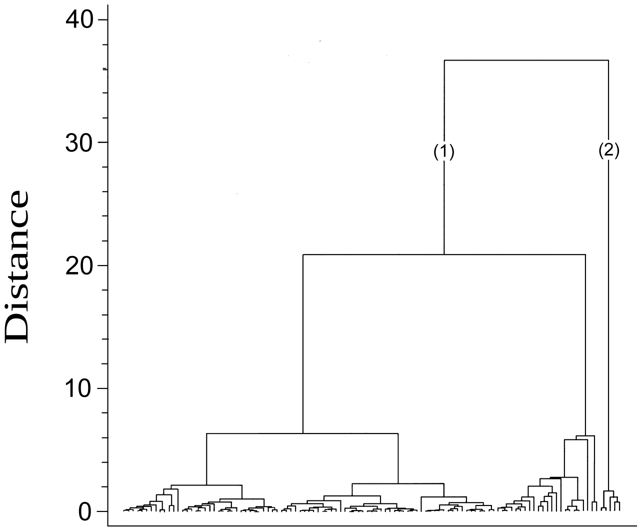


Fig. 5.2. Dendrogram of 111 *Coelogyne* sect. *Fuliginosae* specimens based on the six morphological characters with the highest loadings on PC1, PC2 and PC3 (see Materials & Methods for details of the clustering methods). Two main groups can be recognized, one with specimens with plate-like keels on the epichile and long projections on the epichile margin (1) and one with specimens with bar-shaped keels and short projections on the epichile margin (2).

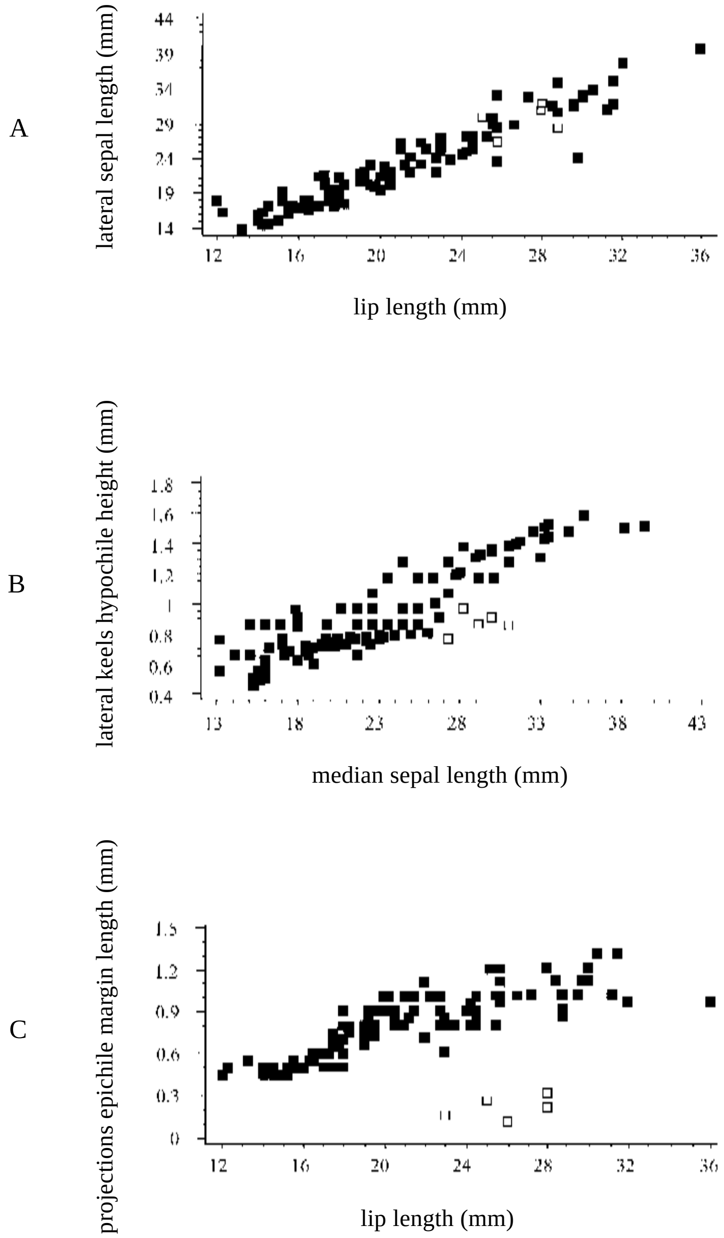


Fig. 5.3. Scatter diagrams of the morphological variation within 111 *Coelogyne* sect. *Fuliginosae* specimens. – A. Individuals of *C. triplicatula* do not form a discrete group based on their lip length. – B. Individuals of *C. triplicatula* have relatively low lateral keels on the hypochile, but there is some overlap in this character with *C. fimbriata*. – C. Individuals of *C. triplicatula* have much shorter projections on the epichile margin than the other specimens studied [*C. fimbriata* (n) and *C. triplicatula* (/)].

size variation, the ordinations were also rerun with all flower measurements converted to ratios. The results were essentially the same as with binary characters or all flower measurements included (data not shown).

Cluster analyses produced a dendrogram with two clusters (Fig. 5.2). The specimens with plate-like keels and long projections on the epichile margin cluster together (cluster 1) and show a high degree of internal dissimilarity. The specimens with bar-shaped keels and short projections on the epichile margin, identified as *C. triplicatula*, form a separate group (cluster 2), with close overall similarity.

Principal component and cluster analyses were also rerun without the specimens assigned to *C. triplicatula* to investigate if the variation between the remainder of the specimens would become more distinct. However, with omission of the specimens of *C. triplicatula*, a large morphological overlap remained among the other specimens studied (data not shown).

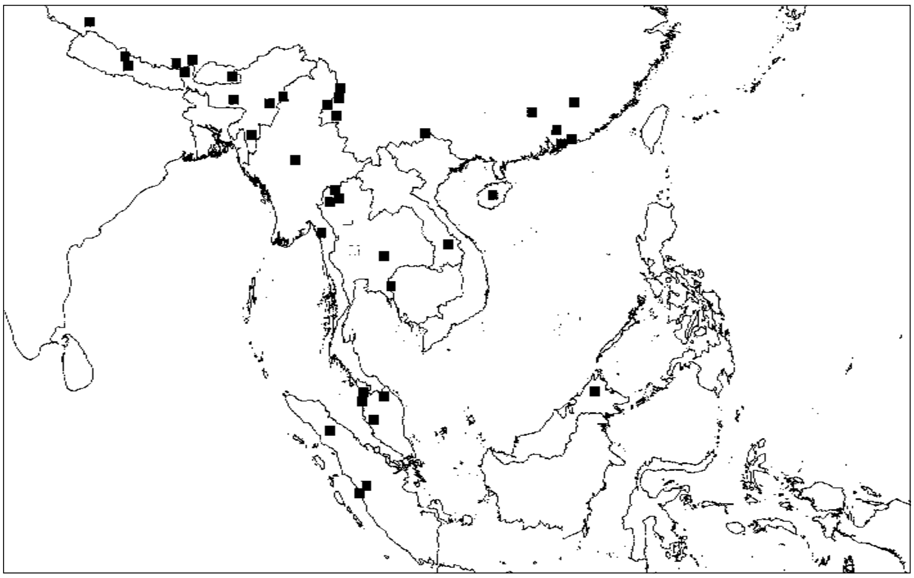
Scatter diagrams of the characters with the highest loadings showed continuous variation in most characters studied (Fig. 5.3). A diagram of lip length against lateral sepal length indicated that specimens of *C. triplicatula* tend to have relatively long lips, but they do not form a discrete group based on this character (Fig. 5.3A). A diagram of median sepal length against height of the lateral keels on the hypochile showed that *C. triplicatula* specimens have slightly lower keels when compared with larger specimens of all other taxa studied in sect. *Fuliginosae*, but there is some overlap in this character, too (Fig. 5.3B). A diagram of lip length against length of the projections on the epichile margin showed that *C. triplicatula* specimens have much shorter projections when compared with all other taxa studied (Fig. 5.3C). Of the key characters used by Pfitzer & Kraenzlin (1907d), only the length of the projections on the epichile margin and the shape of the keels seem to show an interval in the range of variation (Fig. 5.1, 5.3C).

Additional data analysis

Data on flowering period, flower colour, habitat type and elevation of the specimens studied are summarised in Table 5.2. The specimens studied were collected in an area ranging from India to China to Sumatra and Borneo (Map 5.1). The (sub)clusters from Fig. 5.2 could not be characterised by an unique flowering period, flower colour, habitat, elevation or geographical distribution.

Table 5.2. Variation in additional data observed in specimens of the two main clusters of Fig.5.2.

Character	cluster 1	cluster 2
Flowering period	January–December	September–December
Flower colour	Yellow tinged green to salmon to cream-coloured	Yellowish brown to blackish brown
Habitat	Dipterocarpaceae forest, evergreen forest, pine or oak forest, on rock, loam, limestone or dry sandy soils	Unknown
Elevation	50–3300 m	Unknown



Map 5.1. Distribution of *Coelogyne fimbriata* Lindl. (n) and *C. triplicatula* Rchb.f. (/).

TAXONOMIC IMPLICATIONS

SEM studies of the pollinaria of specimens formerly identified as *C. fimbriata, C. fuliginosa* and *C. ovalis* revealed no clear characters for species discrimination. Morphology of the pollinaria, pollinia, pollen grains and pollen seems to be constant for all specimens studied. Morphology of the tetrads appears to be too variable for use as a tool for species identification.

Phenetic analyses of specimens formerly identified as *C. fimbriata, C. fuliginosa, C. ovalis, C. padangensis, C. pallens* and *C. triplicatula* revealed no differences other than the length of the projections on the epichile margin and the shape of the keels on the epichile. No clear differences in other characters could be detected between the different clusters in morphometric space. Cluster 2 of Fig. 5.2 is defined by bar-shaped keels on the epichile and short projections on the epichile margin. All individuals are assigned to one species: *C. triplicatula.* Cluster 1 is defined by plate-like keels on the epichile and long projections on the epichile margin. The specimens of cluster 1 are variable in both vegetative and floral characters, in particular in size of leaves, pseudobulbs and flowers, shape of the lip and colour(pattern)s of the sepals, petals and the lip. The lip of one of the smallest flowers can be virtually identical in shape with the lip of one of the largest flowers. Equal-sized flowers can differ very much in the shape of the lip or even also in the shape of the lateral lobes or the colour(pattern). Due to this enormous variability, even in lower-rank subgroups, an objective subdivision in taxa in this group cannot be made. Unique character (state)s for the subgroups in the complex were not found and therefore all subgroups in this complex have to be reduced to one species: *C. fimbriata,* with high variability in size, shape and colour of both vegetative and floral parts.

DISCUSSION

A first explanation for the large overlap in morphological characters in *C. fimbriata* might be the large impact of the microclimate on shape and size of both vegetative and floral characters. We noticed for instance that cultivated specimens usually had larger leaves, pseudobulbs and flowers than specimens collected in the wild.

Hybridisation between once separated species in this complex might be a second explanation. Hybridisation within the orchid family is not rare, possibly because reproductive isolation did not evolve. Hybrids could not be detected with the morphological methods used in this study. Molecular population methods such as RAPD's, AFLP's, chromosome counts and allozyme studies could be used for identifying hybrids and can possibly give information whether *C. fimbriata* is really one species or consists of several species and/or hybrids. For these studies more living plants need to be sampled from throughout the distribution area. Detailed studies on the ecology (e.g. pollinators) would also improve species delimitation.

SYSTEMATIC TREATMENT

Coelogyne section Fuliginosae

Coelogyne Lindl. sect. *Fuliginosae* Pfitzer & Kraenzl. in Engl., Pflanzenr. 32 (1907) 33; Butzin, Willdenowia 7 (1974) 249; Seidenf., Dansk Bot. Ark. 29 (1975) 13; Pradhan, Indian Orchids: Guide Identif. & Cult. 2 (1979) 704; Butzin in Schltr., Orchideeen 1A (1992) 923; De Vogel, Proc. 14th World Orch. Conf. (1994) 203. — Type species: *Coelogyne fuliginosa* Lindl. ex Hook.f.

Creeping, small-sized epiphytes and lithophytes. Roots attached on the rhizome at or between the nodes. Rhizome creeping; rhizome scales 5–14 between the pseudobulbs, eroding after one growth season, (slightly) imbricate, ovate to ovate-oblong; apex obtuse to acute, sometimes (slightly) mucronate; margin often dark. *Pseudobulbs* oblong to ovate-oblong to fusiform when fresh, oblong to ovate-oblong to terete when dried, slightly flattened, smooth to obtusely angulate and shiny when fresh, obtusely angulate when dried, 2-leafed. *Leaves* thin, coriaceous. Petiole orbicular to ovate in cross section, channelled, clasping the peduncle. Blade ovate-oblong, lanceolate, ovate-lanceolate to linear-lanceolate, slightly striate, smooth; apex acute to long-acuminate, sometimes mucronate; main nerves 5–9. *Inflorescence* suberect, hysteranthous, 1–5-flowered, glabrous. Peduncle orbicular to ovoid in cross section, broadening to the apex; sterile bracts covering the peduncle base 1–6, ovate to ovate-oblong; apex acute to mucronate. Rhachis suberect, slightly zigzag; internodes slightly curved, each with a swollen base bearing a flower. *Floral bracts* deciduous, ovate to ovate-oblong; apex acute, occasionally mucronate; nerves 16 to numerous. *Flowers* widely open, opening in succession, finely papillose. Pedicel ovate in cross section, (slightly) twisted; ovary slightly twisted, 6-ribbed. *Median sepal* ovate-oblong to lanceolate to ovate-lanceolate; apex acute to slightly mucronate; nerves 5–13, midrib rounded, not prominent. *Lateral sepals* sometimes oblique, ovate-oblong to lanceolate; apex acute to mucronate; nerves 5–9, midrib rounded, not prominent. *Petals* not to slightly recurved, with (a)centric midrib, linear; apex acute to slightly obtuse; nerves 1–3, midrib not prominent. *Lip* immobile, boat-shaped, 3-lobed, when flattened pandurate in outline, nerves 13–22.

Hypochile broadly attached, slightly saccate at the base; lateral lobes erect, in front obtuse to rounded to acute, extending in front, front margin not to very fimbriate, with shallowly to deeply rounded sinus; keels 3, starting at the base of the lip, plate-like, smooth to heavily dentate and sometimes undulating at the base, towards the apex of the epichile smooth and undulating, papillate, the lateral keels towards the apex descending, near the apex ascending, the median keel developed on the hypochile only, ending abruptly, sometimes abruptly descending. *Epichile* convex, when flattened ovate to ovate-oblong, with a broad, short claw; base narrow to broadly attached; apex rounded to obtuse, sometimes emarginate; tip absent to acute; margin slightly to heavily fimbriate, recurved; keels 2, a continuation of the keels on the hypochile, sometimes up to 4, plate-like and undulating (*C. fimbriata)* or swollen and bar-shaped (*C. triplicatula)*, ending abruptly or sometimes descending near the apex of the epichile, papillate. *Column* curved to the front, when flattened spathulate; hood with winged margins, widest below the apex, gradually narrowing to the base, its apical margin irregularly dentate. *Anther* broadly bell-shaped in outline, near the place of attachment with an obtuse to rounded projection. *Pollinia* four, flattened to one side, obliquely elliptic, each with a shallow to deep ear-shaped depression, all connate at the apex by a caudicle; caudicle flattened, rectangular in outline, granular. *Stigma* cup-shaped, semi-orbicular with elevated, recurved margin; apex obtuse to rounded; rostellum semi-orbicular to triangular with incurved lateral margins and a longitudinal ridge. *Fruit* body ellipsoid, beaked by the persistent column and remnants of the perianth; valvae keeled, keels plate-like; juga band-like with a pronounced longitudinal ridge.

Distribution — Nepal, Bhutan, India, China, Burma, Laos, Vietnam, Cambodia, Thailand, Peninsular Malaysia, Sumatra and Borneo.

Habitat & Ecology — Epiphytes or lithophytes in lowland to montane forests, sometimes also in secondary vegetations, in the range of 50–3300 m.

Cultivation — Only *C. fimbriata* is widely cultivated.

Artificial hybrids — One cross was registered so far: *Amber*, a hybrid between *C. speciosa* and *C. ovalis* (synonym of *C. fimbriata*), produced by P. Spence (Royal Horticultural Society, 1998).

KEY TO THE SPECIES

1a. Keels on the lip completely plate-like; projections on the lip margin longer than 0.5 mm . . . . **1. C. fimbriata**

b. Keels on the lip partly bar-shaped; projections on the lip margin shorter than 0.3 mm . . . . **2. C. triplicatula**

1. Coelogyne fimbriata Lindl. — Fig. 5.4, Map 5.1, Plate 5.2

Coelogyne fimbriata Lindl., Bot. Reg. 11 (1827) t. 868; Hook. f., Fl. Brit. India 5 (1890) 836; Grant, Orch. Burma (1895) 172; Schltr., Orchideen (1915) 137; Seidenf. & Smitinand, Orch. Thail. 4, 2 (1965) 752, f. 81a–b; S.Y. Hu, Quart. J. Taiwan Mus. 25 (1971) 222, f. 8, 9f; Seidenf., Dansk Bot. Ark. 29 (1975) 15, f. 4; Bechtel, P.J. Cribb & Launert, Orch. Atl. (1980) 101; Seidenf. & J.J. Wood, Orchids Penins. Malaysia and Singapore (1992) 207, f. 87d–e. — *Pleione ovalis* auct. non Lindl.: Kuntze, Rev. Gen. Pl. (1891) 680. — Type: *J.D. Parks* (?/7/1824) (holo K; iso C, P), South China.

Coelogyne ovalis Lindl., Bot. Reg. 24 (1838) 91; Summerh., Bot. Mag. 155 (1929) t. 9255; Seidenf. & Smitinand, Orch. Thail. 2, 1 (1959) 109, 111. — *Pleione fimbriata* auct. non Lindl.: Kuntze, Rev. Gen. Pl. (1891) 680. — Type: *Wallich 1957* p.p. (holo K).

Coelogyne fuliginosa Lindl. ex Hook.f., Bot. Mag. 75 (1849) pl. 4440; Lindl. in Lodd. Cat. 6 (1844) 146, nom. nud.; Miq., Choix Pl. Buitenzorg (1864) t. 25; Hook.f., Fl. Brit. India 5 (1890) 836; Grant, Orch. Burma (1895) 173; Cogn. & Gooss., Dict. Icon. Orch. (1903) 161; Pfitzer & Kraenzl. in Engl., Pflanzenr. 32 (1907) 34; Schltr., Orchideen (1915) 138; Backer & Bakh.f., Bekn. Fl. Java 3, 12 (1952) 128; Fl. Java 3 (1968) 280; Seidenf., Dansk Bot. Ark. 29, 4 (1975) 19, f. 5. — *Pleione fuliginosa* (Lindl.) Kuntze, Rev. Gen. Pl. (1891) 680. — Type: *Loddige's collectors* (?/?/1838) (holo K), India.

Coelogyne pilosissima Planch., Hort. Donat. (1854) 104. — Type: not designated.

Coelogyne longeciliata Teijsm. & Binn., Nat. Tijdschr. Ned.-Indië 27 (1864) 16; Pfitzer & Kraenzl. in Engl., Pflanzenr. 32 (1907) 38. — Type: *Lobb s.n.* (holo ?, not seen).

Coelogyne ovalis var. *latifolia* Hook.f., Fl. Brit. India 5 (1890) 836. — Type: *Clarke s.n.* (holo ?, not seen), Munnipore on Kohima.

Broughtonia linearis Wall. ex Hook.f., Fl. Brit. India 5 (1890) 836. — Type: not designated.

Coelogyne pallens Ridl., J. Straits Branch Roy. Asiat. Soc. 39 (1903) 81; Seidenf., Dansk Bot. Ark. 29, 4 (1975) 13, f. 3, pl. 1a; Seidenf. & J.J. Wood, Orchids Penins. Malaysia and Singapore (1992) 205, f. 87a–c. — Type: *Curtis s.n.* (holo SING?, not seen), Perak, Taiping Hills.

Coelogyne fimbriata var. *annamica* Finet, Notul. Syst. (Paris) 1 (1909) 255; Gagnep., Fl. Gén. Indo-Chine 6 (1933) 309. — Type: *Eberhardt s.n.* (holo P?, not seen).

Coelogyne chrysotropis Schltr., Orchis 5 (1910) 58, pl. 7c; J.J. Sm., Feddes Repert. 32 (1933) 162. — Type: *Schlechter s.n.* (1910) (holo B†), Sumatra.

Coelogyne padangensis J.J. Sm. & Schltr. in Engl., Bot. Jahrb. Syst. 104 (1911) 6; J.J. Sm., Rep. Spec. Beih. 32 (1933) 166. — Type: *Schlechter 15950* (holo B†), Sumatra, Pariaman.

Coelogyne laotica Gagnep., Bull. Mus. Hist. Nat. (Paris) 2 (1930) 425; Fl. Gén. Indo-Chine 6 (1933) 308, 311, f. 26: 9–16; Seidenf. & Smitinand, Orch. Thail. 2, 1 (1959) 112; A.D. Kerr, Nat. Hist. Bull. Siam Soc. 23, 1–2 (1969) 189. — Type: *Thorel s.n.* (holo P?, not seen), Laos.

Coelogyne xerophyta Hand.-Mazz., Symb. Sin. (1936) 1346, 1353, f. 42, no. 1, 2. — Type: *Handel-Mazzetti 8457* (holo W), China, Yunnan.

Coelogyne leungiana S.Y. Hu, Quart. J. Taiwan Mus. 25 (1971) 223. — Type: *S.Y. Hu 9089* (holo AMES, not seen), Hongkong.

Coelogyne primulina Barretto, Orchid Rev. 98, 1156 (1990) 39. — Type: *G. Barretto 315* (holo K; iso HK), Hongkong.

Coelogyne arunachalensis H.J. Chowdhery & G.D. Pal, Nord. J. Bot. 17, 4 (1997) 369. — Type: *G.D. Pal 1790* (holo CAL, not seen), India, Arunachal Pradesh.

Roots 0.5–2 mm diam. Rhizome 2–9 mm thick; rhizome scales 5–14 between the pseudobulbs. *Pseudobulbs* 1.5–11.5 cm apart, 1.6–9.5 by 0.3–2.2 mm. Petiole 2–26 mm long. Blade 3.3–19 by 1–4.4 cm. *Inflorescence* 1–5-flowered. Peduncle 5–53 mm long; sterile bracts 1–6, covering 2/3 up to the entire peduncle. Rhachis up to 11 cm long; internodes 9–22 by 1–2 mm. *Floral bracts* 17–36 by 6–16 mm. Pedicel 5–20 by 1–2 mm; ovary 3–11 by 1–4 mm. *Median sepal* ovate-oblong to lanceolate to ovate-lanceolate, 13–40 by 4–13 mm, nerves 5–13. *Lateral sepals* ovate-oblong to lanceolate, 14–37 by 4–12 mm. *Petals* not to slightly recurved, 13–33 by 1–3 mm. *Lip* 12–36 by 12–25 mm. *Hypochile* when flattened 9–23 by 12–25 mm; base attached

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Plate 5.2. *Coelogyne fimbriata* Lindl. – a. *Leiden cult. 22704*, Thailand. Photograph C.G. Koops. – b. *Leiden cult. 30756*, India. Photograph A. Vogel. – c. *Collection D.A. Clayton*, Peninsular Malaysia. Photograph D.A. Clayton. – d. *Collection J.B. Comber*, Sumatra. Photograph J.B. Comber.

a. *Coelogyne fimbriata* (Thailand)

b. *Coelogyne fimbriata* (India)

c. *Coelogyne fimbriata* (Peninsular Malaysia)

d. *Coelogyne fimbriata* (Sumatra)

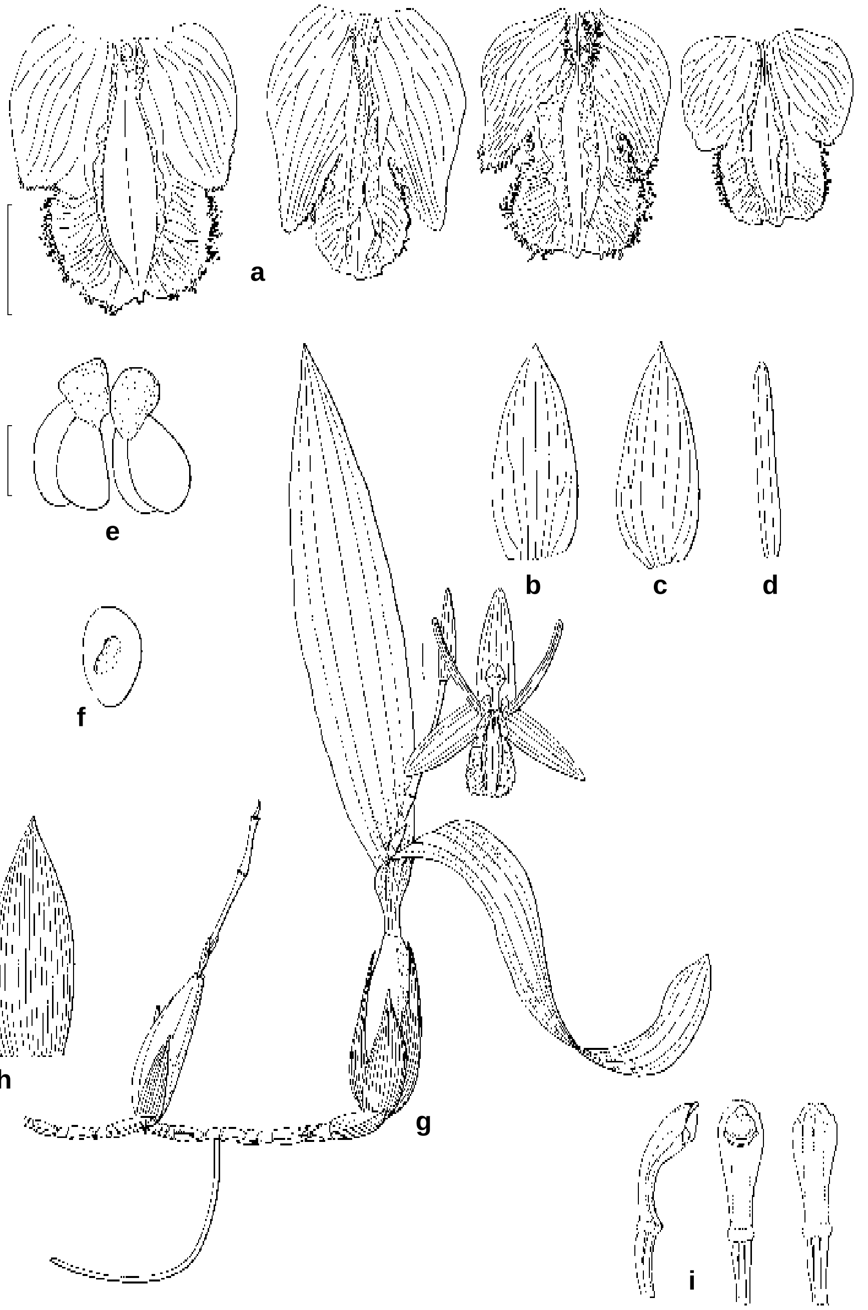

Fig. 5.4. *Coelogyne fimbriata* Lindl. a. Lip ornamentation (from left to right: *Leiden cult. 30756, Comber 1069, Henry 13539, Leiden cult. 23320*); b. median sepal; c. lateral sepal; d. petal (*Leiden cult. 21640*); e. pollinarium; f. pollinium; g. habit (*Leiden cult. 30756*); h. floral bract *(Rock 7707)*; i. column, front, lateral and rear view (*Leiden cult. 23320*). — Scale bars: 1 cm (a–d, g–i); 1 mm (e, f).

over 2–7 mm; lateral lobes in front obtuse to rounded to acute, extending 1–8 mm in front; lateral keels 0.4–1.6 mm high at the base; median keel developed on basal (and sometimes also apical) half of the hypochile, 0.3–1.8 mm high at base. *Epichile* 6–17 by 6–17 mm; claw 0.5–3 mm thick; base attached over 4–12 mm; margin with projections 0.5–1.3 mm long; keels plate-like, undulating, 0.5–2.5 mm high, ending 1–9 mm from the apex of the epichile. *Column* 10–26 by 3–7 mm. *Anther* 3–4 by 2–5 mm. *Pollinia* 1–2 by 1–1.5 mm; caudicle 1–1.5 by 1–2 mm. *Stigma* 1–3 by 3–5 mm; rostellum 2–3 by 2–5 mm. *Fruit* body 18–23 by 7–10 mm; valvae keels 3.5 mm high; juga with a pronounced longitudinal ridge 2 mm high.

Distribution — Nepal, Bhutan, India, China, Burma, Laos, Vietnam, Cambodia, Thailand, Peninsular Malaysia, Sumatra and Borneo.

Habitat & Ecology — Epiphyte or lithophyte in moist upper Dipterocarp, evergreen, pine or oak forest on slopes, sometimes on rocks, on loam, limestone or dry sandy soils, often in the shade. Also recorded as a common pioneer orchid on tree branches and rocks (Sparrow, 1996a, b). Elevation 50–3300 m, with highest abundancy around 1500 m (Sparrow, 1995). Flowering the whole year round (in greenhouse as well).

Notes — 1. Pseudobulb dull to bright light green, scales straw-coloured with brown margins. Leaves green to light green. Floral bracts straw-coloured tinged green, with brown margins. Flower colours are very variable. Sepals, petals and ovary usually pale dull yellow tinged green to salmon, petals sometimes with a small orange spot at the base. Lip often cream-coloured, on the lateral lobes inside with fine brown lines which shimmer through on the outside, some lines continuing on the epichile and there with lighter fine branched brown lines; base of the lip sometimes with a red-brown blotch; plate of the hypochile often with three brown lines between the usually brown crested keels, on the epichile one or three brown lines between the keels; the outside of the lip usually with two brown lines continuing from the hypochile on the epichile and there with lighter fine branched brown lines. Column yellow or cream coloured, brownish-orange at the base; apex of the hood often orange, sometimes tinged brown. Anther orange-yellow. Pollinia orange-yellow. Smell mushroom-like.

2. The epithet *fimbriata* refers to the fringed margins of the lip.

3. Seidenfaden (1975) suggested that *C. leungiana* may be a peloric form of *C. fimbriata*. The specimens he studied had linear instead of ovate-oblong petals, the lip lacked lateral lobes and the margin was entire, not fimbriate. However, we observed flowers with partly or entirely normally developed lips and more or less linear petals as well on a cutting of the plant from which the type was taken. Barretto (1990) observed that some flowers have in addition “abnormalities” such as two anthers, a broadly distended rostellum, or a stigma bearing a swollen lip-like rim. We consider *C. leungiana* a monstrous form of *C. fimbriata*.

2. Coelogyne triplicatula Rchb.f. — Fig. 5.5, Map 5.1, Plate 5.2

Coelogyne triplicatula Rchb.f., Bot. Zeitung (Berlin) (1864) 415; Xenia Orchid 2 (1870) 159, t. 166; Pfitzer & Kraenzl. in Engl., Pflanzenr. 22 (1907) 36. — Type: *Parish s.n.* (holo K), Moulmein.

Roots 0.5–2.5 mm diam. Rhizome 2–5 mm thick; rhizome scales 5–8 between the pseudobulbs. *Pseudobulbs* 1.5–3.5 cm apart, 2.8–6.3 by 1–1.7 cm. Petiole 5–8 mm long. Blade 6.4–11.4 by 1.4–3.8 cm. *Inflorescence* 3-flowered. Peduncle 33–47 mm

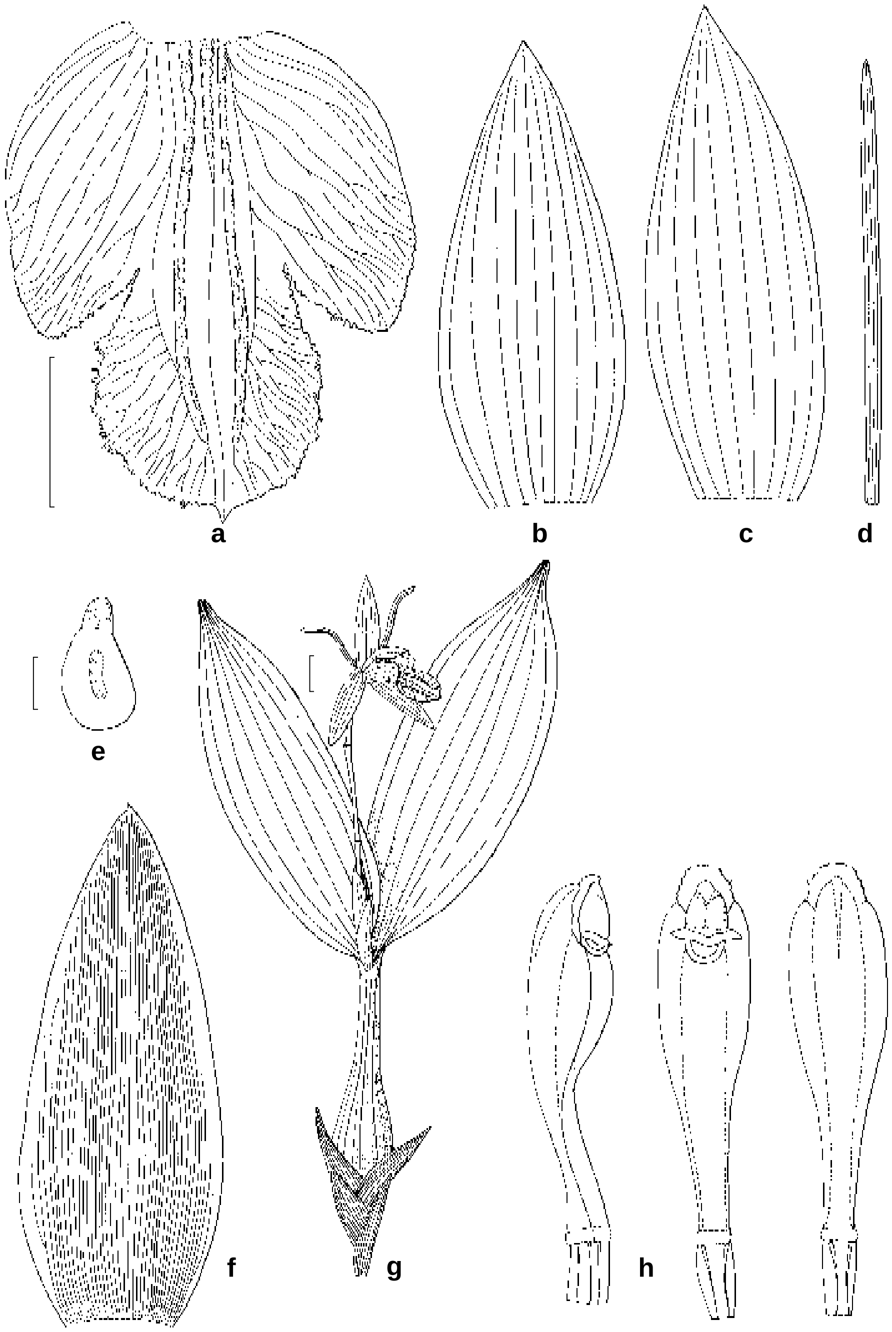

Fig. 5.5. *Coelogyne triplicatula* Rchb.f. a. Lip ornamentation; b. median sepal; c. lateral sepal; d. petal; e. pollinium [*Van Imschoot s.n.* (1889)]; f. floral bract [*Glasnevin s.n.* (8/11/1904)]; g. habit; h. column, front, lateral and rear view [*Van Imschoot s.n.* (1889)]. — Scale bars: 1 cm (a–d, f–h); 1 mm (e).

long; sterile bracts 1 or 2, covering 3/4 of peduncle. Rhachis up to 7.4 cm long; internodes 25–30 by 1–1.5 mm. *Floral bracts* c. 40 by 15 mm. *Pedicel* 13–18 by 1–1.5 mm; ovary 7–8 by 2–3 mm. *Median sepal* ovate-oblong, 27–31 by 9–17 mm; nerves 9–11. *Lateral sepals* ovate-oblong, 26–32 by 9–11 mm. *Petals* slightly recurved, 25–34 by 1–3 mm. *Lip* 25–29 by 19–29 mm. *Hypochile* when flattened 15–21 by 19–29 mm; base attached over 3–5 mm; lateral lobes in front obtuse; extending 4–9 mm in front; lateral keels 0.7–1 mm high at the base, median keel developed on the basal half of the hypochile, 1–1.3 mm high at the base. *Epichile* 13–17 by 11–18 mm; claw 2–3 mm thick; base attached over 7–11 mm; margin with projections 0.1–0.3 mm long; keels swollen and bar-shaped, sometimes slightly longitudinally channelled, 0.8–1.3 mm high, ending 2–4 mm from the apex of the epichile. *Column* 19–21 by 5–6 mm. *Anther* 4–4.5 by 3–4.5 mm. *Pollinia* c. 3 by 2 mm; caudicle not seen. *Stigma* 2–3 by 2–2.5 mm; rostellum 2–3 by 3–4 mm. *Fruit* not seen.

Distribution — Burma (Moulmein).

Habitat & Ecology — Lithophyte. Elevation unknown. Flowering in September (October, December in greenhouse).

Notes — 1. Sepals and petals yellowish brown, labellum blackish brown on midlobe, side lobes horizontally streaked with fine dark brown lines.

2. The epithet *triplicatula* (three-folded) refers to the three keels on the lip.

3. This species is very similar to large specimens of *C. fimbriata*. The main differences are the much shorter projections on the epichile margin and the shape of the keels on the epichile: bar-shaped and swollen instead of plate-like and undulating, as in *C. fimbriata*.

INSUFFICIENTLY KNOWN VARIETY

3. **Coelogyne fimbriata** var. **acuminata** Regel

Coelogyne fimbriata var. *acuminata* Regel, Linnaea 12 (1856) 370. — Type: not designated.

Note — According to the type description (Von Regel, 1856) this variety differs in having acuminate sepals and a lip with an acute midlobe, instead of acute sepals and a midlobe with round to obtuse, sometimes emarginate apex. There is no type specimen assigned and no collections were available for this study.

EXCLUDED SPECIES

4. *Coelogyne micrantha* Lindl., Gard. Chron. (1855) 173; Hook.f., Fl. Brit. India 5 (1890) 836. — Type: *Dick s.n.* (holo K), India.

Note — A lip with smooth margin and three or more equal-sized keels is not present in other species of sect. *Fuliginosae,* hence it is concluded that this species fits better in sect. *Micranthae*.

5. *Coelogyne schilleriana* Rchb.f., Berliner Allg. Gartenzeitung 26 (1858) 189; Hook.f., Fl. Brit. India 5 (1890) 834. — Type: *Veitch s.n.* (holo W), India, Moulmein.

Note — In our view, *C. schilleriana* is better placed in a section of its own, because the pseudobulbs and lip of this species differ markedly in shape from those of the species presently recognised in sect. *Fuliginosae*. The pseudobulbs are obpyriform and clustered instead of oblong to lanceolate and widely spaced on the rhizome. The lip has a much broader epichile with three equal-sized keels instead of a short median keel and two longer lateral keels. The colour pattern of the lip is deviating, too: irregularly yellow-blotched and spotted with orange-red instead of yellowish-green to salmon to yellowish-brown to cream-coloured with fine brown lines.

6. *Coelogyne treutleri* Hook.f., Fl. Brit. India 5 (1890) 837. — Type: *Treutler s.n.* (holo K), India, Sikkim Himalaya.

Note — A lip with smooth margin and three or more equal-sized keels is not present in other species of sect. *Fuliginosae*, hence it is concluded that this species fits better in sect. *Micranthae*.

ACKNOWLEDGEMENTS

The authors would like to thank the directors and curators of the herbaria mentioned under Material and Methods for the loan of dried specimens, spirit collections and living material; Mrs. G. Barretto for sending us living material; André Schuiteman for his help and comments; Jan van Os for the inking of the illustrations; Art Vogel and colleagues from the Hortus Botanicus Leiden for obtaining and cultivating many living plants of the *C. fimbriata* complex; Raymond van der Ham, Bertie Joan van Heuven and Saskia Bodegom for help with the pollen analyses; the keepers and directors of the Botanic Gardens in Meise and Vienna for the supply of cuttings of specimens in their collections and the Leids Universiteits Fonds and Alberta M.W. Mennega Stichting for financing the colour plates.

IDENTIFICATION LIST

Collections used for the principal component analysis are in **bold** type (s.n. collections excluded). Specimens used for the pollen analyses are indicated by (p).

1. *C. fimbriata* 2. *C. triplicatula*

Abraham cult. 3160: 1 — Allen **27/1/1957: 1** — Anonymous 39961: 1; 40130: 1; 305480: 1; ?/?/1872: 1; 17/12/1915: 1; ?/1/1920: 1.

Balston **1/10/1912: 1** — Barretto 221: 1; 222: 1; 315: 1; 413: 1; 48782: 1 — Barriger **785: 1** — Berkeley 25/11/1882: 1 — Berlin cult. 7778: 1; 9326: 1; 9346: 1; 10899: 1; 16951: 1; 17044: 1; 17045: 1; 17046: 1; 23590: 1; 24114: 1; 24258: 1; (Prag) 27506: 1; (Cubr.) 28714: 1 — Bogor cult. **B146 : 1**; 203: 1; F203: 1; (Smith) 209: 1; **(Piepers) 485: 1** — Bor 6608: 1 — Burkidge cult. **26/1/1886: 1** — Burkill & Haniff 12708: 1 — Butterfield cult. 42194: 1 — Buxbaum cult. 284: 1.

Carr 16/11/1934: 1 — Champion 527: 1 — Charoenphol, Larsen & Warncke 4294: 1 — Clarke 25145: 1; **41382: 1** — Clayton ?/1/1997: 1 — Cogniaux 20/8/1897: 1 — Comber **1069: 1**.

Dullupchan 113: 1.

Ehrendorf 9/10/1954: 1.

Falconer 1021: 1 — Forrest 26132: 1; 26147: 1.

Gamble 4017A: 1; **9981: 1**; 23142: 1 — Glasgow cult. 29/10/1920: 1 — Glasnevin cult. 26/11/1894: 1; 8/11/1904: 2 — Godefroy cult. ?/12/1891: 2 — Gravendeel cult. 16/10/1996: 1 — Griffith 5158: 1 — Groeneveldt cult. 595: 1.

Hallier 3/11/1892: 1 — Hance 401: 1; (Lamont) 401A: 1; 401B: 1; **(Faber) ?/9/1883: 1** — Handel-Mazzetti 8457: 1; 9789: 1 — Haniff 9057: 1 — Haniff & Nur **2324: 1** — Hegel ?/11/1848: 1 — Henry **13539: 1**; 13598: 1 — Hooker 127: 1 — How 73235: 1 — Hu 6065: 1; **6176: 1**; 11094: 1; 12454: 1.

Inayat **24100: 1**.

Kadoorie cult. (Barretto 301) 53014: 1; (Barretto 315) 55624: 1 — Keke **1143: 1** — Kerr 200A: 1; 200B: 1; 200C: 1; 0755: 1; **0762: 1** — Kew cult. ?/11/1886: 1; ?/11/1887: 1; ?/11/1888: 1; (Warre) ?/10/1897: 1; ?/2/1920: 1; (Elwes) 247-1922: 1; 14/10/1926: 1; (Hinde) 175-1926: 1; 3-1928: 1; 215-29: 1; 12/10/1931: 1; 310-1948: 1; 636-1954: 1; 638-54.63802: 1; (Matthews 170) 705-6: 1; 705-63.70538: 1; (Rittershauser) 58234: 1 — Kienast cult. ?/12/1895: 1; ?/11/1889: 1 — King ?/5/1874: 1.

Lamont 755: 1 — Latif 6: 1 — Lau 2486: 1; 4667: 1 — Lindley 55: 1 — Leiden cult. (hortus VU Amsterdam) 21405: 1; 21464: 1; 21640: 1; 21764: 1; 21786: 1; (van Vliet) 21789: 1; 22704: 1 (p); 22725: 1 (p); 22767: 1; 23320: 1; 27294: 1; (de Vogel) 27675b: 1; 30723: 1; 30729: 1 (p); 30756: 1; 30759: 1 (p); 30767: 1; 920836: 1; (Barretto) 970702: 1; (Barretto) 970703: 1; 970704: 1 — Loddige's collectors ?/?/1838: 1 — Low cult. ?/10/1894: 1 — Ludlow & Sherriff **1048: 1**.

Macpherson 6/9/1909: 1 — Meise cult. 1907-3824: 1; 30/8/1912: 1; 3/10/1912: 1; 1974-0170: 1 — Metcalf 18045: 1; 18328: 1 — Moore ?/12/1885: 1.

Pal 1790: 1 — Pantling 19: 1 — Parish 118: 1; ?/?/1863: 2 — Parkinson 6404: 2 — Parks (?/7/1824): 1 — Parry 423: 1; 435: 1 — Peradeniya cult. (Jayaweera) 1167: 1 — Polunin, Sykes & Williams 5735: 1 — Prain's collector 117: 1; 173: 1.

Ridley ?/12/1892: 1 — Robinson & Kloss **6085: 1** — Rock 7158: 1; **7707: 1**.

Schlechter 15950: 1 — Shi 15116: 1 — Smith 29: 1 — Stainton **8480: 1**; 8775: 1 — Stainton, Sykes & Williams 8962: 1 — Swinhoe **90: 1**.

Taam 1750: 1 — Ting & Shih 1046: 1 — Tsai 54159: 1; 58531: 1; **58732: 1** — Tsang 24274: 1; 25681: 1; 25910: 1.

Van Beusekom & Phengklai **2466: 1** — Van Imschoot ?/10/1889: 2; ?/11/1890: 1; 29/6/1893: 1; ?/?/1896: 2 — Vienna cult. 18/8/1958: 1.

Wai Tak 8737: 1 — Wallich 1957: 1 — Wang 34701: 1; 36128: 1; 36496: 1; 40130: 1 — Wilford 101: 1 — Wilson 101: 1 — Wood 862: 1.

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Accepted species are in roman type, synonyms, excluded and insufficiently known species are in *italics*. Numbers refer to the species numbers as given in the text.

Chapter 6

REVISION OF COELOGYNE SECTION VERRUCOSAE (ORCHIDACEAE): A NEW SECTIONAL DELIMITATION BASED ON MORPHOLOGICAL AND MOLECULAR EVIDENCE

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SUMMARY

Section *Verrucosae* Pfitzer & Kraenzl. of the genus *Coelogyne* Lindl. is revised using morphological and molecular data. Eight species are recognised, including two new ones (*C. marthae* and *C. verrucosa*). One name is reduced to synonymy. Four species formerly included by several authors in sect. *Verrucosae* (*C. brachyptera, C. papillosa, C. parishii* and *C. virescens*) are excluded. A total evidence analysis of morphological characters and ITS and *matK* sequence data supports the monophyly of the section as here recognised. *Coelogyne virescens* (sect. *Brachypterae*) is identified as nearest neighbour to the species of sect. *Verrucosae*. The number of sterile bracts on the rhachis and the shape of the ornamentation on the epichile appear to be phylogenetically informative characters, in contrast with the inflorescence type, ovary indumentum and number of keels on the hypochile.

Key words: *Coelogyne* sect. *Verrucosae*, *matK*, orchids, phylogeny, ribosomal ITS, systematics.

INTRODUCTION

The orchid genus *Coelogyne* Lindl. comprises approximately 200 species, distributed from southeast Asia to the south-western Pacific Islands. Pfitzer & Kraenzlin (1907d), in their revision of subtribe Coelogyninae, subdivided the genus into 14 different sections, among which is sect. *Verrucosae*. All later authors maintained this section. According to Pfitzer & Kraenzlin sect. *Verrucosae* consists of plants with large pseudobulbs and leaves, with very large flowers having an unusual combination of colours (green with black markings), and a lip with keels and a mass of papillae. In their key to the sections of *Coelogyne* they state in addition that sect. *Verrucosae* is distinguished from sect. *Tomentosae* by a glabrous rhachis, peduncle (probably pedicel is intended), and ovary. As a matter of fact, not all species originally included in sect. *Verrucosae* by Pfitzer & Kraenzlin have green flowers with black markings, and the rhachis, pedicel, and ovary are hairy in some taxa. The size of the flowers and the vegetative parts vary considerably as well.

In this study the following combination of character states was found to be diagnostic for sect. *Verrucosae*: pseudobulbs rounded to strongly flattened, 2-leafed; rhachis at the base with a few sterile bracts, but no such bracts at the base of the peduncle; scattered minute scale-like hairs on rhachis, pedicel, ovary, and the outside of the sepals and petals; flowers opening simultaneously; three keels on the hypochile; ornamentation on the midlobe of the lip consisting of various kinds of warts or teeth; base of column in front forming a very small to pronounced column foot.

Pfitzer & Kraenzlin (1907a) listed a total of 10 species in sect. *Verrucosae*: *C. asperata* Lindl., *C. brachyptera* Rchb.f., *C. densiflora* Ridl., *C. edelfeldtii* F. Muell. & Kraenzl., *C. mayeriana* Rchb.f., *C. pandurata* Lindl., *C. papillosa* Ridl., *C. parishii* Hook., *C. peltastes* Rchb.f., and *C. pustulosa* Ridl. They failed to designate a type species. We have here chosen *C. pandurata* Lindl. as the type species, as this agrees best with the description of the section as given by Pfitzer & Kraenzlin.

Rolfe (1908) added *C. virescens*. Smith (1920, 1927) added *C. imbricans* J.J. Sm. and *C. peltastes* var. *unguiculata* J.J. Sm. Carr (1934) included *C. zurowetzii* Carr. In our view, the two newly described species *C. marthae* S.E.C. Sierra and *C. verrucosa* S.E.C. Sierra should also be placed in sect. *Verrucosae*.

Coelogyne densiflora was reduced to *C. tomentosa* by De Vogel (1992). In this study, *C. edelfeldtii*, *C. lowii*, and *C. pustolosa* are reduced to *C. asperata* and *C. peltastes* var. *unguiculata* is considered to be a synonym of *C. pandurata*. De Vogel (1994) and Clayton (in prep.) place *C. brachyptera*, *C. parishii*, and *C. virescens* in sect. *Brachypterae*, because of the hysteranthous inflorescence and imbricate bracts at the base of the peduncle.

The sectional classifications of *Coelogyne* in current use are based on a few diagnostic characters only, and no phylogenetic analyses with all species assigned to sect. *Verrucosae* were performed so far. The main objectives of this study were: 1) to check the monophyly of sect. *Verrucosae* as here recognised; 2) to study interspecific relationships within the section. A taxonomic revision was made, and phylogenetic analyses were performed based on morphological and molecular characters obtained by sequencing the plastid *matK* gene and the nuclear ITS1-5.8S-ITS2 regions.

MATERIALS AND METHODS

Sampling

For the phylogenetic analysis with morphological characters 18 taxa were studied, representing 16 species assigned to *Coelogyne* sect. *Brachypterae*, *Cristatae*, *Rigidiformes*, *Tomentosae* and *Verrucosae* by various authors, and two outgroups. Representatives of two closely related genera in Coelogyninae, *Bracisepalum* and *Dendrochilum*, were chosen as outgroups. These genera are placed in the same clade as species of sect. *Verrucosae* in a molecular phylogeny of *Coelogyne* based on plastid RFLPs, *matK* and ITS sequence data (Gravendeel et al., in prep.). For the molecular analyses plant material was obtained from the living orchid collections of the botanical gardens in Leiden and Zurich and from private orchid collections. Unfortunately, living collections of only 12 taxa were available for the molecular and total evidence analysis. DNA extracted from herbarium collections turned out to be too degraded. Voucher specimens of all accessions surveyed, with their origins, are listed in Table 6.1 and deposited at L.

Taxonomic study

Collections were examined from the following herbaria: A, AMES, BM, BO, C, HBG, K, KEP, L, NY, P, SAR, SING and W. Depending on the availability of the ma-

Table 6.1. List of species analysed in the molecular analyses. Arranged by genus according to Dressler (1993). All belong to subtribe Coelogyninae. *B.* = *Bracisepalum*; *C.* = *Coelogyne*; *D.* = *Dendrochilum*; PNG = Papua New Guinea.

Genus and species	Section	Voucher[1]	Origin	ITS1-5.8S-ITS2[2]	*matK*[2]
B. selebicum J.J. Sm.		*Leiden cult. 20446*	Sulawesi	AF281120	AY003873
D. longifolium Rchb.f.		*Leiden cult. 32110*	PNG	AF281121	AY003874
C. virescens Rolfe	*Brachypterae*	*Clayton cult. s.n.*	Unknown	AF281122	AY003875
C. foerstermannii Rchb.f.	*Cristatae*	*Leiden cult. 970591*	Sarawak	AF281123	AY003876
C. sanderiana Rchb.f.	*Cristatae*	*Leiden cult. 30765*	Unknown	AF281124	AY003877
C. plicatissima Ames & C. Schweinf.	*Rigidiformes*	*Leiden cult. 980409*	Sarawak	AF281125	AY003878
C. dayana Rchb.f.	*Tomentosae*	*Leiden cult. 20247*	Unknown	AF281126	AY003879
C. rhabdobulbon Schltr.	*Tomentosae*	*Leiden cult. 26597*	Sabah	AF281127	AY003880
C. asperata Lindl.	*Verrucosae*	*Leiden cult. 22279*	PNG	AF281128	AY003881
C. mayeriana Rchb.f.	*Verrucosae*	*Leiden cult. 30728*	Unknown	AF281129	AY003882
C. pandurata Lindl.	*Verrucosae*	*Leiden cult. 21532*	Unknown	AF281130	AY003883
C. verrucosa S.E.C. Sierra	*Verrucosae*	*Leiden cult. 970584*	Sarawak	AF281131	AY003884

1) All voucher specimens are deposited in L.
2) GenBank accession number.

terial the dimensions given in the descriptions are based on living, spirit or dry material. Dried flowers were rehydrated before measurements were taken. A data matrix of 27 morphological characters was constructed, of which 5 relate to vegetative and 22 to reproductive structures. The following characters and character states were used.

1. Rhizome scales: 1 = long persistent; 2 = soon disintegrating.
2. Leaves: 1 = herbaceous; 2 = coriaceous.
3. Pseudobulbs: 1 = ovate to ovate-lanceolate; 2 = elliptic to lanceolate; 3 = cylindrical.
4. Pseudobulbs: 1 = slightly to extremely flattened; 2 = terete.
5. Pseudobulbs: 1 = unifoliate; 2 = bifoliate.
6. Flowers per inflorescence: 1 = up to 25; 2 = more than 25.
7. Inflorescence: 1 = heteranthous; 2 = proteranthous; 3 = synanthous; 4 = hysteranthous.
8. Rhachis: 1 = internodes straight to slightly zigzagging; 2 = internodes zigzagging.
9. Sterile bracts on peduncle: 1 = present; 2 = absent.
10. Sterile bracts on rhachis: 1 = 0–2; 2 = more than 2.
11. Floral bracts: 1 = patent; 2 = ascending.
12. Floral bracts: 1 = caducous; 2 = persistent.
13. Ovary: 1 = sparsely hairy; 2 = densely hairy; 3 = glabrous.
14. Petals: 1 = obovate-lanceolate; 2 = lanceolate; 3 = linear-lanceolate.
15. Petals nerves: 1 = 0–3; 2 = 4–9; 3 = more than 9.
16. Hypochile base: 1 = emarginate; 2 = subtruncate; 3 = rounded; 4 = saccate.
17. Median keel compared to lateral keels: 1 = longer; 2 = shorter.
18. Keels on hypochile: 1 = 1; 2 = 2; 3 = 3; 4 = more than 3.
19. Lateral lobes of hypochile: 1 = distinctly developed; 2 = hardly developed or absent.

20. Venation colour on lateral lobes of hypochile: 1 = brown or black; 2 = blackish green; 3 = white; 4 = pink.
21. Venation on lateral lobes of hypochile: 1 = prominent; 2 = not prominent.
22. Claw on epichile: 1 = present; 2 = absent.
23. Lateral lobes of epichile: 1 = with keels or warts; 2 = without keels or warts.
24. Ornamentation on epichile: 1 = swollen, bar-shaped keels; 2 = high, plate-like keels; 3 = low, rounded keels; 4 = keels broken up in flat irregular teeth and warts; 5 = molar or tooth-like warts; 6 = calli; 7 = irregularly rounded warts.
25. Epichile margin: 1 = with regular undulations; 2 = smooth.
26. Column hood margin: 1 = with pronounced teeth; 2 = smooth.
27. Apex of anther: 1 = V-shaped; 2 = obcordate; 3 = triangular; 4 = truncate.

Only characters were used which could be easily divided into discrete, non-overlapping states. A graph of the length of the lip of all taxa analysed did not show discrete gaps. This character was therefore omitted from the analyses. Character states were evaluated from herbarium and spirit collections, where possible from at least 5 collections per species. Distinct species are recognised when at least two morphological characters indicate differences (Van Steenis, 1957). Maps were made with the programme MapInfo Professional version 5.0 (© Media Cybernetics), using the coordinates stated on specimen labels whenever available, otherwise various gazetteers were used.

DNA extractions

Total genomic DNA was extracted from 50 mg of fresh young leaf tissue following the CTAB method of Doyle & Doyle (1987) without further cleaning procedures. Leaf material was taken from one individual per species.

matK and ITS amplifications

The *matK* gene and ITS1-5.8S rDNA-ITS2 regions were chosen because of their proved utility in Coelogyninae at the subgeneric level (Gravendeel et al., in prep.). A large portion of the *trnK* region (mostly *matK*) was amplified with the following four primers: –19F (5’- CGTTCTGACCATATTGCACTATG-3’) and 881R (5’-TMTTCATCAGAATAAGAGT-3’); 731 F (5’- TCTGGAGTCTTTCTTGAGCGA-3’) and 2R (5’- AACTAGTCGGATGGATGGAGTAG-3’). All primers were designed at the Royal Botanic Gardens, Kew, except for 2R (Johnson & Soltis, 1994). The thermal cycling protocol comprised 28 cycles, each with 1 min. denaturation at 94 °C, 30 sec. annealing at 48 °C, an extension of 1 min. at 72 °C, concluding with an extension of 7 min. at 72 °C. All PCR products were sequenced directly after purification with QIA quick purification columns (QIAGEN, Amsterdam, The Netherlands). ITS1 and ITS2 spacers along with the 5.8S gene were amplified with the primers 17 SE (5’-ACGAATTCATGGTCCGGTGAAGTGTTCG-3’) and 26SE (5’- TAGAATTCCCCGGTTCGCTCGCCGTTAC-3’) from Sun et al. (1994). The thermal cycling protocol comprised 26 cycles, each with 10 sec. denaturation at 96 °C, 5 sec. annealing at 50 °C and extension of 4 min. at 60 °C. All PCR products were cloned following the protocol of Promega’s pGEM-T Easy Vector System and then reamplified from transformed bacterial clones by touching them with a sterile pipet tip and using that sample as template. Amplified, double-stranded DNA fragments were purified using Wizard PCR minicolumns (Promega, Madison, USA) and sequenced on an ABI 377 automated sequencer, using standard dye-terminator chemistry and following the protocols of PE Applied Biosystems, Inc. Two to four sequencing reactions were performed for each completed sequence, one with each of the two PCR primers, and these generated nearly complete overlapping single-strand sequences for the entire ITS1-5.8-ITS2 region and *matK*-3'*trnK*-fragments .

Phylogenetic analyses

All characters were assessed as independent, unordered and equally weighted, using Fitch parsimony (Fitch, 1971). Only discrete morphological characters were used in the phylogenetic analyses, with multistate coding. When multiple states occurred within one species, they were treated as polymorphisms. Sequences were aligned with Meg-Align version 4.03 (DNASTAR, Inc. 1999) and subsequent adjustment by hand. Gaps in the sequence data were coded as missing values. The morphological data matrix and *matK* and ITS alignments are available from the second author upon request (gravendeel@nhn.leidenuniv.nl). All sequences are submitted to Genbank (see Table 6.1 for accession numbers). Maximum parsimony (MP) analyses were performed on the morphological and sequence data with PAUP* version 4.0b64 (Swofford, 1999) using random additions and the MULPARS option. *Bracisepalum selebicum* and *Dendrochilum longifolium* were used as outgroups in all analyses. 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. Congruence of the separate data sets was assessed by visual inspection of the individual bootstrap consensus trees. Bootstraps trees were considered incongruent only if they displayed hard (> 80% supported) incongruencies (Wiens, 1998). Character state evolution of all morphological characters was reconstructed using the assumptions of maximum parsimony with the Trace Character facility in MACCLADE version 3.04 (Maddison & Maddison, 1992).

RESULTS

Morphology

Of the 27 characters scored, 4 were autapomorphies and the remaining 23 were synapomorphies (Table 6.2). The MP analyses yielded 31 most parsimonious trees (length = 69; CI = 0.65; RI = 0.67). The bootstrap consensus topology and the corresponding branch supports are shown in Fig. 6.1. Resolution of the morphological bootstrap consensus is low. Only three clades receive strong to moderate support: *Coelogyne* (100%), sect. *Rigidiformes* (100%), and sect. V*errucosae*, excluding *C. papillosa* and *C. virescens* (76%).

matK and ITS sequences

Length ranges of the *matK* gene and its flanking *trnK* sequences were 1536–1544 and 221–245 bp. Boundaries of the *matK* gene were taken from Johnson & Soltis (1994). The alignment has a total number of 1908 sites, of which 78 were variable and 30 were phylogenetically informative (Table 6.2). The MP analyses yielded a single most parsimonious tree (length = 87; CI = 0.89; RI = 0.87). The topology of this tree

Table 6.2. Values and statistics from parsimony analyses of morphology, *matK* and ITS1-5.8S-ITS2 sequences, and combined data.

	Morphology	*matK*	ITS1-5.8S-ITS2	Total evidence
Total number of characters	27	1908	723	2658
Number of variable characters	27 (100%)	78 (4%)	250 (34%)	354
Number of phylogenetically informative characters	23	30	85	135
Average number of changes per variable site	2.6	1.1	1.4	–
Number of MPTs	31	1	2	1
Tree length (steps)	69	87	344	498
CI	0.65	0.89	0.82	0.80
RI	0.67	0.87	0.55	0.61
Number of clades in bootstrap consensus with >80% support	2	3	2	3

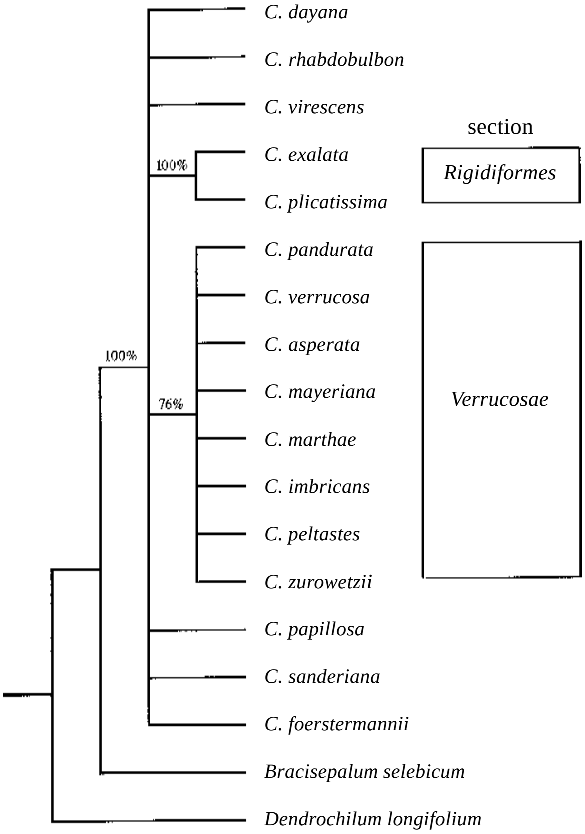


Fig. 6.1. Bootstrap consensus of 31 trees from parsimony analysis of morphological data (only percentages >50% are given).

and the corresponding branch supports are shown in Fig. 6.2. Resolution of this *matK* tree is low, too. Three clades receive high support: *Coelogyne* (100%), sect. *Tomentosae* (93%), and sect. *Verrucosae* excluding *C. virescens* (98%).

Length ranges of the ITS-5.8S-ITS2 sequences were 204–253, 159–163 and 242–271 bp respectively. Boundaries of the 5.8S gene were taken from Hershkovitz & Lewis (1996). The alignment has a total number of 723 sites, of which 250 were variable and 85 were phylogenetically informative (Table 6.2). The MP analyses yielded two most parsimonious trees (length = 344; CI = 0.82; RI = 0.55). The bootstrap consensus topology and the corresponding branch supports are shown in Fig. 6.3. Resolution of the ITS consensus is low, too. Three clades receive moderate to strong support: *Coelogyne* (62%), sect. *Verrucosae* excluding *C. virescens* (92%), and *C. asperata*, *C. mayeriana* plus *C. verrucosa* (81%).

Total evidence analysis

Differences in tree topologies between the different analyses are probably due to sampling error (Huelsenbeck et al., 1996). To improve sampling, a combined analysis of all three data sets was performed. Bootstrap analysis of the combined data set provides more resolution and higher internal support for relationships than did any of the individual data sets. The data matrix of the combined molecular and morphological analyses contains 2658 sites, of which 354 were variable and 135 phylogenetically informative (Table 6.2). The MP analyses yielded a single most parsimonious tree (length = 498; CI = 0.80; RI = 0.61), which is indicated in Fig. 6.4 with the corresponding branch supports. Resolution of the total evidence analysis is higher than any of the individual data sets. Three strongly supported clades are present: *Coelogyne* (100%), sect. *Verrucosae* excluding *C. virescens* (100%), and sect. *Tomentosae* (87%). A clade consisting

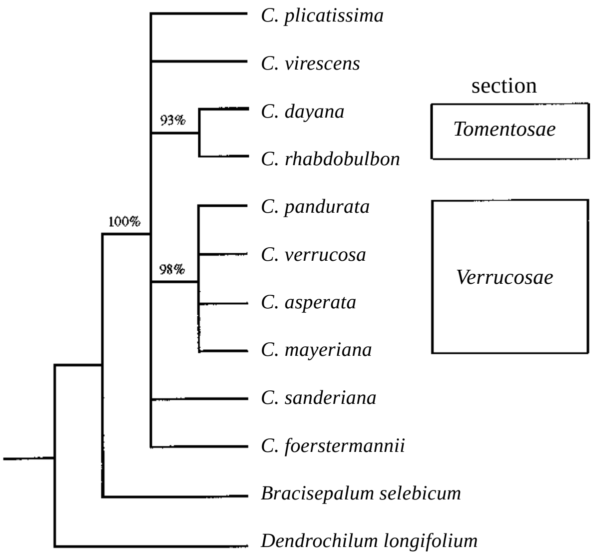


Fig. 6.2. Single MPT from parsimony analysis of *matK* sequences (only percentages >50% are given).

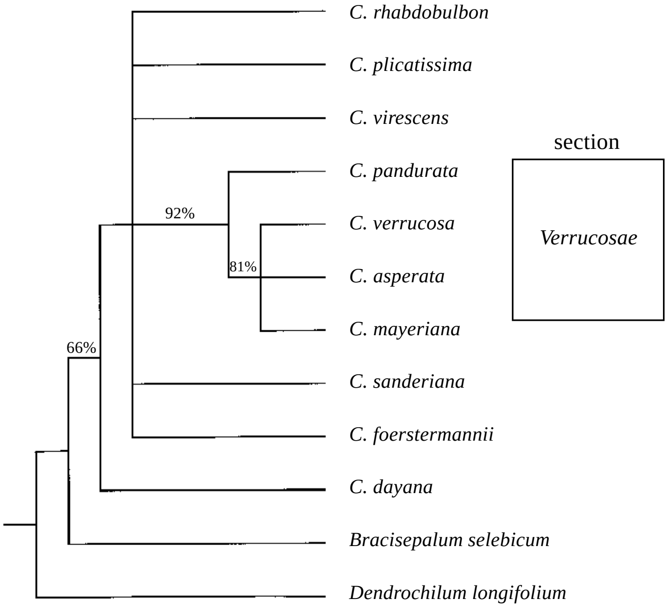


Fig. 6.3. Bootstrap consensus of two trees from parsimony analysis of ITS1-5.8S-ITS2 sequences (only percentages >50% are given).

of *C. asperata*, *C. mayeriana* and *C. verrucosa* receives moderate support (71%). Two weakly supported clades unite *C. sanderiana* with *C. plicatissima* (57%) and sect. *Verrucosae* with sect. *Brachypterae,* sect. *Coelogyne* and sect. *Rigidiformes* (52%).

DISCUSSION

Separate and combined analyses of morphological and molecular data indicate that sect. *Verrucosae* excluding *C. papillosa* and *C. virescens* is monophyletic. The species of sect. *Verrucosae* as here recognised have the following unique synapomorphies: warts, teeth or calli on the epichile and a column hood with smooth margin. All other species analysed have bar-shaped, plate-like or rounded keels and a column hood with a dentate margin. Within sect. *Verrucosae*, a smaller clade, consisting of *C. asperata, C. mayeriana* and *C. verrucosa* receives weak support (71%). These species all have an emarginate hypochile base, in *C. pandurata* this can be emarginate to subtruncate.

Neither morphological data nor *matK* or ITS sequences provided sufficient resolution to study interspecific relationships within sect. *Verrucosae*. Variation of *matK* on species level appeared to be too low (only 4%; Table 6.2). In contrast, the ITS1-5.8S-ITS2 regions seem to lack resolution due to high internal conflict among the sequences collected, as can be deduced from the relatively low RI (0.55; Table 6.2). This higher level of homoplasy could be caused by a problem of alignment in such a rapidly evolving region. To produce a final phylogeny of the section, data from other DNA regions should be collected.

The results of the total evidence analysis identified *C. virescens* as nearest neighbour to the species of sect. *Verrucosae*. This species shares the herbaceous leaves and the presence of a claw on the hypochile with most of the species of sect. *Verrucosae*. *Coelogyne virescens* has quite a few autapomorphic characters, however, such as a hysteranthous inflorescence, imbricate bracts at the base of the peduncle, a glabrous ovary and linear-lanceolate petals, supporting the view that this species should not be considered as a member of the same section. These characters are also present in *C. brachyptera* and *C. parishii*. A phylogenetic analysis with all three species might show whether they should be placed in a section of their own (sect. *Brachypterae*) as suggested by De Vogel (1994) and Clayton (in prep.).

The results of the morphological analysis support our view that *C. papillosa* should be removed from sect. *Verrucosae* because of its significant morphological differences. *Coelogyne papillosa* has a pronounced zigzagging rhachis, a column hood with dentate margin, a lip with six keels, and nerves on the lateral lobes of the hypochile which are pronounced as low rounded keels. In contrast, the species of sect. *Verrucosae* all have a more or less straight rhachis, a column hood with smooth margin, a lip with three keels, and nerves on the lateral lobes of the hypochile which are not prominent. The characters described for *C. papillosa* occur also in species of sect. *Coelogyne* and sect. *Tomentosae*. Therefore, this species might belong to one of these sections.

Another well supported clade in the total evidence analysis consists of species of sect. *Tomentosae* (87%). They are characterized by the relatively high number of sterile bracts on the base of the rhachis, more than 25 flowers per inflorescence, a subtruncate hypochile base, and white veins on the lateral lobes of the hypochile. This section seems clearly separated from the other *Coelogyne* species sampled (although support for this is weak, only 52%), which all have a relatively low number of sterile bracts on the rhachis, less than 25 flowers per inflorescence, an emarginate or subtruncate hypochile base, and brown, black or green veins on the lateral lobes of the hypochile.

Another weakly supported clade consists of *C. plicatissima* and *C. sanderiana* (57%). These species share one apomorphy: obovate-lanceolate petals. In many other characters, however, such as the shape of the pseudobulbs, type of inflorescence, shape of the hypochile base and lateral lobes, number of the keels on the hypochile, ornamentation of the lateral lobes, plate and margin of the epichile, and shape of the apex of the anther, they show considerable differences. A larger taxon sampling is needed to find out if these species belong to one monophyletic group.

To determine whether traditionally used key characters for sectional delimitation in *Coelogyne* are phylogenetically informative, their character state evolution was reconstructed on the single MPT from the total evidence analysis (Fig. 6.4). Characters with high phylogenetic potential are the number of sterile bracts on the rhachis and the shape of the ornamentation on the epichile. Less than two sterile bracts on the rhachis seem to be the plesiomorphic condition for the set of taxa analysed, and more than two bracts the derived condition. Swollen, bar-shaped keels on the epichile are the plesiomorphic condition for the set of taxa analysed and molar, tooth like or irregularly rounded warts the apomorphic condition. The inflorescence type, amount of ovary indumentum and number of keels on the hypochile show many parallelisms and appear not to be phylogenetically useful for the set of taxa analysed.

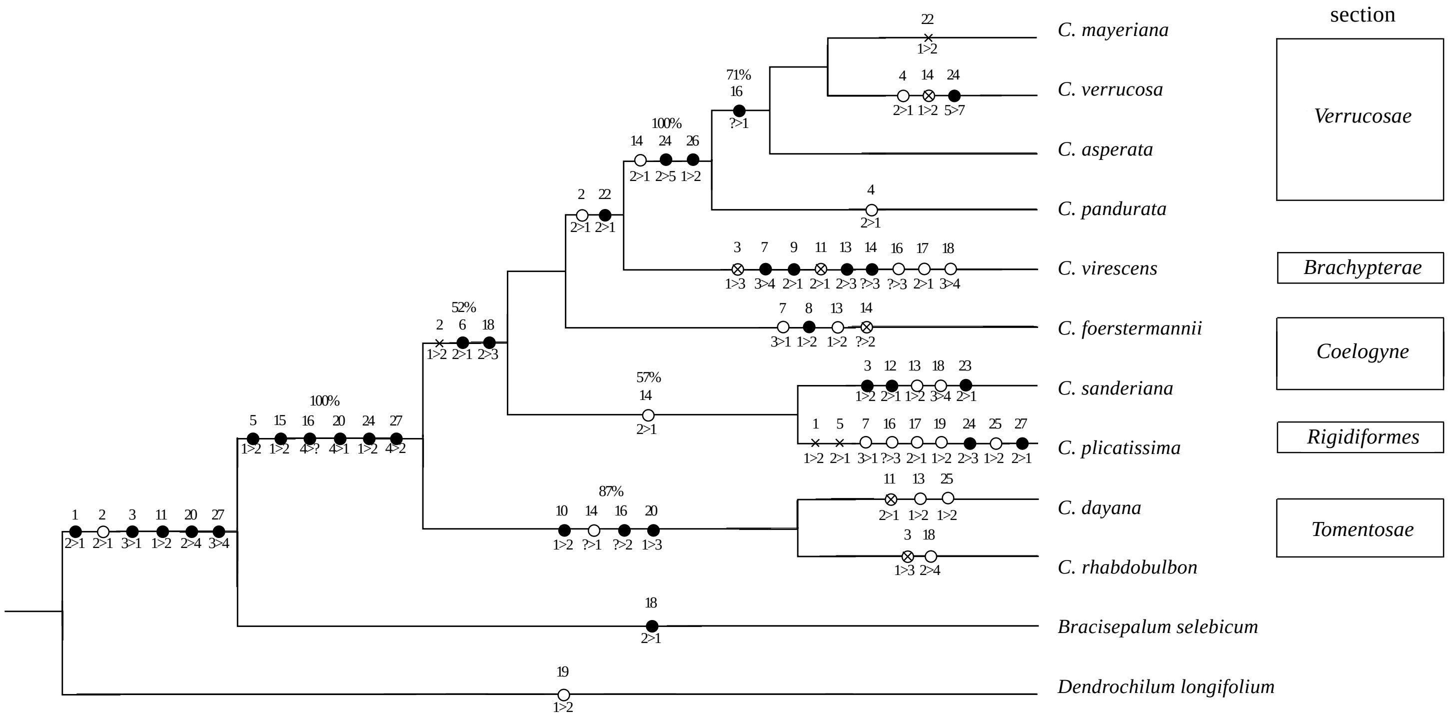


Fig. 6.4. Single MPT from total evidence analysis with bootstrap support values (only percentages >50% are given). The character state changes of the morphological characters used were traced with MACCLADE version 3.04 (Maddison & Maddison, 1992). ● = unique apomorphy; ○ = parallelism; **x** = reversal; ⊗ = parallel reversal.

CHARACTERS

For easy reference, diagnostic characters and their states for sect. *Verrucosae* are briefly described below. Characters diagnostic for the genus *Coelogyne* are omitted here. These can be found in Butzin (1992a) and Dressler (1993).

Pseudobulbs

The outline of the pseudobulbs varies from ovate to ovate-lanceolate to elliptic to lanceolate. The pseudobulbs are round in cross section as in *C. asperata* and *C. mayeriana*, slightly flattened as in *C. pandurata* or strongly flattened as in *C. marthae*, *C. verrucosa*, *C. peltastes*, *C. imbricans* and *C. zurowetzii*. The pseudobulbs of the last four species have an incurved margin.

Inflorescence

The inflorescence is proteranthous or synanthous, and in most cases both conditions are present within one species. Usually the inflorescence is curved from a more or less erect base.

Rhachis

The rhachis is more or less straight to slightly zigzagging, and has scattered minute scale-like hairs. The number of internodes varies from 4 to 24. *Coelogyne asperata* and *C. pandurata* have the largest number.

Floral bracts

Persistent sterile and fertile bracts are present in all species of the section. Both types of bracts have many fine nerves, a midrib which is not prominent, and dense minute scale-like hairs outside. There are one to three sterile imbricate bracts at the base of the rhachis; these are elliptic to oblong or (ovate-)oblong to (ovate-)lanceolate, and more or less appressed to the rhachis. The fertile bracts are elliptic to oblong or (ovate-)oblong to (ovate-)lanceolate with incurved margins, and they clasp the base of the pedicel.

Flowers

The flowers are medium-sized to large, distichous, opening widely, more or less simultaneously, often more or less curved to one side and with scattered minute scale-like hairs on pedicel, ovary and the outside of the sepals and petals. On average most of the species have 3–15 flowers in an inflorescence, with the exception of *C. asperata*, which may have up to 35 flowers.

Hypochile

The hypochile is boat-shaped, when flattened emarginate, subtruncate or rounded at the base. The lateral lobes sometimes project backwards at the back, and are triangular-ligulate or (broadly) rounded in front, with a rounded to semi-orbicular apex. There are three keels on the hypochile in all species of the section. They have an entire margin and are low and rounded at the very base. The median keel is usually low, rounded, single crested and smooth (with the exception of *C. mayeriana*, where it has projections over the entire length). The lateral keels are higher than the median keel, thin to thick plate-like and single- or double-crested.

Epichile

The epichile is spathulate or not depending on the presence or absence of a claw. When present, the claw is more or less rectangular and has straight or irregular margins. The blade is usually irregularly rectangular, quadrangular, ovate or triangular. The margin of the blade is in most species broadly undulate; in *C. zurowetzii* it is finely undulate. The ornamentation varies within the species and consists of molar-like warts (*C. asperata*, *C. pandurata*, *C. peltastes*, *C. zurowetzii*), tooth-like warts (*C. peltastes*, *C. mayeriana*), flattened calli (*C. imbricans*), rounded papillae (*C. verrucosa*, *C. zurowetzii*), or keels that are broken up in flat irregular teeth or warts (*C. marthae*).

SYSTEMATIC TREATMENT

Coelogyne section Verrucosae

Coelogyne Lindl. sect. *Verrucosae* Pfitzer & Kraenzl. in Engl., Pflanzenr. 32 (1907) 73; Schltr., Feddes Repert. Beih. 1 (1911) 101; Butzin, Willdenowia 7 (1974) 252; Seidenf., Dansk Bot. Ark. 29 (1975) 66; Butzin in Schltr. et al., Die Orchideen 1A (1992) 935; De Vogel, Proc. 14th World Orch. Conf. (1994) 204. — Type species: *Coelogyne pandurata* Lindl. (here chosen).

Small to large epiphytes, terrestrials or lithophytes. Roots terete, glabrous. Rhizome creeping or climbing, terete, 3–14 internodes between two pseudobulbs; rhizome scales overlapping or not (*C. mayeriana*), chartaceous, long persistent, densely covered with minute scale-like hairs. *Pseudobulbs* close together to wide apart, in cross section round to strongly flattened, in outline elliptic to lanceolate or ovate to ovate-lanceolate, sometimes with incurved margins, 2-leafed; scales (cataphylls) covering the pseudobulb chartaceous, with dense minute scale-like hairs, long persistent or soon disintegrating in short persistent fibres. *Leaves* herbaceous; petiole semi-terete, channelled, with scattered minute scale-like hairs; blade obovate to obovate-lanceolate or oblong to lanceolate, base gradually narrowing into the petiole, top acute to acuminate, main nerves 3–11, above sunken, below quite prominent, additional nerves not conspicuous. *Inflorescence* proteranthous or synanthous, curved from a more or less erect base, 3–35-flowered. Scape with scattered minute scale-like hairs. Rhachis about straight to slightly zigzagging, with scattered minute scale-like hairs; internodes 4–37. *Bracts* persistent, herbaceous, with manyfine nerves and dense minute scale-like hairs on the outside, midrib not prominent; sterile bracts 1–3 at the base of the rhachis, elliptic to oblong or ovate-oblong to ovate-lanceolate, more or less appressed to the rhachis, overlapping; fertile bracts elliptic to oblong or ovate-oblong to ovate-lanceolate, clasping the base of the pedicel, the margins incurved. *Flowers* medium-sized to large, distichous, opening widely, more or less simultaneously, often more or less curved to one side, with scattered minute scale-like hairs on pedicel, ovary and the outside of the sepals and petals; lip in lowermost position due to curving of rhachis or irregular curving or twisting of pedicel and ovary. Pedicel straight to curved, terete; ovary about straight to curved, terete, with 6 broad longitudinal ribs. *Median sepal* ovate-oblong to ovate-lanceolate; top acute; nerves 9–15, median nerve prominent. *Lateral sepals* slightly falcate to falcate, ovate-oblong to ovate-lanceolate; top acute; nerves 7–11. *Petals* (obovate-)lanceolate; top acute; midrib rather prominent to slightly pronounced as a low rounded keel; nerves 3–11. *Lip* 3-lobed, glabrous. *Hypochile* boat-shaped, at the base emarginate, subtruncate or rounded; lateral lobes projecting backwards or not, in front triangular-ligulate, (broadly) rounded, with rounded to semi-orbicular apex; keels 3 with entire margin, low and rounded at the base, the median keel low, rounded, single crested, smooth, or with projections over the entire length (*C. mayeriana*), the lateral keels higher than the median keel, thin to thick plate-like, single or double crested. *Epichile* without or with a more or less rectangular claw with straight or irregular margins; blade irregularly rectangular, quadrangular, ovate or triangular; top truncate, retuse, acute or rounded, tip mostly acute with a small notch on either side, margins broadly and regularly undulate or finely undulate (*C. zurowetzii*), when flattened about straight or irregular, ornamentation consisting of molar-like warts (*C. asperata*, *C. pandurata*, *C. peltastes*, *C. zurowetzii*), tooth-like warts (*C. peltastes*, *C. mayeriana*), flattened calli (*C. imbricans*), rounded papillae (*C. verrucosa*, *C. zurowetzii*), or keels broken up in flat irregular teeth or warts (*C. marthae*). *Column* (narrowly) spathulate, with scattered minute scale-like hairs; base very slightly thickened to distinctly swollen, in front projecting into a very small to pronounced column foot, on the junction with the stalk with a low cross ridge; stalk slightly and gradually widening from the base; margins slightly winged; hood about rectangular, triangular, rounded, obovate or ovate, top truncate, rounded or broadly rounded, with slightly irregular margin. *Anther* about quadrangular, obovate or obcordate; base triangular or ligulate; top broadly rounded to truncate, emarginate. *Pollinia* four, obovate, each with an oblique central depression which becomes shallower towards the base, all connate at the base by a flattened, broadly triangular caudicle. *Stigma* semi-elliptic; lower margin distinctly raised; rostellum about rectangular. *Fruit* ellipsoid; margins flat; valves with a low keel. *Seeds* shortly fusiform; embryo ellipsoid.

Distribution — Eight species distributed from Sumatra to the Santa Cruz Islands. *Coelogyne asperata* covers the entire distribution area of the section: Java, Sumatra, Peninsular Malaysia, Borneo, Sulawesi, Philippines, Moluccas, New Guinea, Solomon Islands and Santa Cruz Islands. *Coelogyne mayeriana* has been found in Sumatra, Singapore, Peninsular Malaysia and Borneo. *Coelogyne pandurata* occurs in Sumatra, Peninsular Malaysia, Borneo, and possibly the Philippines. The other species are endemic to Borneo, which is the centre of diversity.

Habitat & Ecology — Epiphytes, terrestrials or lithophytes. In peat-swamp and mixed Dipterocarp lowland forest, heath forest, and montane forest, in shaded to quite exposed positions, on granite or ultramafic substrate. Elevation 0–2050 m. Flowering all year round, but only once or twice a year in any given locality.

Conservation status — As far as could be ascertained *Coelogyne mayeriana* has not been collected from the wild for more than 50 years, except for a collection from Sabah. As this conspicuous orchid is not easily overlooked it is probably seriously endangered. *Coelogyne imbricans*, *C. marthae*, *C. peltastes* and *C. zurowetzii* are known from very few collections only, they must be considered rare and vulnerable. *Coelogyne pandurata* is widespread but rather uncommon and *C. verrucosa* is fairly common in North and West Borneo, whereas *C. asperata* is a common and widespread species.

Cultivation — Only *C. asperata* and *C. pandurata* are widely cultivated.

Artificial hybrids — Several hybrids have been produced. Erfkamp & Gruß (1996) mention the following: *C. x brymeriana*, a hybrid between *C. asperata* Lindl. and *C. dayana* Rchb.f., made by W.E. Brymer in 1906. *Coelogyne x burfordiense*, a hybrid between *C. asperata* Lindl. and *C. pandurata* Lindl., made by Trevor Lawrence in 1907 (Plate 6.1b). *Coelogyne x albanense*, a hybrid between *C. pandurata* Lindl. and *C. sanderiana* Rchb.f., made by C.F. Sander, F.K. Sander & L.L. Sander in 1913. *Memoria Soedjana Kassan*, a hybrid between *C. speciosa* Lindl. and *C. asperata* Lindl., made by A.S. Parnata in 1976. Sander et al. (1927) mention *C. x sanderiana*, a hybrid between *C. pandurata* Lindl. and *C. x albanense*, made by C.F. Sander, F.K. Sander & L.L. Sander in 1913. The Royal Horticultural Society (1993, 1997) mentions *Green dragon*, a hybrid between *C. pandurata* Lindl. and *C. massangeana* Rchb.f., made by the Burnham Nurseries in 1992, and *South Carolina*, a hybrid between *C. x burfordiense* and *C. pandurata* Lindl., made by Carter & Holmes in 1996.

Explanation of terms — Definitions of peduncle and rhachis are given in Vermeulen (1995). A scape is here considered as the part of the peduncle, not covered by the scales of the young shoot.

KEY TO THE SPECIES

1a. Pseudobulbs in cross section circular 2
b. Pseudobulbs in cross section slightly to strongly flattened 3
2a. Rhizome scales not overlapping; pseudobulbs (3.5–)8–24 cm apart . . . . **4. C. mayeriana**
b. Rhizome scales overlapping; pseudobulbs (1.2–)2.5–6.5 cm apart . . . . **1. C. asperata**
3a. Claw on midlobe of lip present, longer than or equal to 2.5 mm 4
b. Claw on midlobe of lip absent, or if present shorter than 2.5 mm 5
4a. Pseudobulb 1.5–3 cm diam. when fresh, margins not incurved; ornamentation on the midlobe of the lip consisting of a patch of molar-like warts, the whole patch 8–17 by 7–18 mm . . . . **5. C. pandurata**
b. Pseudobulb 0.7–1.3 cm diam. when fresh, margins incurved; ornamentation on the midlobe of the lip consisting of a patch of big rounded, projecting warts, the whole patch 4.5–13 by 3–7 mm . . . . **7. C. verrucosa**
5a. Claw on midlobe of lip present; 2, 4 or 6 swollen nerves on the claw and base of the epichile 6
b. Claw on midlobe of lip absent; swollen nerves on the base of the epichile absent 7
6a. Margin of midlobe very finely undulate; ornamentation on midlobe consisting of short rows or patches of scattered, single or connected, rounded and molar-like warts . . . . **8. C. zurowetzii**
b. Margin of midlobe broadly undulate; ornamentation on midlobe consisting of two irregular flattened calli, which together have a more or less ovate shape . . . . **2. C. imbricans**
7a. Median keel on the lip continuing on the base of the midlobe; ornamentation on the midlobe consisting of a patch of tooth-like, more or less flattened warts, often arranged in radiating rows, the whole patch 7–12 by 5–10 mm . **6. C. peltastes**
b. Median keel on the lip not reaching the base of the midlobe; ornamentation on the midlobe consisting of a patch of 4–6 single-crested, parallel keels which are broken up in flat irregular teeth or warts, the whole patch 5–9 by 5–8 mm . . . . **3. C. marthae**

1. **Coelogyne asperata** Lindl. — Fig. 6.5, Plate 6.1a, Map 6.1

Coelogyne asperata Lindl., J. Hort. Soc. London 4 (1849) 221, t. 7; Fol. Orchid. (1854) 3; Miq., Fl. Ned. Ind. 3 (1859) 666; Rchb.f., Ann. Bot. Syst. 6 (1861) 224; Hook.f., Fl. Brit. India 5 (1890) 835; H.J. Veitch, Man. Orchid. Pl. 6 (1890) 31; Ridl., J. Linn. Soc., Bot. 31 (1896) 287, 326; Pfitzer & Kraenzl. in Engl., Pflanzenr. 32 (1907) 76, f. 25C–D, 26A; Ridl., Mat. Fl. Malay. Penins. 1 (1907) 129; J.J. Sm., Nova Guinea 8 (1911) 20, 527; Engl., Bot. Jahrb. Syst. 48 (1912) 96; J.J. Sm., Nova Guinea 12 (1915) 196; Ridl., Trans. Linn. Soc. London II, 9 (1916) 202; J.J. Sm., Teysmannia 31 (1920) 255; Ridl., Fl. Malay. Penins. 4 (1924) 131; Ames in Merr., Enum. Philipp. Flow. Pl. 1 (1924) 280; Burkill & M.R. Hend., Gard. Bull. Straits Settlem. 3 (1925) 438; C.F. Sander, F.K. Sander & L.L. Sander, Sander's Orch. Guide (1927) 212; J.J. Sm., Bull. Jard. Bot. Buitenzorg III, 10 (1928) 104; III, 11 (1931) 105; Ames, J. Arnold Arbor. 13 (1932) 129; J.J. Sm., Bot. Jahrb. Syst. 65 (1933) 464; Feddes Repert. Beih. 32 (1933) 161; Carr, Kew Bull. (1934) 377; Dakkus, Orch. Ned. Ind. 3 (1935) 75, f. 30; Quisumb., Philipp. Orchid Rev. (1951) 9; Davis & Steiner, Philipp. Orchid Rev. (1952) 75; Latif, Bunga Anggerik (1953) 90; Holttum, Orchids of Malaya 3 (1964) 253; Andrée Millar, Orchids of Papua New Guinea (1978) 74; Bechtel in P.J. Cribb & Launert, Orch. Atl. (1980) 100; Chadim, Orchadian 7, 3 (1982) 60, f. 1, 2; B.A. Lewis & P.J. Cribb, Orchids of the Solomon Islands and Bougainville (1991) 88; Seidenf. & J.J. Wood, Orchids of Penins. Malaysia and Singapore (1992) 217, f. 92a–b, pl. 12d. — *Pleione asperata* (Lindl.) Kuntze, Rev. Gen. Pl. 2 (1891) 680. — Type: *Twisden Hodges cult. s.n.* (30/5/1849) (holo K-LINDL, not found), Borneo. Neotype (here chosen): *Lobb s.n. (Veitch & Son)* (holo K-LINDL), Borneo.

Coelogyne lowii Paxton, Paxton's Mag. Bot. 16 (1849) 225; Ames in Merr., Enum. Philipp. Flow. Pl. 1 (1924) 283. — Type: *Low s.n.* (?/?/1845) (holo K, not found), Borneo.

Coelogyne edelfeldtii F. Muell. & Kraenzl., Oesterr. Bot. Z. 44 (1884) 421; Pfitzer & Kraenzl. in Engl., Pflanzenr. 32 (1907) 76. — Type: *Edelfeldt s.n.* (?/?/1884) (holo HBG, not found), New Guinea.

Coelogyne pustulosa Ridl., J. Bot. 24 (1886) 353; Pfitzer & Kraenzl. in Engl., Pflanzenr. 32 (1907) 73, f. 26D; Schltr., Feddes Repert. Beih. 1 (1914) 105; Rendle, J. Bot. (Hooker) 61 (1923) 55. — Type: *Forbes s.n.* (?/?/1886) (holo BM), New Guinea, South Cape.

Roots 3–5 mm diameter. Rhizome creeping, 1–1.8 cm thick, 7–14 internodes between two pseudobulbs; scales overlapping. *Pseudobulbs* (1.2–)2.5–6.5 cm apart, in cross section terete, with shallow groves, in outline (ovate-)lanceolate, 7–25 by 3–5.6 by 2–4.5 cm; scales covering the pseudobulb 7–23 by 4–6 cm. *Leaf* petiole 5.5–38 by 0.7–1.5 cm; blade lanceolate, 26–110 by 4.5–20 cm; main nerves 5–9. *Inflorescence* proteranthous or synanthous, 6–35-flowered. Scape 6–22 cm long including the part covered by the scales of the young shoot. Rhachis 12–33 cm long; internodes 7–24, 0.8–4.2 cm long. *Sterile bracts* 1 or 2 (or 3), elliptic to oblong, 2.6–4.7 by 1–2.8 cm; fertile bracts elliptic, 2.5–4 by 1.3–3 cm. Pedicel 10–37 by 2–3 mm; ovary 5–15 by 3–4 mm. *Median sepal* ovate-oblong, 30–45 by 10–17 mm; nerves 9–11, the median one prominent. *Lateral sepals* slightly falcate, ovate-oblong to ovate-lanceolate, 30–42 by 7–15 mm; nerves 7–9. *Petals* obovate-lanceolate, 30–45 by 4.5–8 mm; nerves 3–5, midrib slightly prominent. *Hypochile* 15–25 by 20–32 mm, base emarginate; lateral lobes 15–25 by 5–10 mm, at the base projecting backwards for 2–3 mm, in front triangular-ligulate, projecting for 5–8 mm, with rounded or rarely acuminate apex; keels 3, with entire margin, low and rounded at the base, the median keel low and rounded, gradually lowering to the front, rarely very short, at the top often bifurcate, on the top part of the hypochile continuing into two longitudinal rows of irregular, rounded to acute, raised molar-like structures, the lateral keels higher than the median keel, thick plate-like, continuing into similar raised structures as the median one.

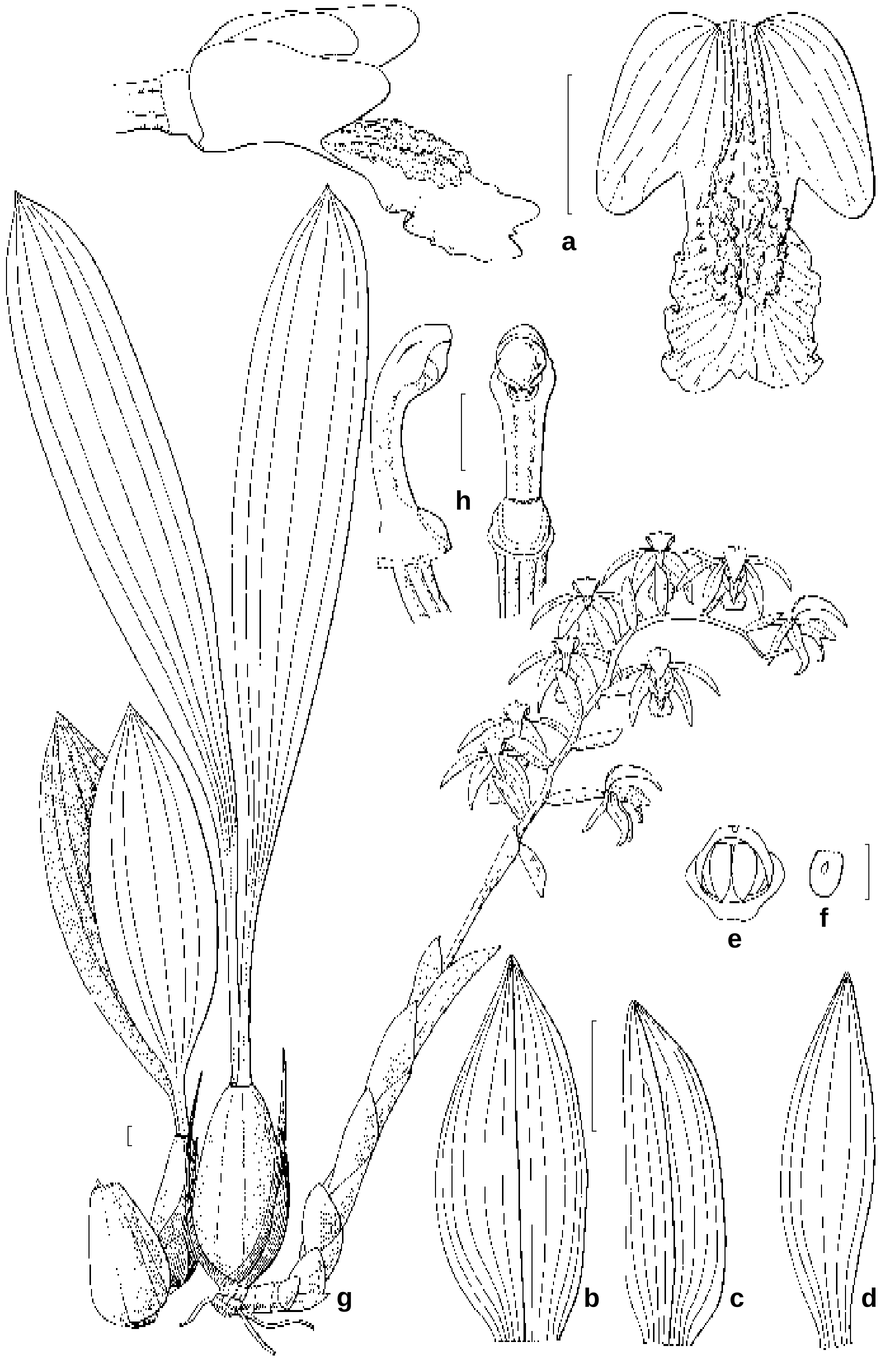


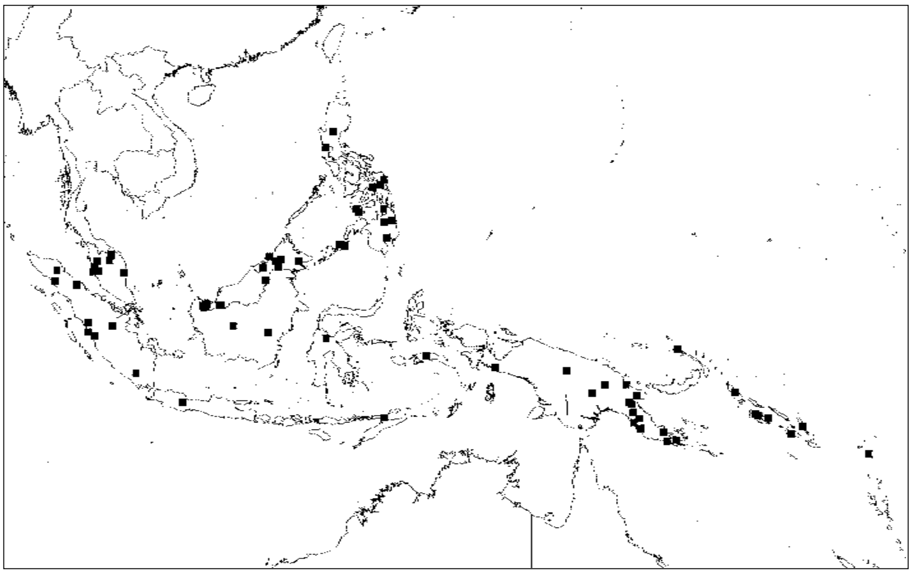
Fig. 6.5. *Coelogyne asperata* Lindl. a. Lip ornamentation, lateral and front view (*Leiden cult. 21480*); b. median sepal; c. lateral sepal; d. petal; e. anther; f. pollinium; g. habit; h. column: lateral and front view (*Leiden cult. 22279*). — Scale bars: 1 cm (a–d, g); 2 mm (e, f); 5 mm (h).

Epichile about spathulate, 16–26 by 10–17 mm; claw about rectangular, (2–)5–10 by 8–12 mm, margins straight, ornamentation consisting of two raised bands of molar-like structures as on the hypochile, continuing on the blade; blade irregularly rectangular to quadrangular to ovate, 9–15 by 10–17 mm, the top truncate to acute, the tip acute, triangular, mostly with a small notch on either side, the margin broadly and regularly undulate, when flattened about straight, ornamentation consisting of two bands of molar-like structures, the whole patch of these structures on claw and midlobe in outline more or less elliptic, 12–17 by 8–12 mm. *Column* in outline spathulate, 8–17 by 3–4.5 mm; column foot small; stalk 5.5–14 by 2–3 mm; hood about triangular, 4–7 by 3–4.5 mm, top broadly rounded, with slightly irregular margin. *Anther* about quadrangular, 3–4 by 3–4 mm, base triangular, top broadly rounded, tip emarginate. *Pollinia* obovate, 1–1.5 by 1–1.2 mm. *Stigma* semi-elliptic, 2.5–3.5 by 3–4 mm; rostellum about rectangular, 1.3–2 by 2.2–2.7 mm. *Fruit* ellipsoid; body 5–9 by 2.5–5 cm; margins flat, 3–5 mm wide; valves 30–45 mm wide, with a low keel. *Seeds* shortly fusiform, to 2–3 mm long; embryo 0.5–1 mm long.

Distribution — Sumatra, Peninsular Malaysia, Borneo (Sabah, Brunei, Sarawak, Kalimantan), Java, Sulawesi, Philippines, Moluccas, New Guinea (Irian Jaya, Papua New Guinea), Solomon Islands, Santa Cruz Islands.

Habitat & Ecology — Epiphytes on trunks and big branches of trees, lithophytes or terrestrials. Lowland and montane forest, in partial shade to quite exposed, also along rivers, in forest on limestone and in swamp forest. Elevation 10–2042 m. Flowering all the year when considered over its entire range, but in any given area flowering only once or twice a year.

Notes — 1. Pseudobulbs and leaves green. Sepals and petals creamy yellow to almost white, or pale greenish. Lip white or pale greenish, at the extreme base orange; keels white; lateral lobes with 3–5 brown veins; claw and blade with orange-brown



Map 6.1. Distribution of *Coelogyne asperata* Lindl.

molar-like projections. Column creamy yellow, or sometimes pale greenish, with scattered brown scale-like hairs; cross ridge on column foot orange. Anther creamy yellow or pale greenish; pollinia light yellow. Ovary cream coloured or pale greenish, with brown scale-like hairs. Root tip pale orange. Fragrant. Colour description based on living material, slides, and notes on the labels of the collections.

2. The epithet *asperata* (which is Latin for rough, uneven) refers to the raised patch of projections on the midlobe of the lip.

3. The dimensions are based on living and spirit material.

4. The species can be recognised by the non-flattened pseudobulbs that are close together and the presence of two raised patches of molar-like projections on the claw and the epichile.

5. O'Byrne (1994) reports this species to be pollinated by beetles.

2. Coelogyne imbricans J.J. Sm. — Fig. 6.6, Map 6.2

Coelogyne imbricans J.J. Sm., Bull. Jard. Bot. Buitenzorg III, 2 (1920) 26; Dakkus, Orch. Ned. Ind. 2 (1931) 70; 3 (1935) 86. — Type: *Bogor cult. s.n.* (?/?/1918) (H.L.B. 9226298) (holo L; iso L), Borneo.

Roots not seen. Rhizome creeping or climbing (type description), not seen. *Pseudobulbs* 4–5.5 cm apart (type description), in cross section very flattened, thickness not known, imbricate over each other like roof tiles, in outline oblong, with incurved margins, 6–11.5 by 4–8 cm; scales covering the pseudobulb not seen. *Leaf* petiole 1.5–7.5 by 0.4–0.6 cm; blade obovate-oblong or oblong, 11.5–23 by 4–7.6 cm; main nerves 7–11. *Inflorescence* synanthous (type description), 6–10-flowered. Scape 4–7 cm long including the part covered by the scales of the young shoot. Rhachis 11.8–24 cm long; internodes 7–11, 2–4 cm long. *Sterile bract* 1, elliptic to oblong, 2–2.7 by 1–1.2 cm; fertile bracts elliptic, 2–3 by 1.3–1.9 cm. Pedicel 25–42 by 0.8–1.5 mm; ovary 7–9.5 by 1–2 mm. *Median sepal* ovate-lanceolate, 29–35 by 7–11 mm; nerves 9–11, the median one prominent. *Lateral sepals* falcate, ovate-oblong to ovate-lanceolate, 23–32 by 7–12 mm; nerves 7–9. *Petals* obovate-lanceolate, 23–33 by 4–8 mm; nerves 7, midrib slightly prominent. *Hypochile* 11.5–15 by 12–14 mm, when flattened the base subtruncate; lateral lobes 11.5–15 by 3.5–6 mm, at the base not projecting backwards, in front the free part triangular, projecting for 2–3 mm, with rounded apex; keels 3, with entire margin, low and rounded at the base, the median keel low and rounded, gradually lowering to the front, ending near the junction of hypo- and epichile, the lateral keels at the basal half higher than the median keel, plate-like, gradually ascending towards the top of the epichile and there abruptly lowering into the median raised nerves on the claw of the epichile. *Epichile* about spathulate, 10–13 by 7.8–9.5 mm; claw about rectangular, 1.7–2.3 by 4–4.8 mm, margins straight, with 4–6 swollen nerves which continue on the blade; blade irregularly rectangular to quadrangular to ovate, 9–10 by 7.8–9.5 mm, the top truncate, to acute, the tip acute, triangular, mostly with a small notch on either side, the margin broadly and regularly undulate, when flattened about straight, at the base with 4–6 raised nerves, median continuing into two irregular flattened calli which are together more or less ovate, covering a patch 6–6.5 by 4.5–6 mm. *Column* in outline club shaped, distinctly curved, 17–18.4 by 2–2.2 mm; column foot small; stalk 8.4–9 by 1.3–1.8 mm; hood broadly

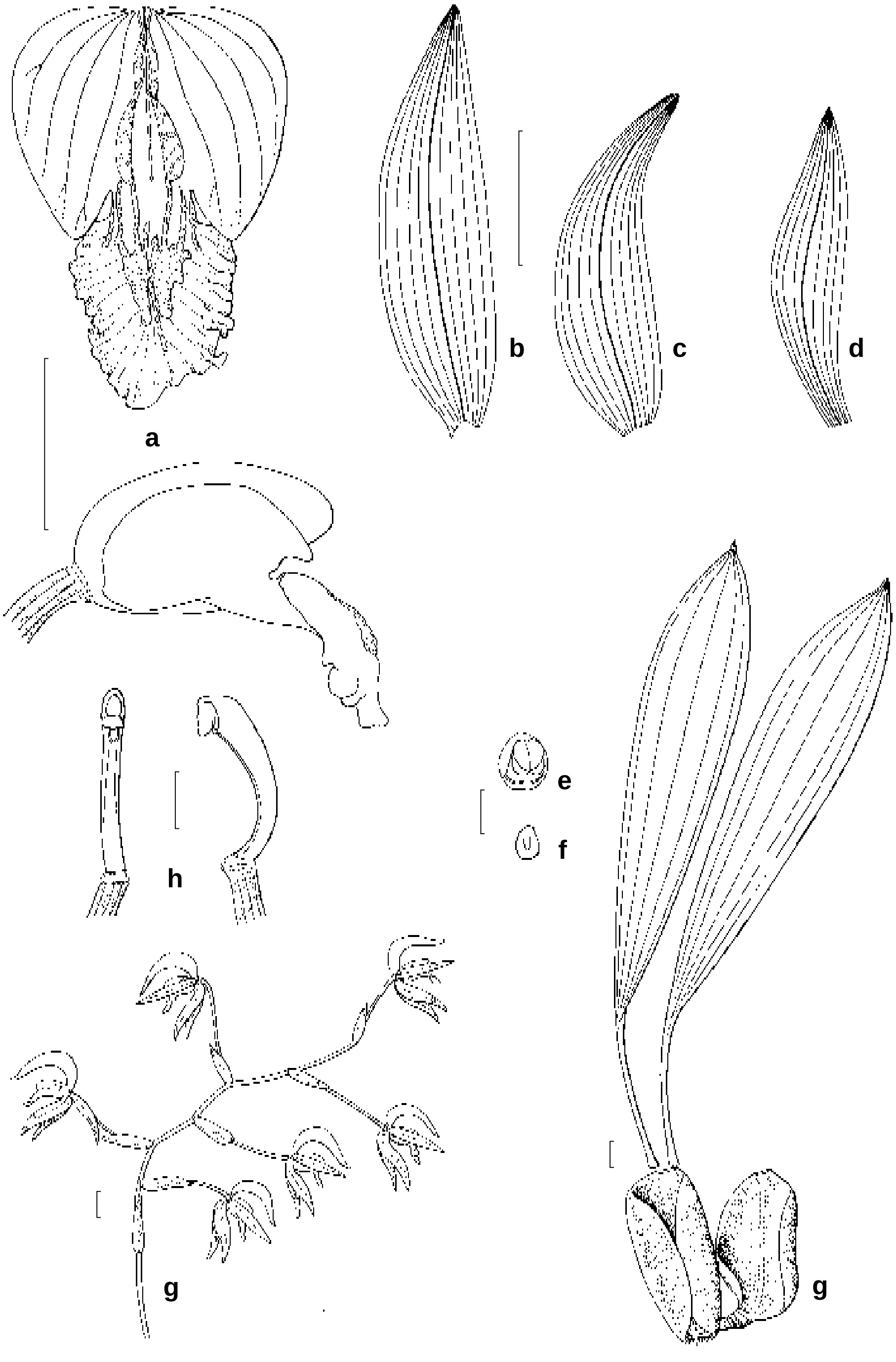
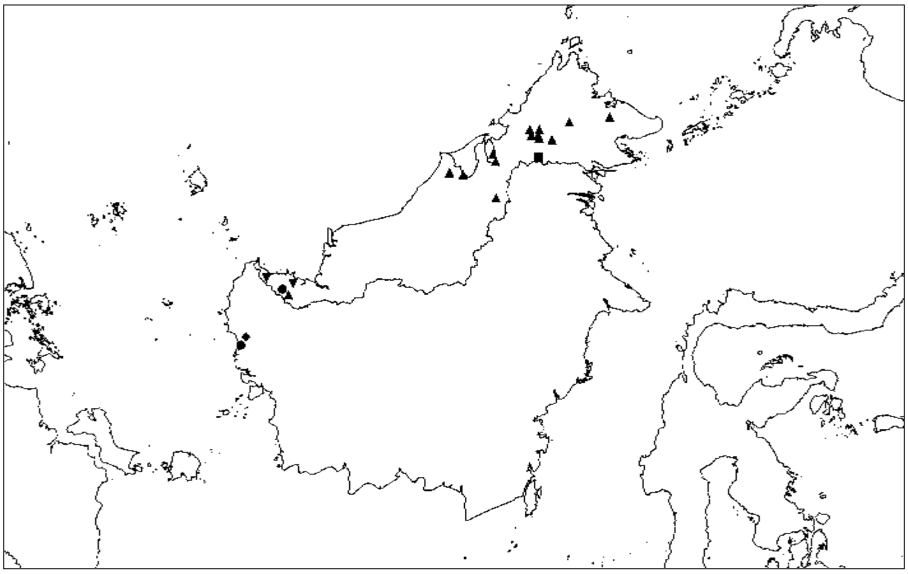


Fig. 6.6. *Coelogyne imbricans* J.J. Sm. a. Lip ornamentation, front and lateral view; b. median sepal; c. lateral sepal; d. petal; e. anther; f. pollinium; g. habit; h. column: front and lateral view (*J.J. Sm. cult., H.L.B. 9226298*). — Scale bars: 1 cm (a–d, g); 2 mm (e, f); 5 mm (h).



Map 6.2. Distribution of *Coelogyne imbricans* J.J. Sm. (l), *C. marthae* S.E.C. Sierra (t), *C. peltastes* Rchb.f. (u), *C. verrucosa* S.E.C. Sierra (s) and *C. zurowetzii* Carr (n).

rounded, with slightly irregular margin, 8–10 by 2–2.2 mm, top rounded, with irregular margin. *Anther* obcordate, 2.2–2.8 by 2–2.4 mm, base triangular; top broadly rounded, tip emarginate. *Pollinia* obovate, 1.2–2.5 by 0.7–0.8 mm. *Stigma* semi-elliptic, 2–2.5 by 1.5–2 mm; rostellum about rectangular, 1.2–1.5 by 1–1.2 mm. *Fruit* and *seeds* not seen.

Distribution — Borneo (Kalimantan, Sarawak).

Habitat & Ecology — Epiphytes. Flowering months unknown.

Notes — 1. Pseudobulbs and leaves green. Sepals and petals pale green. Lip pale greenish, at the extreme base yellow; keels yellow at the base, at the top light green and on the claw light brown; lateral lobes with 6–8 brown veins; claw brown and blade green. Column light greenish; cross ridge on column foot brown, with scattered brown scale-like hairs. Ovary light greenish, with brown scale-like hairs. Scent not recorded. Colour description based on the type publication and on the labels of the specimens seen.

2. The epithet *imbricans* (which is Latin for overlapping like roof tiles) refers to the overlapping pseudobulbs.

3. The dimensions are based on dry material.

4. The species can be recognised by the very thin imbricate pseudobulbs with flattened incurved margins, two calli on the epichile, and by the brown patch on the top of the lateral lobes.

5. According to Smith (1920) *C. imbricans* is similar to *C. peltastes*, but with more compressed pseudobulbs, smaller and differently coloured flowers, and broader lip with nearly smooth ‘keels’ (= calli). Although Smith also mentions remarkably small leaves for the size of the pseudobulbs, some leaves of his herbarium specimens are not particularly small.

6. The collection *Maxwell s.n.* (1895) differs in the details of the calli on the epichile, because instead of two single calli, there are a number of rather elliptic, low raised, smooth warts.

3. Coelogyne marthae S.E.C. Sierra, *spec. nov.* — Fig. 6.7, Plate 6.2b, Map 6.2

> Pseudobulbis parvis planis, labello ungue carenti carinis solitariis cristatis serialibus in lobo mediali dentis vel verrucis irregularibus fractis recognita. — Typus: *Vermeulen 1156* (holo L), Borneo, Sarawak.

Roots 1–3 mm diam. Rhizome climbing, 0.6–0.8 cm thick, 3–6 internodes between two pseudobulbs; scales overlapping. *Pseudobulbs* 0.6–1.3 cm apart, in cross section flattened (in juvenile specimens apparently thicker), in outline ovate-oblong, 1.5–5 by 0.7–2.3 cm, by 0.6–1 cm; scales covering the pseudobulb 6.4–9.7 by 2.8–4 cm. *Leaf* petiole 1–4 by 0.1–0.3 cm; blade lanceolate, 6–28 by 1.2–4.5 cm; main nerves 3–5. *Inflorescence* proteranthous or synanthous, 3–5-flowered. Scape 3.7–8 cm long including the part covered by the scales of the young shoot. Rhachis 7–16.2 cm long; internodes 4–6, 2.3–3.7 cm long. *Sterile bracts* 1 or 2, ovate-lanceolate, 2.3–3.2 by 0.4–1 cm; fertile bracts, ovate-oblong to ovate-lanceolate, 2.4–3 by 0.6–1.2 cm. Pedicel 12–14 by 1.8–2 mm; ovary 5–6 by 2.2–2.5 mm. *Median sepal* ovate-lanceolate, 34–38 by 9–13 mm; nerves 11, the median one prominent. *Lateral sepals* slightly falcate, ovate-lanceolate, 31–35 by 9–10 mm; nerves 7. *Petals* lanceolate, 29–32 by 4–6 mm; nerves 5, midrib slightly prominent. *Hypochile* 14–16 by 17–19 mm, when flattened base emarginate or rounded; lateral lobes 14–16 by 5–7 mm, at the base projecting backwards for 1.8–2.2 mm; in front triangular-ligulate, projecting for 3.8–4.2 mm, with broadly rounded apex; keels 3, with entire margin, low and rounded at the base, the median keel gradually higher, thin plate-like, continuing up to two-thirds of the hypochile or sometimes continuing almost to the top of the epichile, the lateral keels towards the epichile higher than the median keel, widening, thick plate-like, double crested, continuing on the epichile. *Epichile* not spathulate, 13–14 by 15–16 mm; claw absent, blade about irregular quadrangular, the top truncate, the tip acute, triangular, mostly with a small notch on either side, the margin broadly and regularly undulate, when flattened about straight, ornamentation consisting of 4–6 single crested parallel keels, broken up in flat irregular teeth or warts, ending in the top half of the blade, whole patch of ornamentation 5–9 by 5–8 mm. *Column* in outline narrowly spathulate, 14–17 by 3.2–4 mm; column foot rather pronounced; stalk 5–7.3 by 1.8–2.5 mm; hood about rectangular to broadly rounded, 7–10 by 3.2–3.8 mm, top broadly rounded, with slightly irregular margin. *Anther* more or less obcordate, 2.8–3.2 by 2.2–2.5 mm, base triangular to ligulate; top broadly rounded, tip emarginate. *Pollinia* obovate, 1.4–1.7 by 1–1.2 mm. *Stigma* semi-elliptic, 2.2–2.8 by 1.9–2.1 mm; rostellum about rectangular, 1.2–1.5 by 1–1.2 mm. *Fruit* and *seeds* not seen.

Distribution — Borneo (Sarawak: Bahagian Kuching).

Habitat & Ecology — Epiphytes. In the lower part of trunks of undergrowth trees. Heath forest, c. 20–30 m high, on level terrain with deep sandy soil overlain by a layer of raw humus, locally with pools of stagnant brown water. Elevation 50–300 m. Flowering: March, December.

Notes — 1. Pseudobulbs and leaves green. Sepals and petals light green. Lip white tinged green, at the very base orange; lateral lobes with 4 or 5 brown veins; hypochile

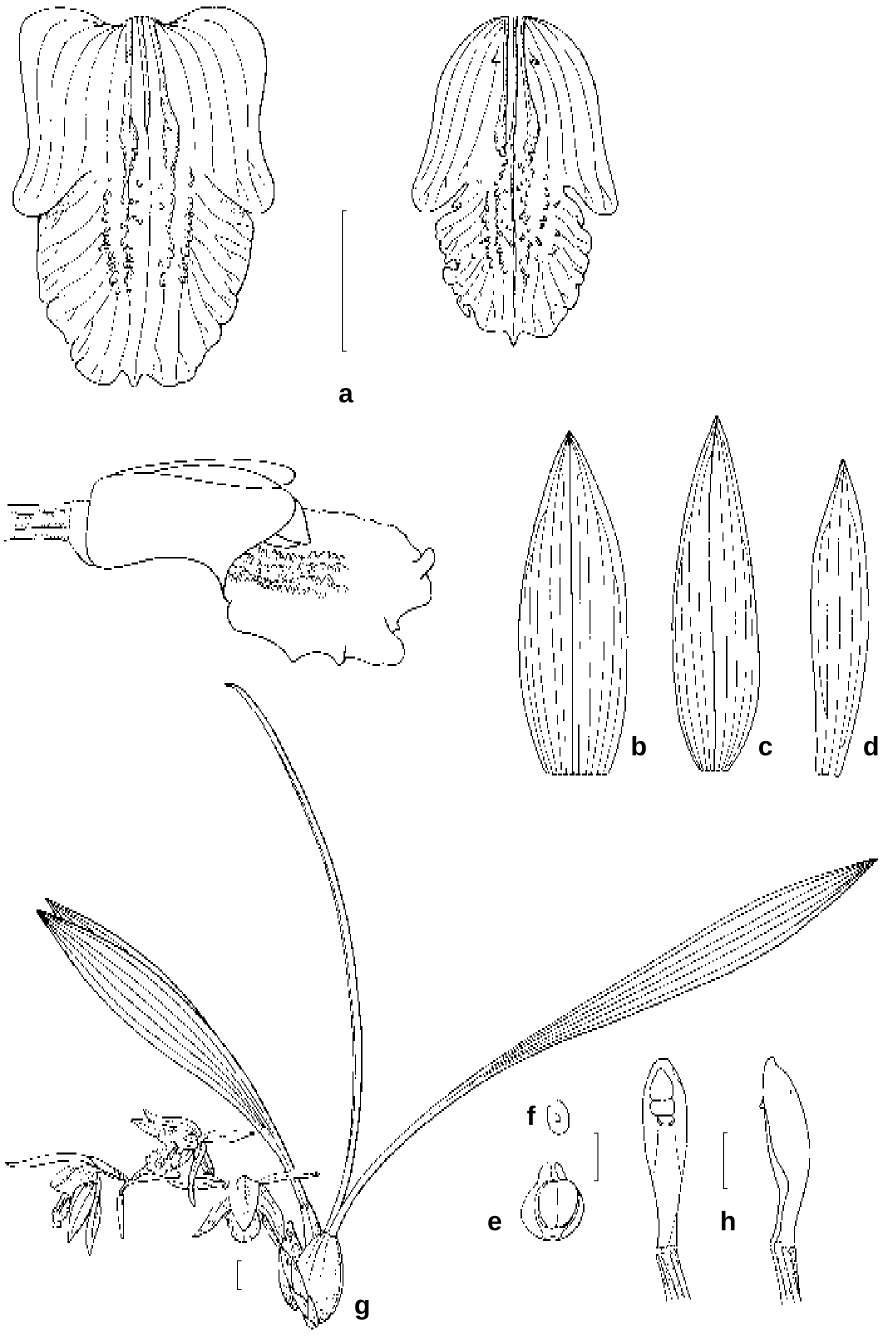


Fig. 6.7. *Coelogyne marthae* S.E.C. Sierra. a. Lip ornamentation, front view (from left to right: *Leiden cult. 27496, De Vogel 8836*) and lateral view (*Leiden cult. 27496*); b. median sepal; c. lateral sepal; d. petal; e. anther; f. pollinium; g. habit; h. column: front and lateral view (*De Vogel 8836*). — Scale bars: 1 cm (a–d, g); 2 mm (e, f); 5 mm (h).

light green, keels at the back light green, in front yellow with brown crests; epichile near the margins light green, middle part with brown rows of papillae. Column, ovary and anther light green. Scent not recorded. Colour description based on slides and notes on the labels of the collections.

2. *Coelogyne marthae* is named after Dr. Martha Tilaar, the benefactor of the newly established Martha Tilaar Chair of Ethnobotanical Knowledge Systems with special reference to Medicinal Plants in Developing Countries at Leiden University, The Netherlands.

3. The dimensions are based on living and spirit material.

4. The species can be recognised by the small flattened pseudobulbs, and a lip with rows of single crested keels breaking up in flat irregular teeth or warts on the midlobe, which lacks a claw.

4. Coelogyne mayeriana Rchb. f. — Fig. 6.8, Plate 6.2a, Map 6.3

Coelogyne mayeriana Rchb. f., Gard. Chron. 2, 8 (1877) 134; Ridl., J. Linn. Soc., Bot. 32 (1896) 324; Zörnig, Bot. Jahrb. Syst. 33 (1904) 649, f. 20, 21; Pfitzer & Kraenzl. in Engl., Pflanzenr. 32 (1907) 75; J.J. Sm., Teysmannia 31 (1920) 258; Ridl., Kew Bull. (1925) 91; C.F. Sander, F.K. Sander & L.L. Sander, Sander's Orchid Guide (1927) 125; J.J. Sm., Feddes Repert. Beih. 32 (1933) 165; Bull. Jard. Bot. Buitenzorg III, 16 (1939) 124; Latif, Bunga Anggerik (1953) 95; Holttum, Orchids of Malaya 3 (1964) 254, f. 53; Backer & Bakh. f., Fl. Java 3 (1968) 283; J.B. Comber, Orchids of Java (1990) 116; Seidenf. & J.J. Wood, Orchids of Penins. Malaysia and Singapore (1992) 217, f. 92d. — Type: *Reichenbach Herb. 21506* (?/?/1876) (holo W-RCHB; iso W-RCHB), from cultivated specimens of unknown origin.

Roots 1–2 mm diam. Rhizome creeping, 0.4–0.8 cm thick, 5–12 internodes between two pseudobulbs; scales not overlapping. *Pseudobulbs* (3.5–)8–24 cm apart, in cross section terete, in outline ovate, 3.5–9.5 by 3–5 by 1.7–3.4 cm; scales covering the pseudobulb 4–11 by 2.5–5 cm. *Leaf* petiole 1.2–8.5 by 0.5–0.7 cm; blade lanceolate, 12–40 by 2.7–9 cm; main nerves 5–7. *Inflorescence* proteranthous or synanthous, 3–10-flowered. Scape 5–13 cm long including the part covered by the scales of the young shoot. Rhachis 9–30 cm long; internodes 5–12, 1.6–5.5 cm long. *Sterile bracts* 1 or 2, elliptic, 1.7–5 by 1–3.4 cm; fertile bracts elliptic, 1.6–3 by 0.8–1.9 cm. Pedicel 16–40 by 1–2 mm; ovary 5–15 by 1.5–3 mm. *Median sepal* ovate-lanceolate, 28–42 by 9–15 mm; nerves 9–11, the median one prominent. *Lateral sepals* slightly falcate, ovate-lanceolate, 30–40 by 8–15 mm; nerves 7–9. *Petals* obovate-lanceolate, 20–40 by 8–11 mm; nerves 5–7, midrib slightly prominent. *Hypochile* 8–19 by 11–20 mm, when flattened the base emarginate; lateral lobes 8–19 by 7–8 mm, at the base projecting backwards for 2–4 mm, in front rounded, projecting for 2.5–3 mm, with round apex; keels 3, over the entire length with small projections, with entire margin, low and rounded at the base, the median keel low and rounded, gradually lowering to the front, continuing to the junction of hypo- and epichile and there ending forming a crest, the lateral keels higher than the median keel, thick plate-like, continuing into the keels on the epichile. *Epichile* about trapeziform, 10–17 by 9–15 mm; claw absent; blade irregularly rectangular to quadrangular, the top truncate, the tip acute, triangular, with a small notch on either side, the margin broadly and regularly undulate, when flattened about straight, with 2 keels as on the hypochile, sometimes with 2 additional rows of cushion-like projections, both continuing in four patches of tooth-like projec-

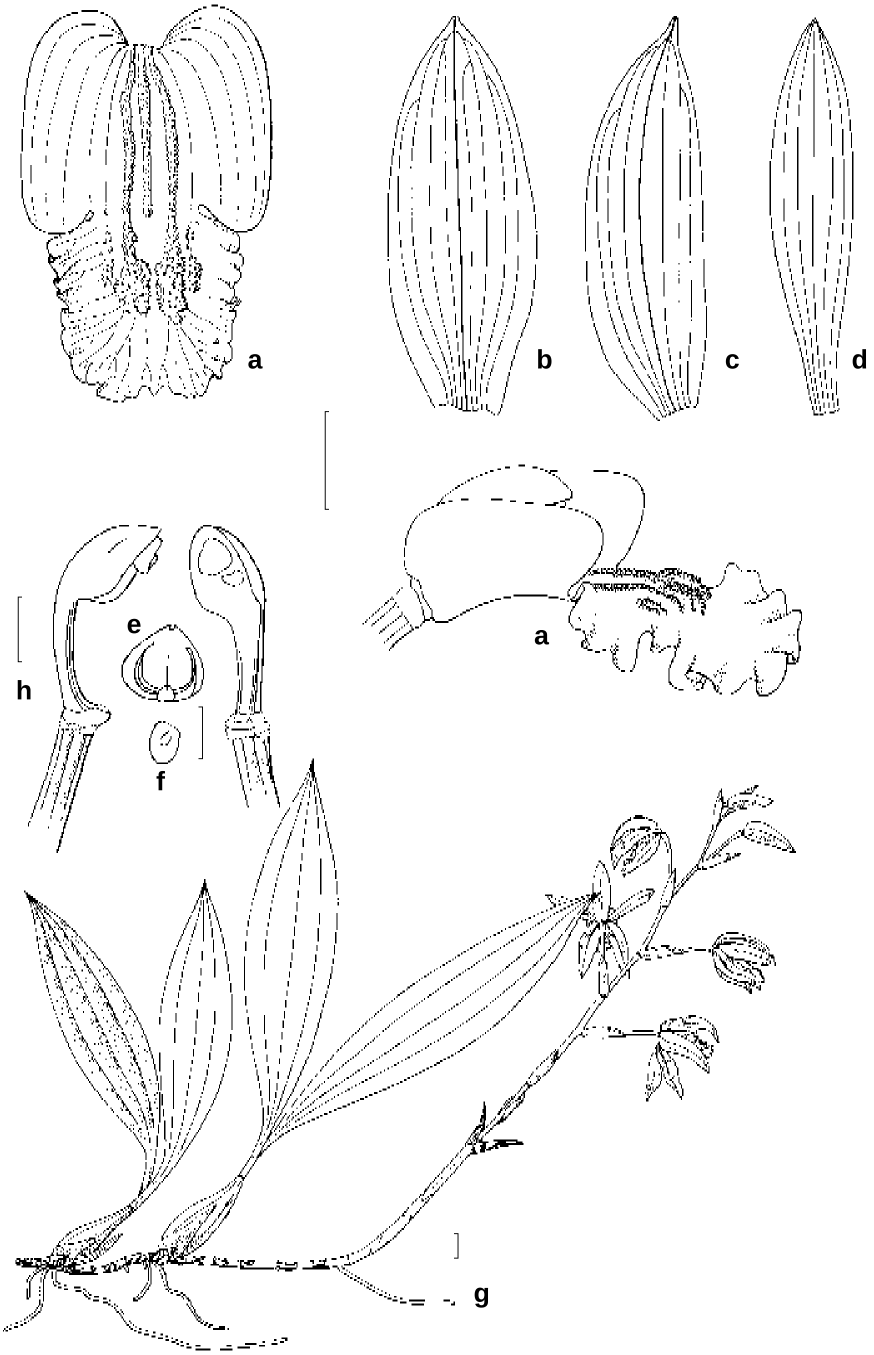
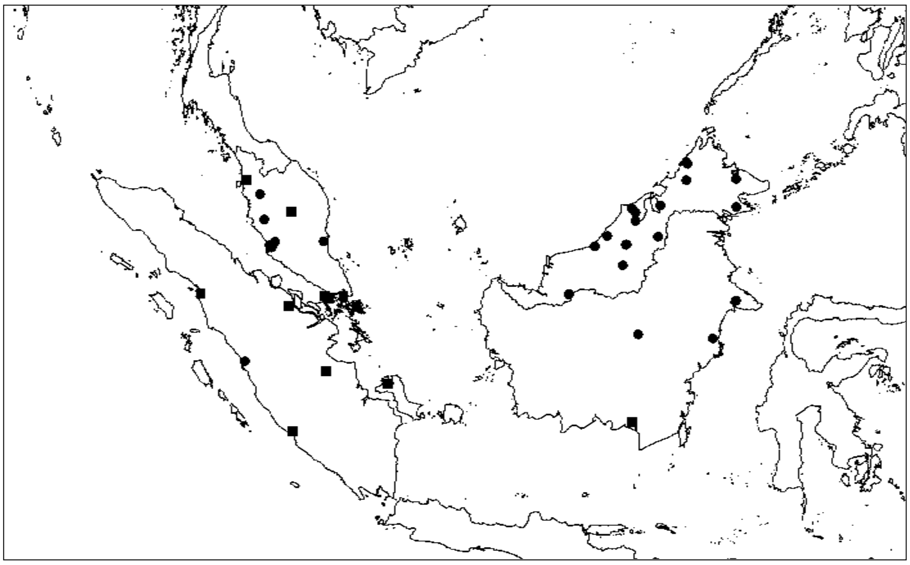


Fig. 6.8. *Coelogyne mayeriana* Rchb.f. a. Lip ornamentation, front and lateral view; b. median sepal; c. lateral sepal; d. petal; e. anther; f. pollinium; g. habit; h. column: lateral and front view (*Leiden cult. 27297*). — Scale bars: 1 cm (a–d, g); 2 mm (e, f); 5 mm (h).



Map 6.3. Distribution of *Coelogyne mayeriana* Rchb.f. (n) and *C. pandurata* Lindl. (l).

tions which are in outline more or less elliptic, the two middle patches 3.5–6 by 2–4 mm, the lateral patches 2–3.5 by 1–2 mm. *Column* in outline spathulate, 10–16 by 4–6 mm; column foot pronounced; stalk 5–8.5 by 1–1.2 mm; hood about triangular, 6–9 by 4–6 mm, top broadly rounded, with slightly irregular margin. *Anther* obovate, 2.8–3 by 2–3.2 mm, base triangular, top broadly rounded, tip emarginate. *Pollinia* obovate, 1.2–1.5 by 0.8–1 mm. *Stigma* semi-elliptic, 2–2.8 by 2.5–4 mm; rostellum about rectangular, 1.8–2 by 2–2.5 mm. *Fruit* ellipsoid, 5–5.5 by 2.5–3.2 cm; margins flat, 2.8–3.2 mm wide; valves 18–24 mm wide, with a low keel. *Seeds* shortly fusiform, to 2.2–3 mm long; embryo 0.7–1 mm long.

Distribution — Sumatra, Peninsular Malaysia, Singapore, Borneo (one doubtful record from Nusa Kambangan Island, Java).

Habitat & Ecology — Epiphytes, lithophytes or terrestrials. Lowland forest, at the base of *Oncosperma* in sandy places on the coast near mangrove swamps, in partial shade to exposed areas. Elevation 0–100 m. Flowering all the year when considered over its entire range, but in any given area flowering only a few times per year.

Notes — 1. Pseudobulbs and leaves green. Sepals and petals light green. Lip light green, at the extreme base orange; central keel whitish, with blackish brown tips, crest green; lateral keels green, with blackish brown tips; lateral lobes inside with 3–5 longitudinal blackish brown veins. Cushion-like projections pale green. Column pale green, lateral lines on each side of the stalk blackish brown; cross ridge on column foot orange. Anther yellow greenish; pollinia light yellow. Root tip pale orange. Fragant. Colour description based on living material, slides, and notes on the labels of the collections.

2. The epithet *mayeriana* refers to the names of two curators, father and son Mayer of Karlsruhe, Germany, who sent Reichenbach the material from which he described this species.

3. The dimensions are based on living and spirit material.

4. The young parts of the plants are covered with a sticky substance.

5. The species can be recognised by the distant, non-flattened pseudobulbs and the presence of lateral rows of cushion-like projections on the midlobe of the lip.

6. Carr (1928) reported this species to be pollinated by wasps which are attracted by the scent of the flowers. The keels are described as guide structures which ensure that the insect reaches the orange swelling at the centre base of the lip where the nectar is stored.

7. There are no recent collections from the wild of this species. It is probably extinct throughout most of its range.

5. Coelogyne pandurata Lindl. — Fig. 6.9, Plate 6.1c, 6.1d, Map 6.3

Coelogyne pandurata Lindl., Gard. Chron. 1 (1853) 791; Fol. Orchid. (1854) 3; Bot. Mag. 84 (1858) t. 5084; Rchb.f., Ann. Bot. Syst. 6 (1861) 224; H.J. Veitch, Man. Orchid. Pl. 6 (1890) 47; Ridl., J. Linn. Soc., Bot. 31 (1896) 286; 32 (1896) 325; Zörnig, Bot. Jahrb. Syst. 33 (1904) 651, f. 22; Pfitzer & Kraenzl. in Engl., Pflanzenr. 32 (1907) 75, f. 26C; J.J. Sm., Teysmannia 31 (1920) 294; Ames in Merr., Enum. Born. Pl. (1921) 144; Enum. Philipp. Flow. Pl. 1 (1924) 283; C.F. Sander, F.K. Sander & L.L. Sander, Sander's Orch. Guide (1927) 127; M.R. Hend., Gard. Bull. Straits Settlem. 4 (1928) 334; J.J. Sm., Feddes Repert. Beih. 32 (1933) 166; Carr, Gard. Bull. Straits Settlem. 8 (1935) 76; Quisumb., Philipp. Orchid Rev. (1951) 12, 20; Latif, Bunga Anggerik (1953) 96, pl. 20; Holttum, Orchids of Malaya 3 (1964) 254; Bechtel in P.J. Cribb & Launert, Orch. Atl. (1980) 104; Valmayor, Orchid. Philipp. 1 (1984) 38; Seidenf. & J.J. Wood, Orchids of Penins. Malaysia and Singapore (1992) 217, f. 92C, pl. 13A. — *Pleione pandurata* (Lindl.) Kuntze, Rev. Gen. Pl. 2 (1891) 680. — Type: *Loddiges (Low) s.n.* (1/12/1853) (holo K-LINDL), Borneo.

Coelogyne peltastes Rchb.f. var. *unguiculata* J.J. Sm., Mitt. Inst. Allg. Bot. Hamburg 7 (1927) 33, f. 23, syn. nov. — Type: *Winkler 347* (holo HAMB), Borneo.

Roots 2–3 mm diam. Rhizome creeping or climbing, 0.9–1.3 cm thick, 6–14 internodes between two pseudobulbs; scales overlapping. *Pseudobulbs* 4.5–10 cm apart, in cross section rather flattened, in outline (ovate-)oblong, with slightly flattened sides, 6.5–19 by 4–7 by 1.5–3 cm; the downwards facing side with a distinct swollen ridge; scales covering the pseudobulb 4.5–18 by 4–7 cm. *Leaf* petiole 5–15 by 0.3–0.9 cm; blade lanceolate, 15–66 by 3.5–10.5 cm; main nerves 5–9. *Inflorescence* proteranthous or synanthous, (3–)6–15-flowered. Scape 5.7–21.5 cm long including the part covered by the scales of the young shoot. Rhachis 15–47 cm long; internodes 4–17, 2–5.7 cm long. *Sterile bracts* 1 or 2, oblong, 2.7–5.5 by 1–2.2 cm; fertile bracts oblong, 2.7–4.7 by 1–2.4 cm. Pedicel 10–52 by 2–3 mm; ovary 10–20 by 3–5 mm. *Median sepal* ovate-lanceolate, 35–75 by 7–21 mm; nerves 11–15, the median one prominent. *Lateral sepals* falcate, ovate-lanceolate, 32–68 by 8–18 mm; nerves 7–11. *Petals* obovate-lanceolate, 33–70 by 8–16 mm; nerves 7–9(–11), midrib rather prominent. *Hypochile* 12–25 by 15–34 mm, when flattened base emarginate to subtruncate; lateral lobes

Plate 6.1. – a. *Coelogyne asperata* Lindl. (*Leiden cult. 27621*, Sarawak). Photograph A. Vogel. – b. *C. x burfordiense* (*Leiden cult. 21413*, unknown origin). Photograph B. Kieft. – c. *C. pandurata* Lindl. (*Leiden cult. 21532*, unknown origin). Photograph C.G. Koops. – d. *C. pandurata* Lindl. (*Leiden cult. 930916*, Sarawak). Photograph A. Schuiteman.

a. *Coelogyne asperata*

b. *Coelogyne x burfordiense*

c. *Coelogyne pandurata*

d. *Coelogyne pandurata*

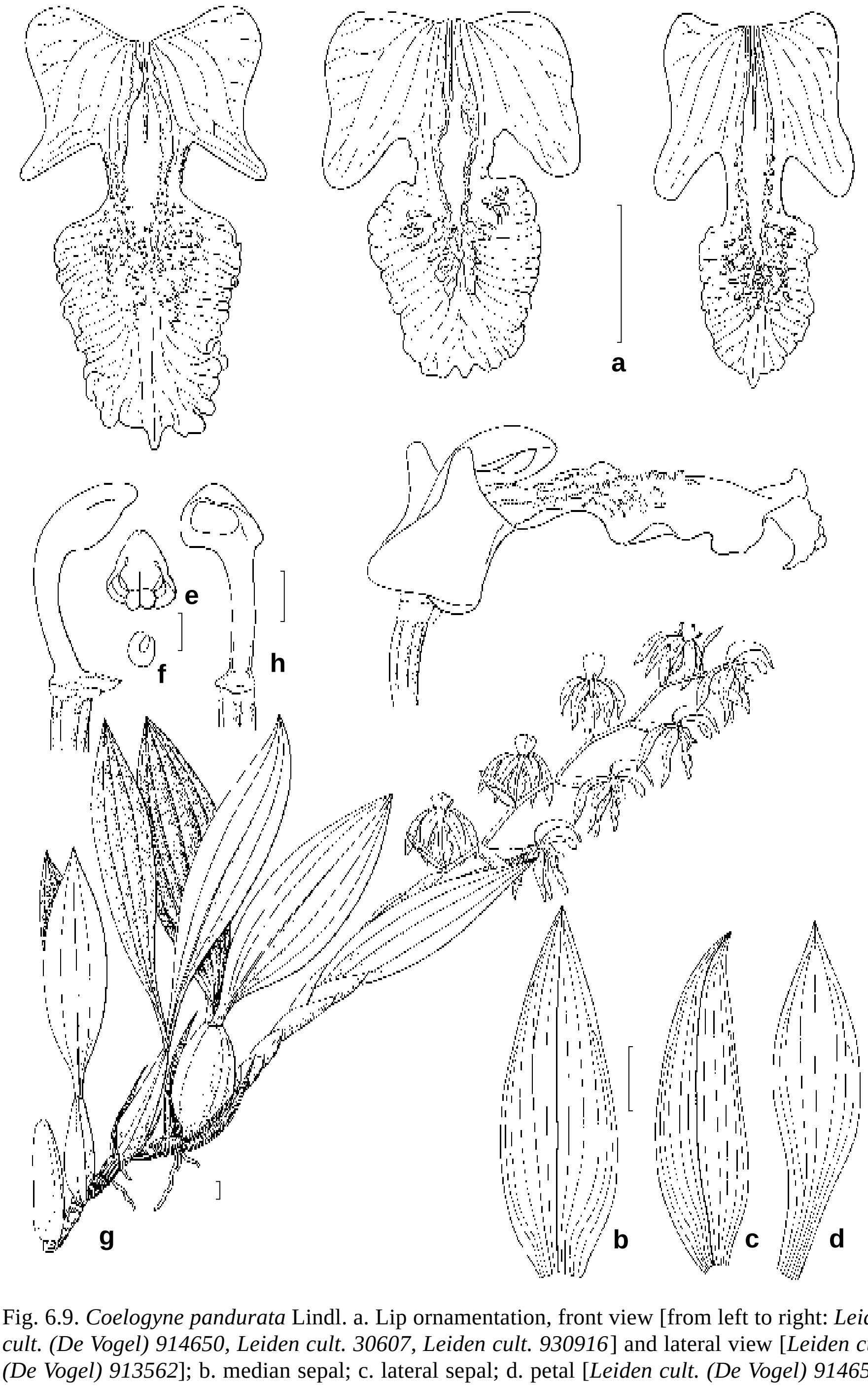


Fig. 6.9. *Coelogyne pandurata* Lindl. a. Lip ornamentation, front view [from left to right: *Leiden cult. (De Vogel) 914650, Leiden cult. 30607, Leiden cult. 930916*] and lateral view [*Leiden cult. (De Vogel) 913562*]; b. median sepal; c. lateral sepal; d. petal [*Leiden cult. (De Vogel) 914650*]; e. anther; f. pollinium; g. habit; h. column: lateral and front view [*Leiden cult. (De Vogel) 913562*]. — Scale bars: 1 cm (a–d, g); 2 mm (e, f); 5 mm (h).

12–25 by 6–12 mm, at the base projecting backwards for 1.5–5 mm; in front triangular-ligulate, projecting for 3–10 mm, with rounded apex; keels 3, with entire margin, low and rounded at the base, the median keel low, in the basal half of the hypochile rounded and swollen, gradually lowering to the front, ending below or close to the junction of hypo- and epichile, the lateral keels in the basal half of the hypochile distinctly swollen, with irregularly indentate margin and sides, in the front half of the hypochile distinctly raised, plate-like, in lateral view semi-elliptic, single or double crested, each margin undulate or not undulate, continuing into the much lower keels on the epichile. *Epichile* about spathulate, 17–40 by 9–23 mm; claw about rectangular, 3–8 by 5–10 mm, margins straight, sometimes coarsely dentate, keels 2, low plate-like with a rather irregularly and coarsely broken up single or double top margin, at the top sometimes with molar-like structures on each side which continue into the blade; blade irregularly rectangular to quadrangular to ovate, 15.5–30 by 10–23 mm, the top truncate to acute, the tip acute, triangular, mostly with a small notch on either side, the margin broadly and regularly undulate, when flattened about straight, with molar-like structures as on the claw converging towards the middle of the blade, and there they are lost among a series of higher, transverse, molar-like warts, the whole patch of molar-like structures on midlobe about ovate, 8–17 by 7–18 mm. *Column* in outline spathulate, (12–)15–25 by 3–5 mm; column foot pronounced; stalk 8–15 by 1–3 mm; hood about triangular, 7–10 by 3–5 mm, top broadly rounded, with slightly to very irregular margin. *Anther* obcordate, 2.8–5 by 3–5 mm, base triangular, top broadly rounded to truncate, tip emarginate. *Pollinia* obovate, 1–2 by 0.8–1.5 mm. *Stigma* semi-elliptic, 2.2–3.5 by 3–4 mm; rostellum about rectangular, 1.3–3 by 2.2–3 mm. *Fruit* ellipsoid, 6–8.5 by 4.5–6 cm; margins flat, 3–5 mm wide; valves 40–50 mm wide, with a low keel. *Seeds* shortly fusiform, to 3–4 mm long; embryo 0.7–1.3 mm long.

Distribution — Sumatra [Smith (1933b), based on *Bünnemeijer 32*, not seen], Peninsular Malaysia, Borneo (Sabah, Brunei, Sarawak, Kalimantan), and possibly the Philippines [Valmayor (1984), based on specimens from Agusan, Bontoc, Samar and Surigao, not seen].

Habitat & Ecology — Epiphytes on trunks and big branches of trees, lithophytes or terrestrials. Lowland forest and hill forest, in partial shade to quite exposed. Among rocks, on granite or ultramafic substrate. Elevation 10–1000 m. Flowering all the year when considered over its entire range, but in any given area flowering only once or twice a year.

Notes — 1. Pseudobulbs and leaves green. Sepals and petals light greenish. Lip light greenish with black or brown patches, at the extreme base orange; keels pale green with blackish brown tips, at the base white; lateral lobes with 4–8 brown to black veins; midlobe claw and blade with black or brown and light green molar-like projections. Column light greenish; sometimes with blackish brown lateral lines on each side of the stalk; cross ridge on column foot orange. Anther light greenish; pollinia

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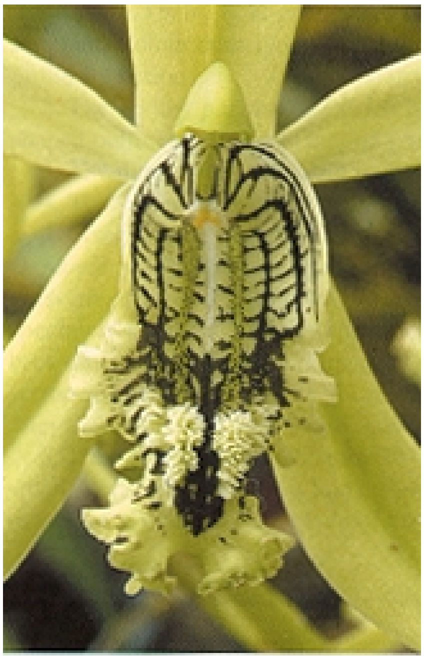
Plate 6.2. – a. *Coelogyne mayeriana* Rchb.f. (*Leiden cult. 970767*, unknown origin). Photograph C.G. Koops. – b. *C. marthae* S.E.C. Sierra (*Leiden cult. 27496*, Sarawak). Photograph P. Jongejan. – c. *C. verrucosa* S.E.C. Sierra (*Leiden cult. 970597*, Sarawak). Photograph A. Schuiteman. – d. *C. zurowetzii* Carr (*Liem K.W. cult. 2.84*, Kalimantan). Photograph J. Comber.



a. *Coelogyne mayeriana*

b. *Coelogyne marthae*

c. *Coelogyne verrucosa*

d. *Coelogyne zurowetzii*

dull yellow. Ovary light greenish, with brown scale-like hairs. Root tip pale orange. Fragrant. Colour description based on living material, slides, and notes on the labels of the collections.

2. The epithet *pandurata* (which is Latin for violin-shaped) refers to the violin-shaped outline of the lip in natural position.

3. The dimensions are based on living and spirit material.

4. The young parts of the plant are covered with a sticky substance.

5. Considerable variation in size and colour is present among the specimens of *C. pandurata*. Most orchid growers know the large form of this species with the big grass green flowers with pitch black markings on the lip. There are, however, many specimens among the collections which are much smaller or intermediate in size, with brown instead of black markings on the lip (Plate 6.1d). Pelser et al. (2000) also describe size plasticity for the species of sect. *Fuliginosae*. *Coelogyne peltastes* var. *unguiculata* J.J. Sm. was based on a small-flowered form of *C. pandurata.*

6. This species can be recognised by the rather flattened pseudobulbs, the relatively small lateral lobes of the lip, and the presence of molar-like structures which converge towards the middle of the blade of the epichile.

6. Coelogyne peltastes Rchb.f. — Fig. 6.10, Map 6.2

Coelogyne peltastes Rchb.f., Gard. Chron. 2, 14 (1880) 296; Pfitzer & Kraenzl. in Engl., Pflanzenr. 32 (1907) 73, f. 25, 26c; J.J. Sm., Teysmannia 31 (1920) 295; Dakkus, Orch. Ned. Ind. 2 (1931) 70; 3 (1935) 86. — Type: *Veitch s.n.* (?/8/1880) (*Reichenbach Herb. 21503*) (holo W), Borneo.

Roots c. 2.5 mm diam. Rhizome climbing (from type description), not seen. *Pseudobulbs* in cross section very flattened, in outline oblong, with margins which incurve, forming a sort of convex shield over the scandent stem, 8.2 by 5.5 cm. *Leaf* petiole 4.2–4.4 by 0.3–0.5 cm; blade lanceolate, 27.5–28 by 3.9–4 cm; main nerves 5. *Inflorescence* 3–9-flowered. Scape 4.6–10.5 cm long including the part covered by the scales of the young shoot. Rhachis 6–27 cm long; internodes 4–11, 1.9–4.2 cm long. *Sterile bracts* 1 or 2, ovate-oblong to ovate-lanceolate, 3.5–5.2 by 1–1.6 cm; fertile bracts ovate-oblong to ovate-lanceolate, 3–4.2 by 0.8–1.4 cm. Pedicel 15–27 by 1.5–2.2 mm; ovary 7–12 by 1.7–3 mm. *Median sepal* ovate-lanceolate, 34–47 by 7–14 mm; nerves 9–11, the median one prominent. *Lateral sepals* falcate, ovate-lanceolate, 36–40 by 4.5–10 mm; nerves 7. *Petals* obovate-lanceolate, 40–43 by 6–9 mm; nerves 5–7, midrib slightly prominent. *Hypochile* 12–17 by 11–19 mm, when flattened the base emarginate to subtruncate; lateral lobes 12–17 by 4–7 mm, at the base projecting backwards for 1–2 mm; in front either distinctly descending with broadly rounded apex which is not projecting, to slightly descending, the free part about semi-orbicular, projecting for 2–3 mm; keels 3, with entire margin, low and rounded at the base, the median keel beyond the base slightly higher, continuing as a swollen low keel on the base of the epichile, the lateral keels higher than the median keel, thin plate-like, single crested, continuing into the much lower keels on the claw of the epichile, near the epichile with several molar-like projections. *Epichile* not spathulate, 15–20 by 10–16 mm; claw absent, blade irregularly rectangular the top truncate, the tip acute, triangular, mostly with a small notch on either side, margin broadly and regularly and finely undulate, the median keel at the end elevated and thin plate-like, when flattened about

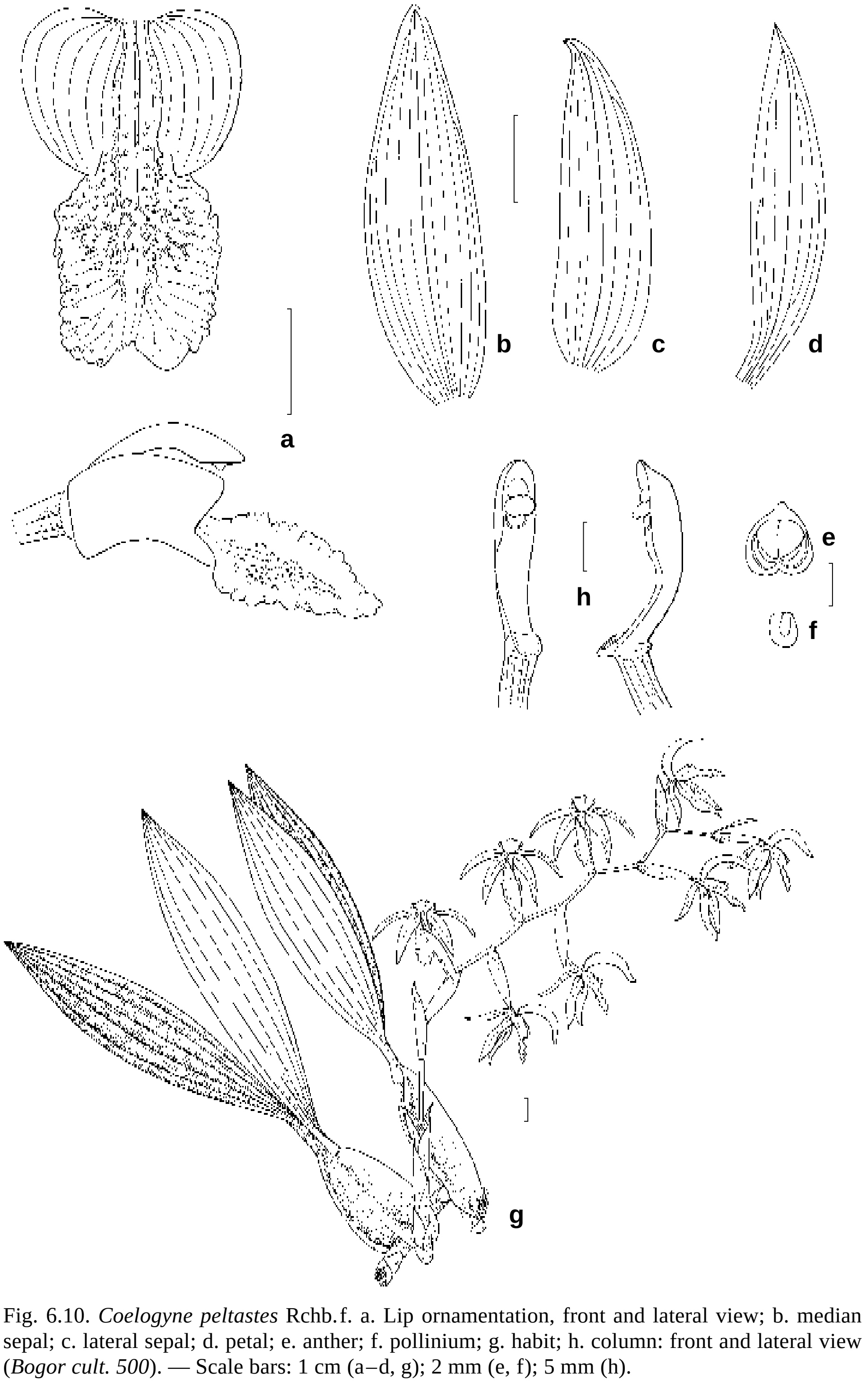


Fig. 6.10. *Coelogyne peltastes* Rchb.f. a. Lip ornamentation, front and lateral view; b. median sepal; c. lateral sepal; d. petal; e. anther; f. pollinium; g. habit; h. column: front and lateral view (*Bogor cult. 500*). — Scale bars: 1 cm (a–d, g); 2 mm (e, f); 5 mm (h).

straight, ornamentation consisting of a patch 7–12 by 5–10 mm, consisting of tooth-like, more or less flattened warts, often arranged in radiating rows, the median ones to the top of the patch higher, more molar-like. *Column* in outline narrowly spathulate, 17–20 by 3.7–5 mm; column foot pronounced; stalk 9–13 by 2.7–3.2 mm; hood about triangular, with slightly irregular margin, 7–9.5 by 3.7–5 mm, top broadly rounded, with irregular margin. *Anther* obcordate, 3.3–3.7 by 2.8–3.2 mm, base triangular; top broadly rounded, tip emarginate. *Pollinia* obovate, 1.6–1.8 by 1.1–1.4 mm. *Stigma* semi-elliptic, 2.5–3 by 4–4.2 mm; rostellum about rectangular, 2.1–2.3 by 2.1–2.4 mm. *Fruit* and *seeds* not seen.

Distribution — Borneo (Kalimantan Barat).

Habitat & Ecology — Epiphytes on tree trunks near the ground in heath forest. Flowering: April, August.

Notes — 1. Pseudobulbs and leaves green. Sepals and petals light yellow to emerald green. Lip white; lateral lobes with 4–8 dark brown veins; midlobe blade with brown and white warts. Column light greenish. Scent not recorded. Colour description based on type description and water colour illustrations from the Reichenbach Herbarium collection (W).

2. The epithet *peltastes* (which is Latin for shield-shaped) refers to the kind of concave shield over the climbing rhizome formed by the pseudobulbs.

3. The dimensions are based on spirit (inflorescence) and dry (vegetative) material.

4. The species can be recognised by the presence of very flattened pseudobulbs with incurved margins, the absence of a claw at the base of the epichile, and the presence of molar-like projections on the midlobe of the lip.

5. The type material present in Reichenbach's Herbarium in Vienna consists of one herbarium sheet with drawings of the plant sent by Veitch in 1880, and a second with dried leaves and pseudobulbs. A watercolour painting made on 1 November 1881 by John Day and preserved in one of his scrapbooks at Kew is based on the same specimen from which Veitch had earlier sent material to Reichenbach.

7. **Coelogyne verrucosa** S.E.C. Sierra, *spec. nov.* — Fig. 6.11, Plate 6.2c, Map 6.2

> A *Coelogyne pandurata* pseudobulbis planissimis, labello in lobo mediali macula magna verrucis satis magnis rotundatis differt. — Typus: *Vermeulen & Lamb 322* (holo L; iso K), Sabah.

Roots 2–4 mm diam. Rhizome climbing, 0.7–1.2 cm thick, 4–10 internodes between two pseudobulbs; scales overlapping. *Pseudobulbs* 1.8–5 cm apart, in cross section very flattened, in outline ovate, with margins which slightly incurve, pressed against the rhizome and the lower part of the subsequent pseudobulb, 5–10 by 3.3–5 by 0.7–1.3 cm; scales covering the pseudobulb 6–9.8 by 3–4 cm. *Leaf* petiole 2–6 by 0.3–0.7 cm; blade lanceolate, 16–38 by 2.5–6 cm; main nerves 7–9. *Inflorescence* proteranthous or synanthous, 6–10-flowered. Scape 3.5–14 cm long including the part covered by the scales of the young shoot. Rhachis 12.5–34 cm long; internodes 8–12, 1.2–5 cm long. *Sterile bracts* 1 or 2, oblong, 2.3–4 by 0.9–1.7 cm; fertile bracts, oblong, 2–3.2 by 0.7–1.8 cm. Pedicel 13–50 by 1–2 mm; ovary 7.5–12 by 1.3–3 mm. *Median sepal* ovate-lanceolate, 18.5–40 by 6–13 mm; nerves 9–11, the median one prominent. *Lateral sepals* falcate, ovate-lanceolate, 20–37.5 by 5.5–9 mm; nerves

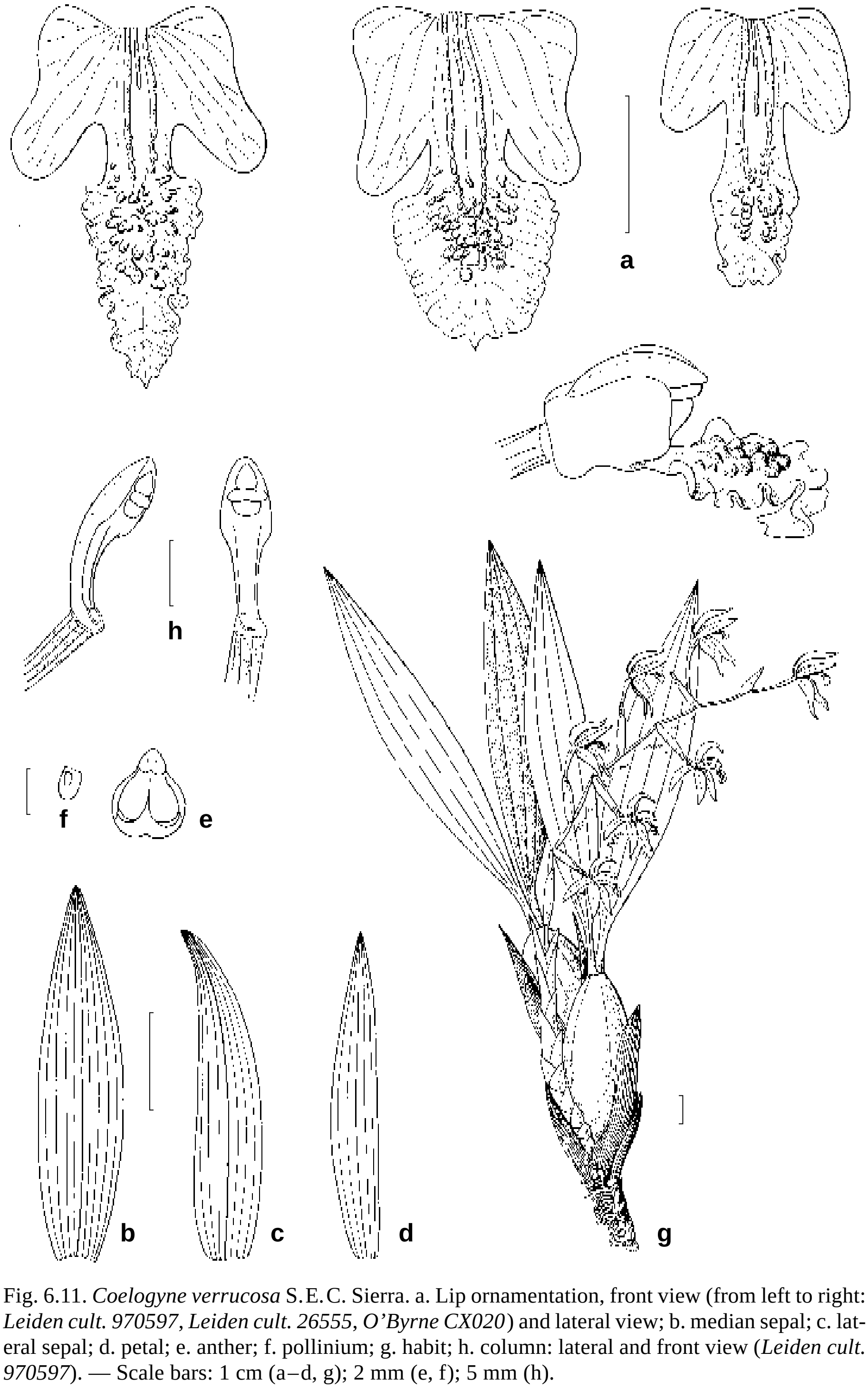


Fig. 6.11. *Coelogyne verrucosa* S.E.C. Sierra. a. Lip ornamentation, front view (from left to right: *Leiden cult. 970597*, *Leiden cult. 26555*, *O'Byrne CX020*) and lateral view; b. median sepal; c. lateral sepal; d. petal; e. anther; f. pollinium; g. habit; h. column: lateral and front view (*Leiden cult. 970597*). — Scale bars: 1 cm (a–d, g); 2 mm (e, f); 5 mm (h).

7–9. *Petals* lanceolate, 17.5–36 by 3.3–6.2 mm; nerves 5–7 rather prominent. *Hypochile* 9–13.5 by 10–19 mm, when flattened base emarginate to subtruncate; lateral lobes 9–13.5 by 4.5–6 mm, at the base projecting backwards for 0–2.2 mm; in front triangular-ligulate, free part projecting for 2.8–5 mm, with broadly rounded apex; keels 3, with entire margin, low and rounded at the base, the median keel low and rounded, gradually lowering to the front, continuing to the middle or sometimes up to the junction of hypo- and epichile, the lateral keels at the base low, more to the front higher than the median one, rounded, or thin to thick plate-like and then the raised part in lateral view semi-elliptic, widened at the crest, single or double crested, continuing on the epichile. *Epichile* about spathulate, 12–16.5 by 6–12 mm; claw about rectangular, 2.5–4.5 by 3.5–6.5 mm, margins straight, keels 2, low plate-like with a rather irregularly and coarsely broken up single crest, at the top and lateral of the keels with few scattered tooth-like projections which continue on the blade; blade irregularly rectangular to quadrangular to ovate, 8–14 by 6–12 mm, the top acute to rounded, the tip acute, triangular, mostly with a small notch on either side, margin broadly and regularly undulate, when flattened about straight, ornamentation on the very base consisting of few molar-like structures as on the claw, beyond that with a more or less ovate, 4.5–13 by 3–7 mm big patch of rather big, rounded, projecting warts. *Column* in outline spathulate, 11.5–16 by 2.5–5 mm; column foot small; stalk 5–9 by 1.5–3 mm; hood distinctly widened, about ovate, 4.5–9 by 2.5–5 mm, top broadly rounded, with slightly to very irregular margin. *Anther* obcordate, 1.5–3.2 by 2.5–5 mm, base triangular, top broadly rounded, tip emarginate. *Pollinia* obovate, 1.2–1.8 by 0.7–1.2 mm. *Stigma* semi-elliptic, 1.5–2 by 2–3 mm; rostellum about rectangular, 1.3–1.7 by 2–3 mm. *Fruit* ellipsoid, 4 by 2.1 cm; margins flat, 1.5 mm wide; valves 18 mm wide, with a low keel. *Seeds* shortly fusiform to 1.8–2.1 mm long; embryo 0.7–1 mm long.

Distribution — Borneo (Sarawak, Brunei, Sabah).

Habitat & Ecology — Epiphytes on trunks and big branches of trees, or terrestrials. Elevation 10–700 m. Heath, peat and mixed Dipterocarp forest. Flowering all year round when considered over its entire range, but in any given area flowering only once or twice a year.

Notes — 1. Pseudobulbs and leaves green. Bracts, sepals and petals light greenish. Lip light greenish with brown patches, at the extreme base yellow; keels in the basal part of the hypochile white, in the middle pale green, at the top with dark brown tips; lateral lobes with 4–8 brown veins; midlobe claw and blade with light greenish molar-like projections. Column light greenish, sometimes with brown lateral lines on each side of the stalk; cross ridge on column foot yellow. Anther light greenish; pollinia dull yellow. Ovary light greenish, with brown scale-like hairs. Root tips pale orange. Fragrant. Colour description based on living material, slides, and notes on the labels of the collections.

2. The epithet *verrucosa* (which is Latin for warty) refers to the big rounded projecting warts on the midlobe of the lip.

3. The dimensions are based on living and spirit material.

4. Young parts of the plant are covered with a sticky substance.

5. The species can be recognised by the strongly flattened pseudobulbs and a lip with a single big patch of rather large, rounded, projecting warts on the midlobe.

8. **Coelogyne zurowetzii** Carr — Fig. 6.12, Plate 6.2d, Map 6.2

Coelogyne zurowetzii Carr, Orchid Rev. 42 (1934) 44; Backer & Bakh.f., Fl. Java 3 (1968) 283. — Type: *Zurowetz s.n.*, Borneo, Kalimantan, Sambas (holo SING, not found). Neotype (here chosen): *L'Horticulture Internationale cult. (Linden) s.n.* (2/7/1890) (holo K), Borneo.
Coelogyne peltastes auct. non Rchb.f.: Rolfe, Gard. Chron. 3, 8 (1890) 529.

Roots 1–1.5 mm diam. Rhizome creeping, 0.6–0.7 cm thick, 5–10 internodes between two pseudobulbs; scales overlapping. *Pseudobulbs* 3–5 cm apart, in cross section very flattened, in outline oblong with slightly incurved margins, 4.5–9 by 4–6 by c. 1.5 cm (from type description); scales covering the pseudobulb 8–8.5 by 3–3.5 cm. *Leaf* petiole 4–5 by 3–5 cm; blade obovate-lanceolate, 16–21 by 3.5–6.5 cm; main nerves 5–7. *Inflorescence* synanthous, 4–11-flowered. Scape 2.8–5.7 cm long including the part covered by the scales of the young shoot. Rhachis 10.5–19 cm long; internodes 5–12, 2.5–3 cm long. *Sterile bracts* 1–3, oblong to lanceolate, 2–3.2 by 1–1.7 cm; fertile bracts, oblong to lanceolate, 1.9–2.7 by 0.6–1 cm. Pedicel 12–35 by 1–2 mm; ovary 8–12 by 2–2.5 mm. *Median sepal* ovate-lanceolate, 27–33 by 8–10 mm; nerves 9, the median one prominent. *Lateral sepals* slightly falcate, ovate-lanceolate, 23–37 by 6–8 mm; nerves 7. *Petals* obovate-lanceolate, 26–34 by 3–5 mm; nerves 5, midrib slightly prominent. *Hypochile* 9–13 by 12–14 mm, when flattened base subtruncate or rounded; lateral lobes 10–13 by 3.5–5 mm, at the base not projecting backwards; in front triangular-ligulate, projecting for 2–4.5 mm, with rounded apex; keels 3, with entire margin, low and rounded at the base, the median keel beyond the base higher, the part up to about the middle of the hypochile long semi-elliptic in lateral view, beyond that continuing as a swollen low keel on the very base of the epichile, the lateral keels similar to the median keel, but the long semi-elliptic part higher, the part up to the base of the epichile thick plate-like, single crested, continuing into the much lower keels on the claw of the epichile. *Epichile* about spathulate, 11–17 by 11–12 mm; claw about transverse rectangular, 1.5–2 by 4–5 mm, margins irregular, keels 3, shaped as swollen nerves, low, with a rather irregularly and coarsely broken up single margin; sometimes near the junction with the blade with few, small, scattered tooth-like projections or with 2 additional swollen nerves which continue on the blade; blade irregularly rectangular to ovate, 12–14 by 10–13 mm, the top broadly rounded to truncate, the tip acute, triangular, mostly with a small notch on either side, the margin very finely undulate, when flattened about irregular, ornamentation consisting of a patch of warts and nerves, 7–11 by 6–9 mm, at the base formed mainly by 2–4 raised nerves with few scattered tooth-like projections, higher up the raised nerves break up into short rows or patches of scattered, single or connected, rounded and molar-like warts, the warts towards the margins of the patch single and scattered. *Column* in outline narrowly spathulate, 13–16 by 2–4 mm; column foot very small; stalk 8–10 by 1–2 mm; hood about triangular, 5–7 by 2–4 mm, top broadly rounded, with slightly irregular margin. *Anther* obcordate, 2.2–2.5 by 1.7–2 mm, base triangular; top broadly rounded, tip emarginate. *Pollinia* obovate, 1–1.2 by 0.8–1 mm. *Stigma* semi-elliptic, 2–2.8 by 2–3 mm; rostellum about rectangular, 1.5–1.7 by 2–2.3 mm. *Fruit* and *seeds* not seen.

Distribution — Borneo (Kalimantan, Sabah).

Habitat & Ecology — Epiphytes or terrestrials. Elevation to c. 900 m. Lowland plains, sandy soils. Flowering: April–November.

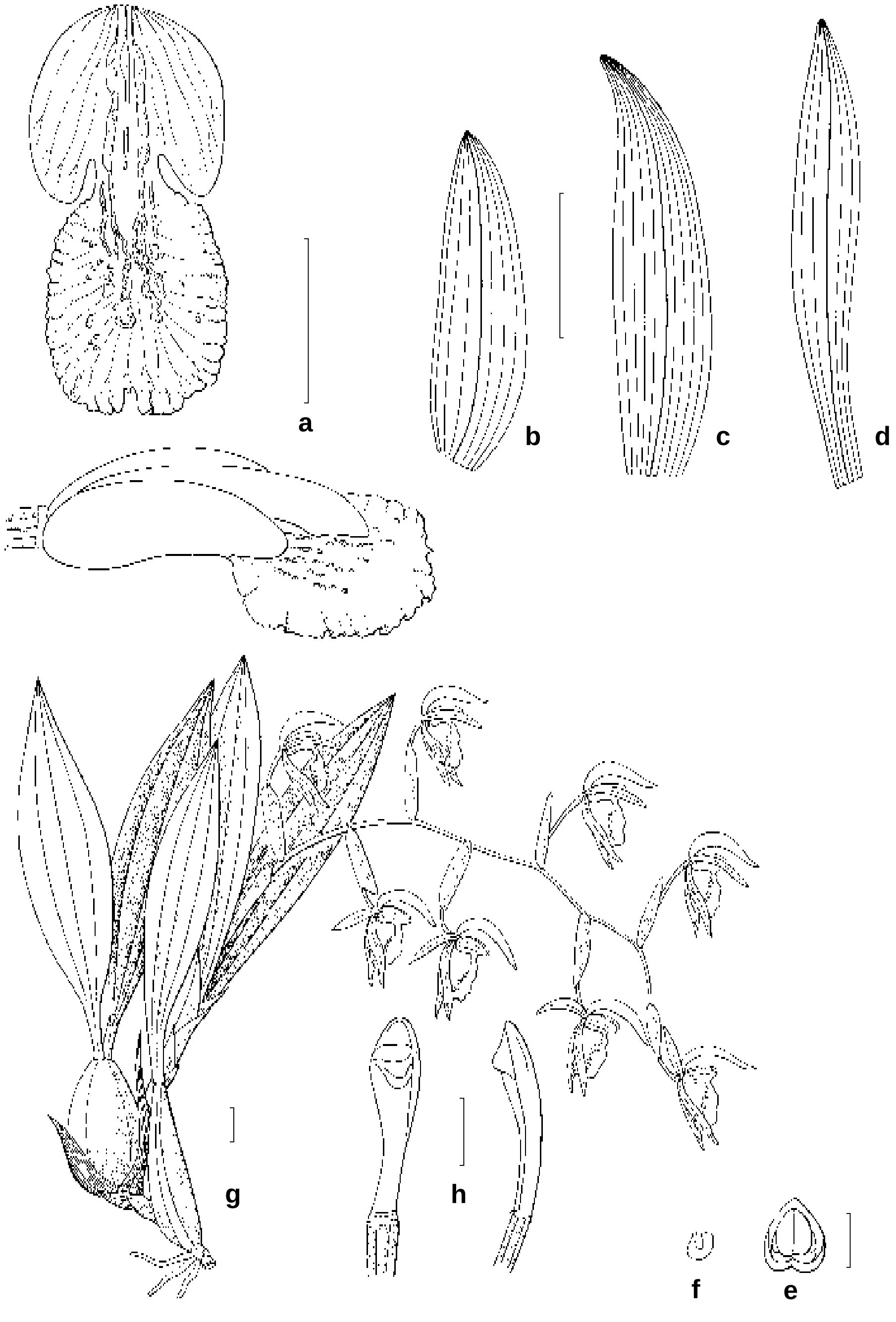


Fig. 6.12. *Coelogyne zurowetzii* Carr. a. Lip ornamentation, front and lateral view; b. median sepal; c. lateral sepal; d. petal [*Le Douse cult. s.n.* (29/7/92)]; e. anther; f. pollinium [*Kew. cult. s.n.* (2/11/1894)]; g. habit; h. column: front and lateral view [*Le Douse cult. s.n.* (29/7/92)]. — Scale bars: 1 cm (a–d, g); 2 mm (e, f); 5 mm (h).

Notes — 1. Pseudobulbs and leaves green. Sepals and petals light greenish. Lip white, at the extreme base yellow; keels white tipped with green; lateral lobes with 4–8 brown veins; midlobe claw and blade with brown swollen nerves and yellowish white warts. Column green with brown lateral stripes on each margin of the stalk. Anther light greenish; pollinia dull yellow. Ovary light greenish, with brown scale-like hairs. Scent not recorded. Colour description based on slides and notes on the labels of the collections.

2. The epithet *zurowetzii* refers to Mr. J.E. Zurowetz, the collector of the type specimen.

3. The dimensions are based on dry material.

4. The species can be recognised by the strongly flattened pseudobulbs, and the very finely undulate margin of the epichile, which is provided with small, scattered rounded to tooth-like projections.

5. The type was not found in Singapore or in any of the other herbaria from which material was requested on loan.

EXCLUDED SPECIES

9. *Coelogyne papillosa* Ridl. in Stapf, Trans. Linn. Soc. London 4 (1894) 238, f. 14, pl. 26B, C; Ridl., J. Linn. Soc., Bot. 31 (1896) 287; Pfitzer & Kraenzl. in Engl., Pflanzenr. 32 (1907) 78; Rolfe in Gibbs, J. Linn. Soc., Bot. 42 (1914) 154; Carr, Gard. Bull. Straits Settlem. 8 (1935) 211. — Type: *Haviland 1098* (holo SING; iso K), Sabah, Mt Kinabalu.

Note — This species is removed from sect. *Verrucosae* based on the results obtained from the morphological phylogenetic analysis. This species has characters which are not present in the other species of sect. *Verrucosae* as here recognised, such as a pronounced zigzagging rhachis, a column hood with dentate margin, a lip with six keels, and nerves on the lateral lobes of the hypochile, which are pronounced as low rounded keels.

10. *Coelogyne brachyptera* Rchb.f., Gard. Chron. 16 (1881) 6; Hook.f., Fl. Brit. India 5 (1890) 842; Pfitzer & Kraenzl. in Engl., Pflanzenr. 32 (1907) 78; Seidenf., Opera Bot. 114 (1992) 116; Bechtel in P.J. Cribb & Launert, Orch. Atl. (1993) 121. — Type: *Low s.n.* (1881) (holo W), Burma, Tenasserim.

11. *Coelogyne parishii* Hook.f., Bot. Mag. 88 (1862) t. 5323; Fl. Brit. India 5 (1886) 837; Pfitzer & Kraenzl. in Engl., Pflanzenr. 32 (1907) 77; Gagnep., Fl. Gén. Indo-Chine 6 (1933) 312; Bechtel in P.J. Cribb & Launert, Orch. Atl. (1993) 124. — Type: *Parishi s.n.* (?/?/1861) (holo K), Burma, Tenasserim, Moulmein.

12. *Coelogyne virescens* Rolfe, Bull. Misc. Inform. (1908) 70. — Type: *Micholitz s.n.* (holo K), Vietnam.

Note — The above mentioned three species have been included in sect. *Verrucosae*, but molecular evidence clearly indicates that at least one of these taxa (*C. virescens*) does not belong to the same clade as the species of sect. *Verrucosae* as here recognised.

Morphologically, *C. brachyptera*, *C. parishii* and *C. virescens* differ from the species of sect. *Verrucosae* by the hysteranthous inflorescence, imbricate bracts at the base of the peduncle, a glabrous ovary, and linear-lanceolate petals. A phylogenetic analysis with all three species might show that they should be placed in a section of their own, as is suggested by De Vogel (1994) and Clayton (in prep.).

ACKNOWLEDGEMENTS

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IDENTIFICATION LIST

Dates are used if the number of the collection is unknown. If only the year is known, it is placed between brackets.

1. *C. asperata*
2. *C. imbricans*
3. *C. marthae*
4. *C. mayeriana*
5. *C. pandurata*
6. *C. peltastes*
7. *C. verrucosa*
8. *C. zurowetzii*

Afriastini 2762: 1; 2777: 1 — Ahwang ?/9/1890: 4 — Alston 13780: 1 — Amdjah 376: 1; 1096: 1 — Anonymous C040: 1; 10/8/1914: 4 — Anthony SA 796: 1 — Argent & Coppins 954: 5.

B series (Murata, Iwatsuki, Kato et al.) 1770: 1 — Bartlett & La Rue 328: 1 — Beaman 7023: 7 — Bogor cult. 10: 5; 32: 6; 33: 6; 39: 5; 40: 6; 56: 1; 87: 6; 88: 1; 97: 4; 153: 1; 158: 4; 500: 6; (1910): 2; (1918) H.L.B. 9226298: 2; (1920): 5 — Brass 3831: 1; 11834: 1; 13804: 1 — Brooks ?/6/1909: 5; (1909/1910): 5; (1916): 1; 4/2/1928: 4 — BS series (Bolster) 294: 1; (Reillo) 15500: 1; 16257: 1 (Ramos) 17624: 1; (Ramos & Concovar) 84145: 1 — Bünnemeijer 1288: 1 — Burley, Tukirin et al. 1429: 1 — Burrage 17/5/1920: 5.

Carr 10017: 1; 10160: 1; 16745: 1 — Carrick & Enoch JC441: 7 — Chan 23/11/1986: 7 — Chaplin 780: 1 — Château du Semont cult. ?/7/1894: 4 — Chew Wee-lek CWL695: 1; CWL990: 7 — Clemens et al. 7524: 1 — Collenette 501: 7; (1960): 7 — Courtauld 8/9/1890: 1 — Creagh (1893): 5 — Cruttwell 961: 1 — Curtis (1880): 5; ?/6/1894: 1; (1897): 1.

Daud 1901: 1 — Day ?/6/1883: 1 — De Vogel 1336: 1; 1431: 1; 8152: 7; 8836: 3; 8879: 7 — De Wilde & De Wilde-Duyfjes 12200: 1; 12523: 1; 13484: 1; 14859: 1 — Dijk 940: 1 — Docters van Leeuwen 83: 1; 11400: 1.

Elmer 10008: 1 — Elsener 190: 1 — Endert 2402: 1.

FB series (Hutchinson) 6103: 1; 6109: 1 — Forbes (1885-6): 1 — Franck 700: 4; 701: 4 — Froidemont 1: 1; 3: 1.

Gamble 29/11/1889: 4 — Garai 57: 1 — Gelder 25: 5 — Gibbs 6232: 1 — Gjellerup 1007: 1 — Glasnevin cult. ?/5/1900: 8 — Groeneveldt 676: 1.

Haegens, Klazenga, Kiew et al. 620: 7 — Hallier 2146: 1; 3058: 1 — Haviland 89: 1; 842: 2; 853: 1; 21/3/1893: 1; Haviland cult. (Kuching Orchid House) 18/4/1893: 5; 5/6/1908: 5 — HBUM cult. (Stone) BCS/12648: 4 — Hewitt 106: 1; 13/3/1906: 1; 30/10/1908: 1.

Kajewski 679: 1 — Keith 7696: 1 — KEP series (Ogata) 110163: 1 — Keßler et al. PK2567: 5 — Kew cult. (Herbarium Hookerianum) (c.1867): 5; ?/5/1890: 5; ?/7/1890: 4; ?/11/1894: 8; (Armstrong & Brown) ?/5/1909: 5; ?/7/1914: 4; 30/10/1914: 5; 4/6/1915: 1; 25/6/1924: 1;

(Armstrong & Brown) 215-1929: 1 — King’s collector 2724: 1; 7176: 5; 7287: 1; (B.P.D.) 8154: 5 — Kleinhoonte 624: 1— Kloss (1912–1913): 1 — Kokawa & Hotta 329: 7 — Kornassi 1239: 1; 1539: 1.

LAE series (Damas, Anos et al.) 74614: 1 — Lamb AL203/84: 8; AL312/85: 5; AL914/88: 5 — Lawrence ?/5/1891: 1; ?/12/1891: 1 — Le Douse cult. 29/7/92: 8 — Leiden cult. 19932: 1; 20721: 4; (Franken & Roos) 20786: 5; 20895: 5; 21480: 1; 21532: 5; 22279: 1; 22731: 4; 24029: 4; 25692: 1; (Vermeulen) 26555: 7; 27019: 4; (Rijksen) 27091: 4; 27092: 1; 27139: 1; 27279: 4; 27297: 4; (De Vogel) 27425: 1; 27621: 1; 28185: 1; 30607: 5; 30728: 4; 30789: 7; 32113: 1; 32243: 1; 913562: 5; 913662: 5; 914650: 5; 914719: 7; (Jenny) 930916: 5; (Schuiteman, Mulder & Vogel) 932800: 5; 933031: 5; (Roelfsema, Vogel & Van Balgooy) 960136: 1; (Roelfsema, Schuiteman & Vogel) 970407: 5; 970584: 7; 970597: 7; 970767: 4; 981187: 7; 990238: 7 — L’Horticulture Internationale cult. 2/7/1890: 8; 21/7/1890: 8; ?/10/1890: 8 — Lobb (Veitch & Sons) s.n.: 1; 1857: 1 — Loddiges (Low) 1/12/1853: 5 — Lörzing 17005: 1 — Loscworthy 20/10/1928: 5 — Lowe (1867): 5 — Lugas 1704: 5.

Maxwell ?/7/1895: 2 — Mendoza 3172: 5 — Mogea 3767: 1; 5448: 1 — Motley 588: 4 — Moulton 218: 7.

Nash 28119: 5 — Native Collector 277: 5; 495: 1 — New York cult. (Nash) 1612: 1; 4334: 1; 5/7/1901: 1 — NGF series (Millar) 18881: 1; (Ridsdale & Lavarack) 30560: 1 — Nongchi 48: 4 — Nooteboom & Chai 1680A: 5 — Nur 189: 1.

Oakes Ames cult. (1896): 5; 1/3/1899: 5 — O’Byrne CX020: 7 — Officers of HMS Penguin (1984-5): 1 — Oxford University 2657: 7.

Phillips & Lamb AL1417/92: 5 — PNH series (Sulit & Conese) 5393: 1; (Sulit) 21725: 1; (Gutierrez et al.) 117009: 1.

Ramos et al. ?/4/1931: 1 — Rappard 202: 4 — Rasip 20/12/93: 1 — Reichenbach Herb. 29851: 6; (Veitch) 21503: 6 ; 21506: 4; 21507: 4; ?/8/1890: 6 — Richards R2657: 7 — Ridley 14400: 1; (1890): 4; 8/1/1890: 4; (1894): 4; ?/5/1896: 5; ?/7/1897: 5; (1898): 4; ?/11/1908: 5; (1909): 4; 26/12/1920: 5 — Royal Society Expedition (Hunt) RSS 3056: 1.

S series (Synge) 4: 7; (Harrison) 413: 5; (Ashton) 18156: 5; (Mohidin) 21682: 5; (Soepadmo, Smith & Chai) 27620: 1; (Mamit) 37433: 1; (Lee) 45427: 5; (Puang Ching) 51244: 1; (Yii et al.) 51662: 1; (Rena, Runi, Rantai et al.) 58375: 1; (Puang Ching) 64751: 1; 65091: 1 — SAN series (Dewol & Kodoh) 88741: 1; (George & Harun) 89553: 5; 89635: 5; (Abang & Sigin) 96278: 7; (Krispinus) 118600: 1; 120242: 1 — San Carlos Univ. 762: 1 — Sanders 16/5/1918: 5 — Sands 778: 1; 3753: 7 — Sands, Chan & Lamb 3740: 1 — Sands, Pattison, Wood et al. 1844: 1 — Schlechter 17126: 1; 18969: 1; 19108: 1 — Scortechini 2113: 5; 2183: 5 — SF series (Haniff & Nur) 7750: 4; (Burkill & Haniff) 16511: 5 — Shah & Sidek MS1154: 1 — Smith cult. (Gravenhorst s.n.) H.L.B. 9226268: 2; H.L.B. 9226283: 2; H.L.B. 92262113: 2; H.L.B. 92262197: 2; H.L.B. 920342352: 2; (1910): 2; (1921): 2.

Tadong 540: 1 — Takeuchi 8884: 1 — Tay & Tan 94-0032: 1 — Tenom Orchid Centre cult. (Chan) 103: 4 — Teijsmann 30: 4 — Trinidad cult. (Broadway) 1/1/1908: 5; 3/3/1920: 5.

UNESCO 48: 1; 166: 1; 218: 1 — UPNG series (Ombas) 1384: 1.

Van Gelder 25: 5 — Van Niel 3794: 5 — Van Royen 5070: 1 — Vermeulen 779: 7; 1156: 3 — Vermeulen & Lamb 322: 7; 753: 7 — Versteeg 1345: 1.

Waterhouse 642: 1; 728: 1 — Weber 55: 1; 250: 1 — Wenzel 532: 1; 602: 1; (1914): 1 — Wickison 125: 1 — Winkler 347: 5 — Wray 2169: 1.

Yates 2160: 1 — Yenny 183: 1 — Yong & Lamb AL437/85: 5.

INDEX

Accepted species are in roman type, new species in bold and synonyms and excluded species in *italics*. Numbers refer to the species number as used in this revision.

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CURRICULUM VITAE

Barbara Gravendeel werd op 2 december 1968 geboren in Utrecht. In 1987 behaalde zij haar VWO diploma aan het Dr. F.H. de Bruijnelyceum in Utrecht. In 1989 begon zij met de studie Biologie aan de Universiteit Utrecht. Tijdens de doctoraalfase werden vier afstudeeronderzoeken afgerond. Het eerste onderzoek deed zij bij de projectgroep Vegetatie-ecologie (Dr. J. Willems). Hierbij werd de voor- en achteruitgang van Rode-Lijstsoorten in een kalkgraslandvegetatie in Zuid-Limburg onderzocht door analyse van karteringen en bodemgegevens. Het tweede afstudeervak werd gevolgd bij de projectgroep Herbarium (Dr. R. Ek). Met behulp van G.I.S werd onderzocht of lianen als indicatorsoorten gebruikt kunnen worden voor verschillende successiestadia in primair bos in Guiana. Het derde afstudeervak werd gedaan bij de vakgroep Natuurwetenschap & Samenleving (Drs. J. Dekker). In opdracht van de wetenschapswinkel Biologie werd de mening van boswachters over natuurontwikkelingsbeheer geanalyseerd. Het vierde afstudeervak werd gedaan bij het voormalige Instituut voor Bos- en Natuuronderzoek (Dr. S. Broekhuizen) in Arnhem. Hiervoor werd het aktiviteitspatroon van geherintroduceerde bevers in de Gelderse Poort in kaart gebracht. In augustus 1995 werd de Biologie studie afgerond. In november van datzelfde jaar werd zij (part-time) Assistente in Opleiding bij het voormalige Rijksherbarium/Hortus Botanicus in Leiden met Prof. P. Baas en Prof. K. Bachmann (UvA) als promotores en Dr. E.F. de Vogel als begeleider. De resultaten van het onderzoek dat zij daar heeft verricht zijn beschreven in dit proefschrift. Moleculaire trainingsperiodes werden gevolgd in Jena in samenwerking met Drs. I. Köhnen en in Kew o.l.v. Dr. M.W. Chase. Het RFLP werk voor dit onderzoek werd grotendeels uitgevoerd in het Hugo de Vries laboratorium van de Universiteit van Amsterdam onder begeleiding van Dr. T.H.M. Mes. Plantenmateriaal werd gedeeltelijk verzameld tijdens drie maanden veldwerk in Peninsular Malaysia en Sarawak. Als prakticumassistent en/of docent werkte zij mee aan de cursussen Biodiversiteit en Patroonanalyse, Plant Families of Southeast Asia en Moleculaire Technieken. Als lid van de onderwijscommissie evalueerde zij de kwaliteit van het cursusaanbod binnen de onderzoeksschool Biodiversiteit. Sinds 15 mei 2000 is zij werkzaam bij de Leidse vestiging van het Nationaal Herbarium Nederland, waar zij het moleculair systematisch onderzoek coördineert.

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NAWOORD

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