

REVISION OF COELOGYNE SECTION MONILIFORMES (ORCHIDACEAE) BASED ON MORPHOLOGY, PLASTID AND nrDNA ITS SEQUENCES

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SUMMARY

Section *Moniliformes* Carr of the orchid genus *Coelogyne* is revised using morphological and molecular data. Twelve species are recognised, including two new ones (*C. chanii* and *C. renae*), and a dubious one (*C. crassiloba*). A combined analysis of morphological characters, and sequences of the nrDNA ITS region, *matK* gene, *trnT-trnL* intergenic spacer, *trnL* intron and *trnL-trnF* intergenic spacer supports the monophyly of the section as here recognised. Persistence of the rhizome scales, shape of the margin of the leaves, inflorescence type, shape of the rachis, its nodes and pedicel scars, indument of the floral bracts, lip size and depth of the sinus of the lateral lobes of the hypochile seem to be phylogenetically informative characters. Shape of the leaf blade, flowering mode, shape of the base and keels of the hypochile, shape of the apex of the lateral lobes and keels of the epichile and shape of the column show many parallelisms.

Key words: *Coelogyne* section *Moniliformes*, *matK*, nrDNA ITS, phylogeny, *trnT-trnF*.

INTRODUCTION

The orchid genus *Coelogyne* comprises over 200 species and is distributed throughout Southeast Asia with main centres of diversity in Borneo, Sumatra and the Himalayas (Clayton, 2002). The genus was subdivided into 5 sections by Lindley (1854a), into 14 sections by Reichenbach (1861a) and Pfitzer & Kraenzlin (1907a) (not identical with the ones of Lindley) and into 5 subgenera and 14 sections by Butzin (1974) (partly different from the ones of Pfitzer & Kraenzlin).

Carr published sect. *Moniliformes* (from the Latin *monile*, a necklace, which refers to the shape of the rachis) in 1935, stating that the species of the affinity of *C. incrassata* (Blume) Lindl. should be considered as forming a separate section, differing from other sections of *Coelogyne* by the single large leaf and the swollen rachis.

In this study, the following combination of character states was found to be diagnostic for sect. *Moniliformes*: pseudobulbs narrowly conico-oblongoid, distally curved, 1-leafed, tinged green to red-brown when fresh; leaves herbaceous, tinged green to red-brown when fresh, sometimes grey-green, base abruptly narrowing into the petiole, margin slightly to distinctly and finely undulating; peduncle without sterile bracts at the base; rachis usually (except in *C. kelamensis*) with swollen, constricted nodes, that are quadrangular to round in cross section; flowers many, arising from the inflorescence in clusters of three or more at the same time or successively over a long period, small to medium-sized; pedicel and ovary (and sometimes also the floral bracts, sepals and

Table 1. List of species analysed for the molecular phylogenetic analyses. Arranged by section according to Pfitzer & Kraenzlin (1907a) and Carr (1935).
C. = *Coelogyne*; *N.* = *Neogyne*; *P.* = *Pholidota*.

Species	Section	Voucher ¹	Origin	nrDNA ITS1-5.8S-ITS2	matK ²	trnT-trnL ²	trnL ²	trnL-trnF ²
<i>C. chunii</i>	<i>Moniliformes</i>	TAP cult. 96	Sabah	AF463355	AF463362	AF464739	AF463384	AF463369
<i>C. gibbifera</i>	<i>Moniliformes</i>	SBGO 201	Sabah	AY101966	AF495864	AF464740	AF463385	AF463370
<i>C. harana</i>	<i>Moniliformes</i>	Leiden cult. 93254	Sarawak	AF463356	AF463363	AF464741	AF463386	AF463371
<i>C. incrassata</i>	<i>Moniliformes</i>	Leiden cult. 932928	Sarawak	AF463357	AF463364	AF464742	AF463387	AF463372
<i>C. kelamensis</i>	<i>Moniliformes</i>	Leiden cult. 930568	unknown	AF302750	AF302715	AF464743	AF463388	AF463373
<i>C. longpasiaensis</i>	<i>Moniliformes</i>	TAP cult. s. n.	Sabah	AF463358	AF463365	AF464744	AF463389	AF463374
<i>C. monilirachis</i>	<i>Moniliformes</i>	Leiden cult. 98003	Sarawak	AF463359	AF463366	AF464745	AF463390	AF463375
<i>C. naja</i>	<i>Moniliformes</i>	Leiden cult. 990122	Sarawak	AF463360	AF463367	AF464746	AF463391	AF463376
<i>C. renae</i>	<i>Moniliformes</i>	Leiden cult. 970768	Sarawak	AF463361	AF463368	AF464747	AF463392	AF463377
<i>C. beccarii</i>	<i>Speciosae</i>	Leiden cult. 32230	New Guinea	AF302751	AF302716	AF464750	AF463395	AF463380
<i>C. macdonaldii</i>	<i>Speciosae</i>	Leiden cult. 25836	Vanuatu	AF302752	AF302717	AF464751	AF463396	AF463381
<i>N. gardneriana</i>		Leiden cult. 970729	unknown	AF302735	AF302700	AF464752	AF463397	AF463382
<i>P. imbricata</i>		Leiden cult. 21540	unknown	AF302738	AF302703	AF464753	AF463398	AF463383

1) All voucher specimens are deposited in L or SING.

2) Genbank accession number.

petals) covered by scattered, minute, brown, scale-like hairs; hypochile with distinctly to slightly saccate base and plate-like keels; epichile with plate-like keels on the claw and no ornamentation or with a patch of swollen, completely fused warty keels on the apex.

Carr listed nine species: *C. crassiloba* J.J. Sm., *C. harana* J.J. Sm., *C. incrassata* (Blume) Lindl., *C. kelamensis* J.J. Sm., *C. macroloba* J.J. Sm., *C. monilirachis* Carr, *C. naja* J.J. Sm., *C. tenuis* Rolfe and *C. vermicularis* J.J. Sm. He failed to designate a type species. We have here chosen *C. monilirachis* Carr as the type species, as this species was published together with the description of the section by Carr (1935).

Carr overlooked *C. bihamata* J.J. Sm. and *C. gibbifera* J.J. Sm., and Wood & Chan (1990) added *C. longpasiaensis* J.J. Wood & C.L. Chan. We describe two new species here, *C. chanii* Gravendeel & de Vogel and *C. renae* Gravendeel & de Vogel, which should also be placed in sect. *Moniliformes*. Furthermore, we reduce *C. macroloba* to *C. gibbifera* and *C. bihamata* to *C. tenuis*.

The traditional sectional classifications of *Coelogyne* are based on few diagnostic characters only. Previous phylogenetic analyses using morphological and molecular characters from a subset of species indicated a monophyletic status of sect. *Moniliformes* (Gravendeel, 2000; Gravendeel et al., 2001). The main objectives of the current study were:

- 1) to check the monophyly of sect. *Moniliformes* as here recognised with a large species sampling;
- 2) to study interspecific relationships;
- 3) to provide an up-to-date revision of all species recognised.

Phylogenetic analyses were performed using morphological characters and sequences from the plastid *matK* gene, the *trnT-trnL* intergenic spacer, *trnL* intron, *trnL-trnF* intergenic spacer, and nrDNA ITS regions. Based on earlier studies, these regions were expected to be useful in reconstructing phylogenetic relationships within the genus *Coelogyne* (Sierra et al., 2000; Gravendeel et al., 2001).

MATERIALS AND METHODS

Sampling

For the morphological phylogeny, 17 taxa were studied, representing species assigned to *Coelogyne* sect. *Moniliformes* and *Speciosae* by various authors, as well as two outgroups. Representatives of two closely related genera in Coelogyneinae, *Neogyne* and *Pholidota*, were chosen as outgroups. These genera are placed in the same clade as species of sect. *Moniliformes* in a molecular phylogeny of *Coelogyne* based on plastid RFLPs, *matK* and nrDNA ITS sequence data (Gravendeel et al., 2001). For the molecular analyses plant material was obtained from the living orchid collections of the botanical gardens in Leiden, The Netherlands, Tenom, Sabah and Singapore Botanic Gardens, Singapore. Unfortunately, living collections of only nine taxa in sect. *Moniliformes* were available for the molecular and total evidence analysis. DNA extracted from herbarium collections turned out to be too degraded to be useful. Voucher specimens of all accessions surveyed, with their origins, are listed in Table 1 and have been deposited at L or SING.

Morphology

Herbarium material was studied from the following herbaria: A, AMES, BM, BO, E, HBG, K, L, P, SAR and SING. The dimensions given in the descriptions are usually based on spirit collections and living material. When only herbarium material was measured, this is mentioned. Maps were made with MapInfo version 5.0. Coordinates were partly found using BRAHMS version 4.8.

For the phylogenetic analyses, only characters were used which could be easily divided into discrete, non-overlapping states. Character states were evaluated from herbarium, living and spirit collections, where possible from at least 5 specimens per species. A data matrix of 39 morphological characters was constructed, of which 5 relate to vegetative and 34 to reproductive structures. The following characters and characters states were used:

1. Rhizome scales: 1 = long persistent; 2 = soon disintegrating.
2. Pseudobulbs: 1 = less than 15 mm apart; 2 = more than 15 mm apart.
3. Pseudobulbs – number of leaves: 1 = one; 2 = two.
4. Leaf blade: 1 = oblong; 2 = (obovate-)oblong; 3 = (obovate-)lanceolate; 4 = lanceolate.
5. Leaf margin: 1 = distinctly finely undulating; 2 = slightly undulating; 3 = flat.
6. Inflorescence type: 1 = synanthous; 2 = hysteranthous.
7. Peduncle: 1 = incrassate; 2 = slender.
8. Rachis: 1 = erect; 2 = pendulous.
9. Rachis at the nodes: 1 = constricted; 2 = not constricted.
10. Rachis – shape of internodes: 1 = disc-shaped; 2 = rectangular.
11. Rachis – pedicel scars: 1 = indistinct; 2 = distinct.
12. Floral bracts – shape: 1 = ovate; 2 = (narrowly) triangular; 3 = oblong to lanceolate.
13. Floral bracts – indument: 1 = glabrous; 2 = sparsely covered with scattered minute brown scale-like hairs.
14. Floral bracts – persistence: 1 = persistent; 2 = deciduous.
15. Lip: 1 = shorter than 25 mm; 2 = between 25 and 30 mm; 3 = longer than 32 mm.
16. Flowers – opening: 1 = in periodic clusters of three or more at the same time; 2 = in succession over a long period.
17. Flowers – resupinate: 1 = yes; 2 = no.
18. Median sepal and petals – indument: 1 = glabrous; 2 = sparsely covered with scattered minute brown scale-like hairs.
19. Lateral sepals – base: 1 = saccate; 2 = flat or concave.
20. Hypochile – base: 1 = distinctly saccate; 2 = slightly saccate or flat.
21. Hypochile – apex of lateral lobes: 1 = decurrent; 2 = truncate; 3 = broadly rounded to obtuse; 4 = acute.
22. Hypochile – sinus of lateral lobes: 1 = absent or less than 2 mm deep; 2 = deeper than 3 mm.
23. Hypochile – number of keels: 1 = two; 2 = three; 3 = more than three.
24. Hypochile – keels at the base: 1 = connected; 2 = free.
25. Hypochile – height of keels: 1 = constant; 2 = ascending.
26. Hypochile – keels ascending: 1 = abruptly; 2 = gradually.

27. Hypochile – ornamentation of keels at the base: 1 = with triangular hooks; 2 = without triangular hooks.
28. Epichile – shape: 1 = (broadly) ovate; 2 = oblong to elliptic; 3 = (slightly) spatulate.
29. Epichile – curvature: 1 = slightly recurved; 2 = distinctly recurved.
30. Epichile – claw: 1 = absent; 2 = present.
31. Epichile – position of keels on claw: 1 = running some distance from the margin; 2 = running closely along the margin.
32. Epichile – keels on claw towards the apex: 1 = descending; 2 = ascending.
33. Epichile – keels on blade: 1 = absent; 2 = present.
34. Epichile – shape of blade: 1 = broadly ovate; 2 = orbicular.
35. Epichile – blade ornamentation: 1 = glabrous; 2 = warty.
36. Epichile – lobules at apex: 1 = not to slightly developed; 2 = well developed.
37. Epichile – shape of apex: 1 = semi-orbicular, widely retuse; 2 = not semi-orbicular, only slightly retuse.
38. Column – shape: 1 = apically reflexed; 2 = entirely curved; 3 = entirely erect.
39. Column – base: 1 = with triangular swelling; 2 = without triangular swelling.

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, or from silica dried leaf material using DNeasy extraction kits and protocols of QIAGEN (Leusden, The Netherlands). Only one individual per species was sampled.

matK, nrDNA ITS and trnT-trnF amplifications

A large portion of the *trnK* region (mostly *matK*) was amplified with the primers: –19F (5'-CGTTCTGACCATATTGCACTATG-3') and 881R (5'-TMTTCATCAGAATAAGAGT-3'); 731 F (5'-TCTGGAGTCTTTCTTGAGCGA-3') and 2R (5'-AACTAGTCGGATGGATGGAGTAG-3') (Gravendeel et al., 2001). 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.

The regions between the *trnT* and *trnF* genes were amplified with the primers a (5'-CATTACAAATGCGATGCTCT-3'), b (5'-TCTACCGATTTCCGCATATC-3'), c (CGAAATCGGTAGACGCTACG-3'), d (GGGGATAGAGGGACTTGAAC-3'), e (GGTTCAAGTCCCTCTATCCC-3') and f (ATTTGAACTGGTGACACGAG-3') from Taberlet et al. (1991). The thermal cycling protocol comprised 35 cycles, each with 1 min. denaturation at 94 °C, 30 sec. annealing at 50–55 °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, Leusden, The Netherlands).

Nuclear ribosomal ITS1 and ITS2 spacers along with the 5.8S gene were amplified with the primers 17 SE (5'-ACGAATTCATGGTCCGGTGAAGTGTTTCG-3') and 26 SE (5'-TAGAATCCCCGGTTCGCTCGCCGTTAC-3') from Sun et al. (1994). The thermal cycling protocol comprised 26 cycles, each with 10 sec. denaturation at

Table 2. Values and statistics from parsimony analyses of morphology, plastid and nuclear sequences, and combined data.

	morphology	<i>matK</i>	<i>trnT-trnF</i>	nrDNA ITS1- 5.8S-ITS2	combined sequences	total evidence
Number of taxa included	17	13	13	13	13	13
Number of characters included	39	1905	1643	685	4233	4273
Number of variable characters	39	48	84	112	244	282
Number of phylogenetically informative characters	30	15	43	48	106	136
Number of MPTs	22	1998	59	961	315	1
Tree length (steps)	99	51	86	127	274	367
CI	0.51	0.94	0.99	0.92	0.91	0.81
RI	0.57	0.89	0.98	0.93	0.89	0.78
Number of clades in bootstrap consensus with > 80% support	2	1	2	0	3	3

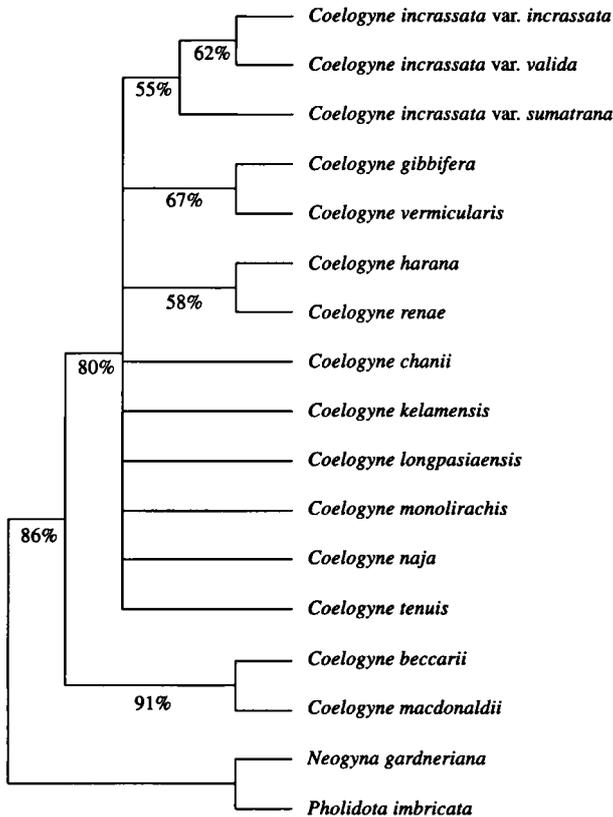


Fig. 1. Bootstrap consensus of 22 trees from parsimony analyses of morphological data (only percentages > 50% are given).

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 pipette tip and using that sample as template.

Amplified, double-stranded DNA fragments were purified using Wizard PCR mini-columns (Promega, Leiden, The Netherlands) 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 nrDNA ITS1-5.8-ITS2 and *trnT-trnF* regions 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. Polymorphisms were coded as "all states possible" and inapplicable or unknown characters by a question mark. Sequences were aligned with MegAlign version 4.03 (DNASTAR) and subsequently adjusted by hand. Gaps in the sequence data were coded as missing values. Synapomorphic indels were coded as present/absent characters. The morphological data matrix and *matK*, *trnT-trnF* and nrDNA ITS alignments are available from the first author upon request (gravendeel@nhn.leidenuniv.nl). All sequences are submitted to Genbank (see Table 1 for accession numbers). Maximum parsimony analyses were performed on the morphological and sequence data with PAUP* version 4.0b10 (Swofford, 1999) using random additions and the MULPARS option. *Neogyne gardneriana* and *Pholidota imbricata* 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. 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 4.0 (Maddison & Maddison, 1992).

RESULTS

Morphology

Of the 39 characters scored, 9 are autapomorphies and the remaining 30 are synapomorphies (Table 2). The MP analyses yielded 22 most parsimonious trees (MPTs) (length = 99; CI = 0.51; RI = 0.57). The bootstrap consensus topology and the corresponding branch supports are shown in Figure 1. Resolution of this consensus tree is relatively high. Seven clades receive moderate to strong support: *Coelogyne* (86%), sect. *Speciosae* (91%), sect. *Moniliformes* (80%), *C. gibbifera* and *C. vermicularis* (67%), *C. incrassata* var. *incrassata* and *C. incrassata* var. *valida* (62%), *C. harana* and *C. renae* (58%), *C. incrassata* (55%).

DNA sequences

matK — The alignment has a total number of 1905 sites, of which 48 were variable and 15 were phylogenetically informative (Table 2). The MP analyses yielded 1998 MPTs (length = 51; CI = 0.94; RI = 0.89). Resolution of the bootstrap consensus tree (not shown) is moderate. Only five clades receive moderate to strong support: *Coelogyne* (100%), sect. *Moniliformes* (72%), all species of sect. *Moniliformes* with the exception of *C. gibbifera* (72%), *C. monilirachis* and *C. naja* (79%), *C. chanii* and *C. harana* (53%).

trnT-trnF — The alignment has a total number of 1643 sites, of which 84 were variable and 43 were phylogenetically informative (Table 2). The MP analyses yielded 59 MPTs (length = 86; CI = 0.99; RI = 0.98). Resolution of the bootstrap consensus tree (not shown) is moderate. Three clades receive strong support: *Coelogyne* (93%), sect. *Speciosae* (90%), *C. gibbifera* plus *C. monilirachis* (79%).

Nuclear ribosomal ITS1-5.8S-ITS2 — The alignment has a total number of 685 sites, of which 112 were variable and 48 were phylogenetically informative (Table 2). The MP analyses yielded 961 MPTs (length = 127; CI = 0.92; RI = 0.93). Resolution of the bootstrap consensus tree (not shown) is very low. Only one clade receives low support: *C. chanii*, *C. harana*, *C. incrassata*, *C. kelamensis*, *C. longpasiaensis*, *C. monilirachis*, *C. naja* and *C. renae* (68%).

Combined sequences — The alignment has a total number of 4233 sites, of which 244 were variable and 106 were phylogenetically informative (Table 2). The MP analyses yielded 315 MPTs (length = 274; CI = 0.91; RI = 0.89). The bootstrap consensus tree is shown in Figure 2. Resolution of this consensus tree is relatively high. Four clades receive moderate to strong support: *Coelogyne* (91%), sect. *Speciosae* (96%), all species of sect. *Moniliformes* with the exception of *C. gibbifera* (81%), sect. *Moniliformes* (70%).

Total evidence analysis

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 4273 characters, of which 282 were variable and 136 phylogenetically informative (Table 2). The MP analyses yielded a single MPT (length = 367; CI = 0.81; RI = 0.78), which is shown in Figure 3. Resolution of the bootstrap consensus tree (not shown) is relatively high. Five clades receive moderate to strong support: *Coelogyne* (100%), sect. *Speciosae* (100%), sect. *Moniliformes* (91%), all species of sect. *Moniliformes* with the exception of *C. gibbifera* (73%), *C. harana* plus *C. renae* (67%).

DISCUSSION

Separate and combined analyses of morphological and molecular data suggest that sect. *Moniliformes* is monophyletic. The species of sect. *Moniliformes* as here recognised have the following unique synapomorphies: pseudobulbs with a single leaf with undulating margin, a rachis with constricted nodes (not constricted in *C. kelamensis*) and (narrowly) triangular to ovate floral bracts. The other species analysed have leaves with a flat margin, a rachis without constricted nodes and ovate to oblong to lanceolate floral bracts.

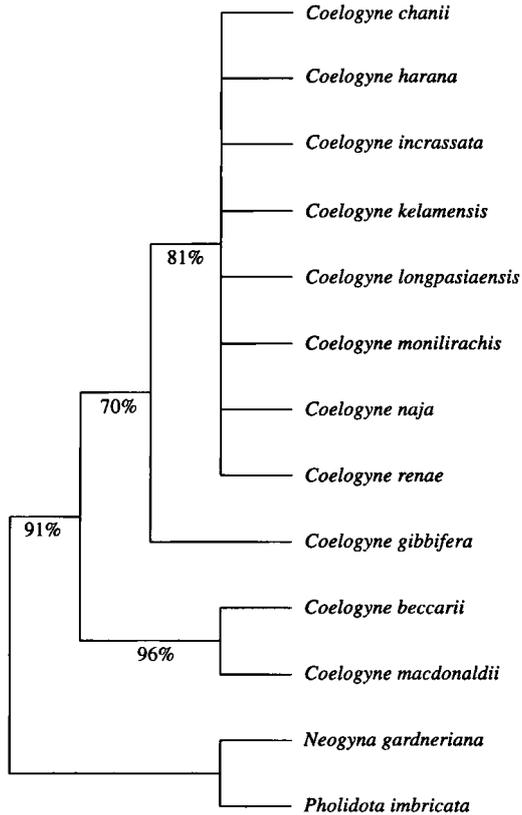


Fig. 2. Bootstrap consensus of 315 trees from parsimony analyses of combined sequence data (only percentages > 50% are given).

Within sect. *Moniliformes*, two smaller moderately supported clades are present (Fig. 3). The first clade comprises all species of the section with the exception of *C. gibbifera* (73%). This clade is characterised by the small flowers and spatulate epichile (with the exception of *C. chanii* and *C. renae*). In contrast with this clade, *C. gibbifera* has large flowers and an ovate epichile. The second clade comprises *C. harana* and *C. renae* (67%), which share hairy floral bracts, and which are glabrous in all other species of sect. *Moniliformes*.

The results of all analyses support placement of *C. kelamensis* within sect. *Moniliformes*, despite its deviating characters, such as the long persistent rhizome scales, widely spaced pseudobulbs, not constricted nodes of the slender rachis and a hypochile with lateral lobes with a deep sinus. All other species of sect. *Moniliformes* have soon disintegrating rhizome scales, closely spaced pseudobulbs, a swollen rachis with constricted nodes and a hypochile with lateral lobes with shallow to deep sinus.

The results of the total evidence analysis identified *C. gibbifera* as nearest neighbour to sect. *Speciosae*. This close relationship is supported by the following characters: an erect rachis, large flower size and ovate epichile. The species of sect. *Speciosae*

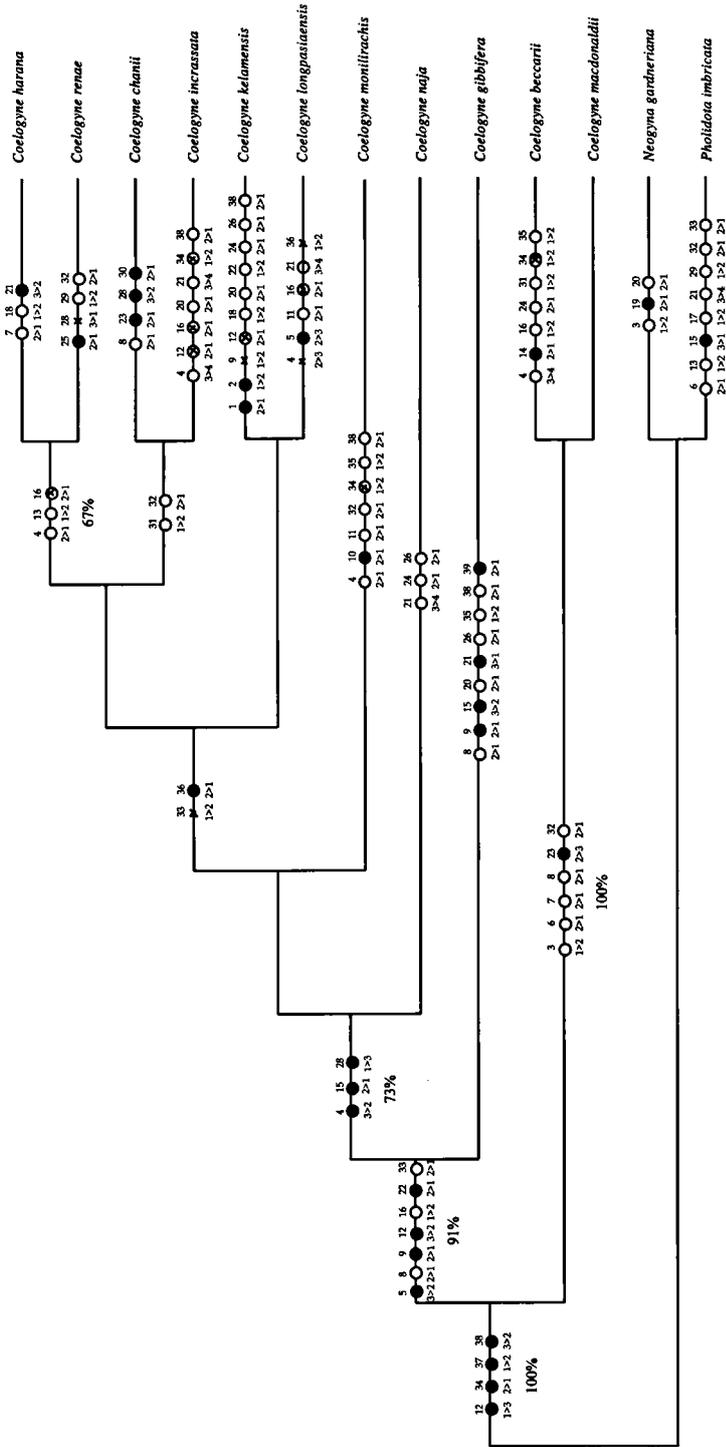


Fig. 3. Single MPT from the total evidence analysis with bootstrap support values (only percentages > 50% are given). ● = unique apomorphy; ⊗ = parallel reversal; X = reversal; ⊗ = parallel reversal.

differ in quite a number of characters from *C. gibbifera* and the other species of sect. *Moniliformes*, too, such as the bifoliate pseudobulbs, synanthous inflorescences, incrassate peduncle, and hypochile with more than three keels. The species of sect. *Moniliformes* all have hysteranthous inflorescences, a slender peduncle (with the exception of *C. harana*), pendulous rachis (with the exception of *C. chanii*, *C. gibbifera*, *C. tenuis* and *C. vermicularis*), small flowers (with the exception of *C. gibbifera* and *C. vermicularis*) and a hypochile with less than three keels.

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 of the total evidence analysis (Fig. 3). According to this reconstruction, characters with high phylogenetic potential are the persistence of the rhizome scales, shape of the margin of the leaves, inflorescence type, shape of the rachis, its nodes and pedicel scars, indument of the floral bracts, lip size, and depth of the sinus of the lateral lobes of the hypochile.

Soon disintegrating rhizome scales, leaves with a flat margin, synanthous inflorescences with an erect rachis with distinct pedicel scars and not constricted nodes, glabrous floral bracts, and a large lip with a hypochile with lateral lobes with a deep sinus seem to be the plesiomorphic condition for the set of taxa analysed. The apomorphic conditions are: persistent rhizome scales, leaves with an undulating margin, hysteranthous inflorescences with a pendulous rachis with indistinct pedicel scars and constricted nodes, hairy floral bracts and a small lip with a hypochile with lateral lobes with a shallow sinus.

Shape of the leaf blade, flowering mode, shape of the base and keels of the hypochile, shape of the apex of the lateral lobes and keels of the epichile and shape of the column show many parallelisms and appear not to be phylogenetically useful for the set of taxa analysed.

CHARACTERS

For easy reference, the most important diagnostic characters and their states for the species of sect. *Moniliformes* are briefly described below.

Rhizome

Disintegrating rhizome scales are predominant in the section. *Coelogyne kelamensis* is the only species with persistent rhizome scales.

Pseudobulbs

All species of the section have closely spaced pseudobulbs, with the exception of *C. kelamensis*, in which the distance between the pseudobulbs is larger than 1.5 cm.

Leaves

Usually the margin of the leaves is slightly undulating, except for the leaves of *C. longpasiaensis* and *C. tenuis*, which have a very finely undulating margin (Fig. 9).

Inflorescence

All species have hysteranthous inflorescences. *Coelogyne harana* is the only species of the section with an incrassate peduncle. All other species have a slender, wiry peduncle.

Rachis

The rachis of most species of the section is pendulous, swollen, and constricted at the nodes. *Coelogyne chanii*, *C. gibbifera*, *C. tenuis* and *C. vermicularis* can be recognised by the erect rachis. *Coelogyne kelamensis* is the only species in which the nodes of the rachis are not constricted. The internodes are usually short and rectangular, with the exception of *C. kelamensis*, which has elongated internodes (Fig. 8) and *C. monilirachis*, which has disc-shaped internodes (Fig. 10). Distinct pedicel scars on the rachis are predominant in the section, except for *C. longpasiaensis* and *C. monilirachis*, in which the pedicel scars are hardly visible.

Floral bracts

Usually the floral bracts are glabrous, but scattered minute brown scale-like hairs occur on the bracts of *C. harana* and *C. renae*.

Flowers

Many ((2–)17–98), small to medium-sized flowers are typical for sect. *Moniliformes*, although the flowers of *C. gibbifera* and *C. vermicularis* are quite large. Most of the species of the section have flowers opening in succession over a long period, with the exception of *C. harana*, *C. incrassata*, *C. longpasiaensis* and *C. renae*, in which the flowers open in periodic clusters of three or more at the same time. The sepals and petals are usually glabrous, with the exception of *C. harana* and *C. kelamensis*, which have scattered minute brown scale-like hairs scattered over all floral parts.

Hypochile — shape of base and lateral lobes

The base of the hypochile (basal part of the lip) is usually slightly saccate, with the exception of *C. gibbifera*, *C. incrassata* and *C. kelamensis*, in which the base is distinctly saccate. *Coelogyne gibbifera* and *C. vermicularis* can be recognised by the decurrent apex of the lateral lobes of the hypochile. *Coelogyne harana* is characterised by the truncate apex of the lateral lobes, whereas *C. incrassata* var. *incrassata*, *C. incrassata* var. *valida*, *C. longpasiaensis* and *C. naja* have an acute apex. The apex of the lateral lobes of the remaining species is broadly rounded.

Hypochile — ornamentation

The number of keels on the hypochile varies from two (*C. chanii*) to three (remaining species). The keels on the base of the hypochile of *C. kelamensis*, *C. naja* and *C. tenuis* are connected, whereas they are free in the remaining species. In *C. tenuis* the base of the lateral keels is abruptly elevated into a triangular hook with recurved, acute top (Fig. 13). The keels of *C. renae* remain low over the entire hypochile, whereas in the remaining species they ascend gradually or abruptly on the basal half of the hypochile.

Epichile

Usually, the epichile (apical part of the lip) is only slightly recurved, with the exception of *C. renae*, which has a distinctly recurved to reflexed epichile (Fig. 12). *Coelogyne chanii* is the only species with an epichile without a claw. In *C. gibbifera*, *C. monilirachis*, *C. naja* and *C. vermicularis* the keels end abruptly in the median

raised nerves at the base of the apex of the epichile. The remaining species have a broadly ovate to triangular patch of swollen, completely fused warty keels on (nearly) the entire blade of the epichile.

Column

The base of the column is usually smooth, with the exception of *C. gibbifera* and *C. vermicularis*, which have a triangular swelling on this position (Fig. 5, 14). The apex is curved to the front in *C. gibbifera*, *C. incrassata*, *C. kelamensis*, *C. monilirachis* and *C. tenuis* (Fig. 8), and erect in the remaining species of the section.

SYSTEMATIC TREATMENT

COELOGYNE section MONILIFORMES

Coelogyne Lindl. sect. *Moniliformes* Carr (1935) 207; de Vogel (1994) 204; J.B. Comber (2001) 323. — Type species: *Coelogyne monilirachis* Carr (here chosen).

Small to medium-sized epiphytes or terrestrials. *Roots* terete, glabrous. *Rhizome* creeping or climbing, terete, with 3–8 internodes between adjacent pseudobulbs; scales soon disintegrating (persistent in *C. kelamensis*). *Pseudobulbs* 2-leafed, close together (widely spaced in *C. kelamensis*), in outline narrowly conico-oblongoid, with slightly swollen base, often distally curved, finely grooved when dried; scales (cataphylls) covering the pseudobulb triangular, soon disintegrating in short persistent fibres. *Leaves* herbaceous; petiole semi-terete, channelled; blade ((ob)ovate-)oblong to (obovate-) lanceolate, base abruptly narrowing into the petiole, margin finely (*C. longpasiaensis* and *C. tenuis*) to slightly undulating, apex acute to acuminate to cuspidate, main nerves 3–9. *Inflorescence* hysteranthous, curved from a more or less erect base, 2–78-flowered. Peduncle incrassate (*C. harana*) to slender; base swollen, without sterile bracts; apex swollen. Rachis erect (*C. chanii*, *C. gibbifera*, *C. tenuis* and *C. vermicularis*) or pendulous, constricted at the nodes (not in *C. kelamensis*); internodes short to elongated (*C. kelamensis*), disc-shaped and round in cross section (*C. monilirachis*) to rectangular and quadrangular with rounded edges in cross section, glabrous when fresh, wrinkled when dried, with indistinct (*C. longpasiaensis* and *C. monilirachis*) to distinct pedicel scars; floral bracts ovate (*C. incrassata* var. *incrassata* and *C. kelamensis*) to (narrowly) triangular, glabrous or sparsely covered with scattered minute brown scale-like hairs (*C. harana*, *C. renae*), deciduous. *Flowers* small to medium-sized, distichous, opening in successive clusters of three (*C. harana*, *C. incrassata*, *C. longpasiaensis*, *C. renae*) or (almost) in succession. Pedicel curved, terete; ovary covered with scattered minute brown scale-like hairs. *Median sepal* (ob)ovate to ovate-oblong to oblong to elliptic, sparsely covered with scattered minute brown scale-like hairs (*C. harana* and *C. kelamensis*) to glabrous; nerves 5–9, the median nerve sometimes slightly prominent towards the base. *Lateral sepals* ovate to ovate-oblong to ovate-lanceolate, oblique, sparsely covered with scattered minute brown scale-like hairs (*C. harana* and *C. kelamensis*) or glabrous; nerves 3–9, the median nerve sometimes slightly prominent towards the base. *Petals* linear, sparsely covered with scattered minute brown scale-like hairs (*C. harana* and *C. kelamensis*) or glabrous; apex acute; midrib abaxially rather prominent to slightly pronounced as a low rounded keel; nerves 1–3. *Lip* 3-lobed, glabrous.

Hypochile boat-shaped; base distinctly (*C. gibbifera*, *C. incrassata*, *C. kelamensis*) to slightly saccate; lateral lobes erect, slightly diverging in front, with decurrent (*C. gibbifera*, *C. vermicularis*) to truncate (*C. harana*) to broadly rounded (*C. chanii*, *C. incrassata* var. *sumatrana*, *C. kelamensis*, *C. monilirachis*, *C. renae*, *C. tenuis*) to acute (*C. incrassata* var. *incrassata*, *C. incrassata* var. *valida*, *C. longpasiaensis*, *C. naja*) apex; sinus 0–5 mm deep; keels 2 (*C. chanii*) or 3, plate-like, basally connected (*C. kelamensis*, *C. naja*, *C. tenuis*) or free, with entire margin, low over the entire lip (*C. renae*) or at the base only and abruptly (*C. gibbifera*, *C. kelamensis*, *C. naja*, *C. tenuis*, *C. vermicularis*) to gradually ascending on the basal fifth to half of the hypochile, the median keel when present occurring on the hypochile only or on the epichile as well (*C. renae*, *C. vermicularis*), the lateral keels just as high as (*C. renae*) or higher than the median keel, slightly descending or ascending (*C. harana*) towards the apex of the hypochile, with (*C. tenuis*) or without triangular hook at the base, continuing on the epichile. *Epichile* (broadly) ovate (*C. gibbifera*, *C. renae*) to oblong to elliptic (*C. chanii*, *C. vermicularis*) to (slightly) spatulate, slightly to distinctly (*C. renae*) recurved; claw absent (*C. chanii*) or present and then with entire margin and 2 or 3 plate-like keels, running some distance from or completely along the margin, slightly diverging and descending (*C. monilirachis*, *C. renae*) or ascending towards the apex (*C. gibbifera*, *C. harana*; *C. incrassata*, *C. kelamensis*, *C. longpasiaensis*, *C. naja*, *C. tenuis*, *C. vermicularis*), ending abruptly in the median raised nerves at the base of the apex (*C. gibbifera*, *C. monilirachis*, *C. naja*, *C. vermicularis*) or continuing on the apex; blade when flattened broadly ovate to orbicular, glabrous to warty, slightly to distinctly recurved, with flat to slightly to distinctly undulating margins, not to slightly to distinctly pronounced lobules and (distinctly) acute to broadly rounded top, ornamentation absent or consisting of 2–9 swollen, completely fused warty keels, forming a broadly ovate (*C. chanii*, *C. harana*, *C. incrassata*, *C. kelamensis*, *C. renae*, *C. tenuis*) to triangular (*C. longpasiaensis*) patch, covering (nearly) the entire blade. *Column* (narrowly) spatulate in outline, apex curved to the front (*C. gibbifera*, *C. incrassata*, *C. kelamensis*, *C. monilirachis* and *C. tenuis*) or erect; base with (*C. gibbifera* and *C. vermicularis*) or without swelling; hood with (slightly) distinct wings; apex with entire to emarginate margin. *Anther* oblong to (broadly) ovate in outline; base near the place of attachment with a rounded projection; apex (slightly) emarginate to entire. *Pollinia* four, (broadly) ovoid, each with an oblique central depression which becomes shallower towards the base, all connate at the base by a flattened, triangular caudicle. *Stigma* broadly ovate, with incurved, emarginate to entire margin; rostellum (broadly) ovate to deltoid, with emarginate to entire margin. *Fruit* ellipsoid; valves with a low keel. *Seeds* fusiform.

Distribution — *Coelogyne incrassata* covers the entire distribution area of the section: Java, Sumatra, Borneo (Sabah, Brunei, Sarawak, Kalimantan). The other species are endemic to Borneo, which is the centre of diversity.

Habitat & Ecology — Epiphytes or terrestrials, found in lower montane or lowland primary rain forest, riverine vegetation and kerangas, on loam, sand, rock or clayish substrate. Elevation usually 500–2900 m with the exception of *C. harana*, *C. incrassata* and *C. kelamensis*, which occur at lower elevations. Flowering in first half of the year (*C. gibbifera* and *C. kelamensis*), second half of the year (*C. chanii*, *C. tenuis* and *C. vermicularis*) or the whole year round (remaining species).

Conservation status — As far as could be ascertained *C. vermicularis* has not been collected from the wild for more than 25 years, except for a collection made in Sarawak in 1991. As this conspicuous species is not easily overlooked it is probably seriously endangered. *Coelogyne chanii*, *C. kelamensis*, *C. renae* and *C. tenuis* are known from very few collections only, they must be considered rare and vulnerable. *Coelogyne gibbifera*, *C. harana*, *C. incrassata*, *C. longpasiaensis*, *C. monilirachis* and *C. naja* are fairly common in North and West Borneo.

Cultivation — Only *C. incrassata* is cultivated, but uncommon in the wild. All species require a rather shady position and should be well-watered throughout the year. Most do well under intermediate conditions in a water-retentive but well-draining mixture. No artificial hybrids of species of sect. *Moniliformes* have been registered so far.

KEY TO THE SPECIES

- 1a. Flowers opening in successive clusters of 3 or more at the same time 2
- b. Flowers opening (almost) in succession over a long period 5
- 2a. Lip with strongly recurved to reflexed epichile **9. *C. renae***
- b. Lip with slightly recurved epichile 3
- 3a. Sinus between the lateral lobes of the lip and the hypochile very shallow or absent; epichile with a triangular patch of several small warts on the blade **6. *C. longpasiaensis***
- b. Sinus between the lateral lobes of the lip and the hypochile shallow to deep; epichile with a broadly ovate patch of 4–7 completely fused, warty keels on the blade 4
- 4a. Hypochile of the lip with slightly saccate base; its lateral lobes broader than 3.5 mm; blade of epichile broadly ovate **3. *C. harana***
- b. Hypochile of the lip with clearly saccate base; its lateral lobes narrower than 3.5 mm; blade of epichile orbicular **4. *C. incrassata***
- 5a. Lip longer than 25 mm; column with a triangular swelling at the base 6
- b. Lip shorter than 25 mm; column without swelling at the base 7
- 6a. Lateral lobes of hypochile longer than 10 mm; epichile with broadly ovate blade **2. *C. gibbifera***
- b. Lateral lobes of hypochile shorter than 10 mm; epichile with obovate blade **11. *C. vermicularis***
- 7a. Lip longer than 18 mm 8
- b. Lip shorter than 18 mm 9
- 8a. Internodes of the rachis short and disc-shaped; keels on the lip in one line, ascending and descending only once **7. *C. monilirachis***
- b. Internodes of the rachis elongated and rectangular; keels on the lip converging and diverging, ascending and ascending twice **8. *C. naja***
- 9a. Leaf petiole longer than 20 mm; lateral lobes of hypochile longer than 7 mm **5. *C. kelamensis***
- b. Leaf petiole shorter than 20 mm; lateral lobes of hypochile shorter than 7 mm 10
- 10a. Lateral keels on the lip without triangular hooks at the base; epichile oblong-elliptic **1. *C. chanii***
- b. Lateral keels on the lip with triangular hooks at the base; epichile broadly ovate **10. *C. tenuis***

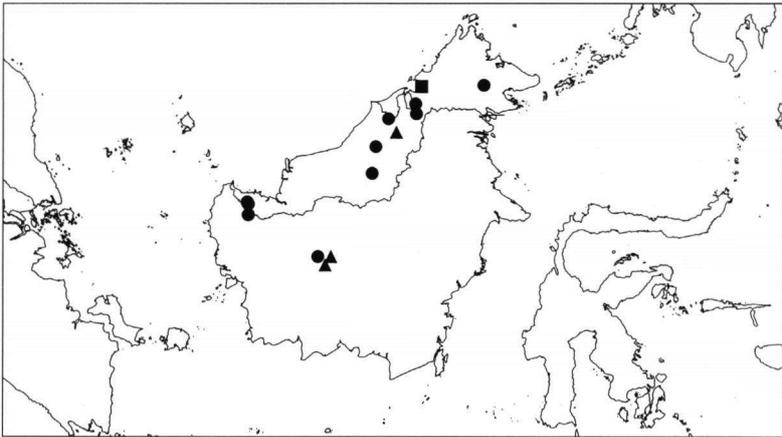


Fig. 4. *Coelogyne chanii* Gravendeel & de Vogel. a. Lip, front view; b. median sepal; c. lateral sepal; d. petal; e. pollinium; f. habit; g. floral bract; h. column, front, lateral and rear view (*Poring Hot Springs cult. (Lohok) B 156-920103*). — Scale bars: 1 cm (a–d, f, h); 1 mm (e); 5 mm (g).

1. *Coelogyne chanii* Gravendeel & de Vogel, *spec. nov.* — Fig. 4, Map 1, Plate 2d

Coelogyne haranae et *C. incrassatae* similis, sed floribus cremeo-viridibus successive florentibus, hypochilii lobis lateralibus latoribus apicibus obtuse rotundatis, epichilii apice crassimo distinguenda. — Typus: *Tenom Agricultural Park cult. 96* (holo L), Sabah.

Roots 1–2 mm diameter. *Rhizome* 5.5–6.5 mm thick, the portion between two pseudobulbs with 4–6 internodes; scales soon disintegrating. *Pseudobulbs* 9–11 mm apart, 12–14 by 0.9–1.9 cm. *Leaf* petiole 9–15 mm long; blade (obovate-)oblong, 20–26 by 6.5–8 cm, margin slightly undulating, apex acuminate to cuspidate, main nerves 5–7. *Inflorescence* 11–25-flowered. Peduncle slender, 11–16 cm long. Rachis erect, swollen, constricted at the nodes, 2.5–5.5 cm long; internodes short, rectangular, quadrangular in cross section and with rounded edges, with distinct pedicel scars, 2.5–3 by 1.5–2 mm; floral bracts triangular, glabrous, 12–14 by 6–7 mm. *Flowers* opening in succession. Pedicel 1.5–2 by 0.5–1 mm; ovary 2.5–3 by 1.5–2 mm. *Median sepal* obovate, 19–21 by 8–10 mm, glabrous, nerves 5–7. *Lateral sepals* ovate-oblong, 19–21 by 6–6.5 mm, glabrous, nerves 5 or 6. *Petals* 15–16 by 0.9–1.2 mm, glabrous, nerves 3. *Hypochile* 9–12 by 8–9 mm, base slightly saccate, lateral lobes 0.9–1.2 by 2.8–3.2 mm, with broadly rounded apex, sinus absent, keels 2, not connected, low at the base, gradually ascending on the basal half of the hypochile, slightly descending towards the apex of the hypochile, without triangular hook at the base. *Epichile* oblong to elliptic, 4.5–5 by 3.5–3.8 mm, slightly recurved, claw absent, blade when flattened broadly ovate, warty, slightly recurved, with slightly undulating margins, sides slightly pronounced as lobules, top acute, ornamentation consisting of 2 swollen, completely fused warty keels, forming a broadly ovate, extremely swollen patch, covering nearly the entire apex. *Column* spatulate in outline, 11–12 by 2.8–3.2 mm, base without swelling, hood with distinct wings, apex with entire margin, not curved to the front. *Anther* oblong to broadly ovate, 1.9–2.1 by 2.4–2.6 mm, apex slightly emarginate. *Pollinia* ovoid, 3–3.5 by 1.2–1.4 mm. *Stigma* 1.5–2 by 1.5–2 mm, with entire margin; rostellum broadly ovate, 1.5–2 by 1.5–2 mm, with entire margin. *Fruit* and *seeds* not seen.



Map 1. Distribution of *Coelogyne chanii* Gravendeel & de Vogel (■), *C. harana* J.J. Sm. (●) and *C. tenuis* Rolfe (▲).

Distribution — Borneo (Sabah).

Habitat & Ecology — Epiphyte in lower montane forest. Elevation 600–1000 m. Flowering: June, November.

Notes — 1. Pseudobulbs and leaves green. Sepals and petals light creamy green. Lip cream-coloured, petiole orange brown. Column creamy green. Anther light yellow. Not fragrant.

2. The epithet *chanii* refers to Chan Chew Lun, who collected the type specimen along the Kallang Waterfalls near Tenom in Sabah, and who, in his capacity as publisher, photographer and illustrator has enriched the orchid literature with several impressive publications.

3. The dimensions are based on living and herbarium collections.

4. The species is very similar to *C. harana* and *C. incrassata*, but can be distinguished by the successively opening creamy green flowers, the hypochile with very broad lateral lobes with obtusely rounded apex and the epichile with extremely thickened blade.

2. *Coelogyne gibbifera* J.J. Sm. — Fig. 5, Map 4, Plate 3c

Coelogyne gibbifera J.J. Sm. (1912a) 53; (1912b) 64; (1930) t. 12, f. 2; Ames (1921a) 144; J.J. Wood & P.J. Cribb (1994) 154. — Type: *Moulton 12* (holo BO), Borneo, Batu Lawi.

Coelogyne macroloba J.J. Sm. (1927d) 30; (1931a) 93. — Type: *Winkler 860* (holo HBG), Borneo, Bukit Raya.

Roots 1.1–1.5 mm diameter. *Rhizome* 6–7 mm thick, the portion between two pseudobulbs with 3 or 4 internodes; scales soon disintegrating. *Pseudobulbs* 8–12 mm apart, 13–21 by 0.8–2 cm. *Leaf* petiole 6–12 mm long; blade (obovate-)lanceolate, 22–36 by 4–8 cm, margin slightly undulating, apex acuminate to cuspidate, main nerves 5–7. *Inflorescence* 2–44-flowered. Peduncle slender, 9–15 cm long. Rachis erect, constricted at the nodes, 6–15 cm long; internodes short, rectangular, quadrangular in cross section and with rounded edges, with distinct pedicel scars, 3.5–4 by 1.8–2 mm; floral bracts narrowly triangular, glabrous, 33–37 by 9.5–11 mm. *Flowers* opening in succession. Pedicel 6–8 by 2–2.5 mm; ovary 5–6 by 2–3 mm. *Median sepal* ovate-oblong, 40–43 by 14–16 mm, glabrous, nerves 5–7. *Lateral sepals* ovate-lanceolate, 33–35 by 8–9 mm, glabrous, nerves 5–7. *Petals* 32–34 by 2–2.4 mm, glabrous, nerves 3. *Hypochile* 13–15 by 12–14 mm, base slightly saccate, lateral lobes 12–13 by 5–5.5 mm, with decurrent apex, sinus 0–1 mm deep, keels 3, not connected, low at the base, abruptly ascending on the basal fifth of the hypochile, slightly descending towards the apex of the hypochile, the median keel present on the entire hypochile, the lateral keels higher than the median keel, without triangular hook at the base. *Epichile* broadly ovate, 16–18 by 19–21 mm, slightly recurved, claw 1–3 by 7–9 mm, keels running some distance from the margin, ascending towards the apex; blade when flattened broadly ovate, 16–18 by 17–19 mm, glabrous, slightly recurved, with distinctly undulating margins, sides pronounced as lobules, top distinctly acute, ornamentation consisting of 2 plate-like keels ending abruptly in the median raised nerves at the basal half of the apex of the epichile. *Column* spatulate in outline, 13–15 by 3–3.5 mm, base with triangular, apically warted swelling 1.9–2.1 by 2.2–2.4 mm, hood with slightly distinct wings, apex emarginate, curved to the front. *Anther* broadly ovate,

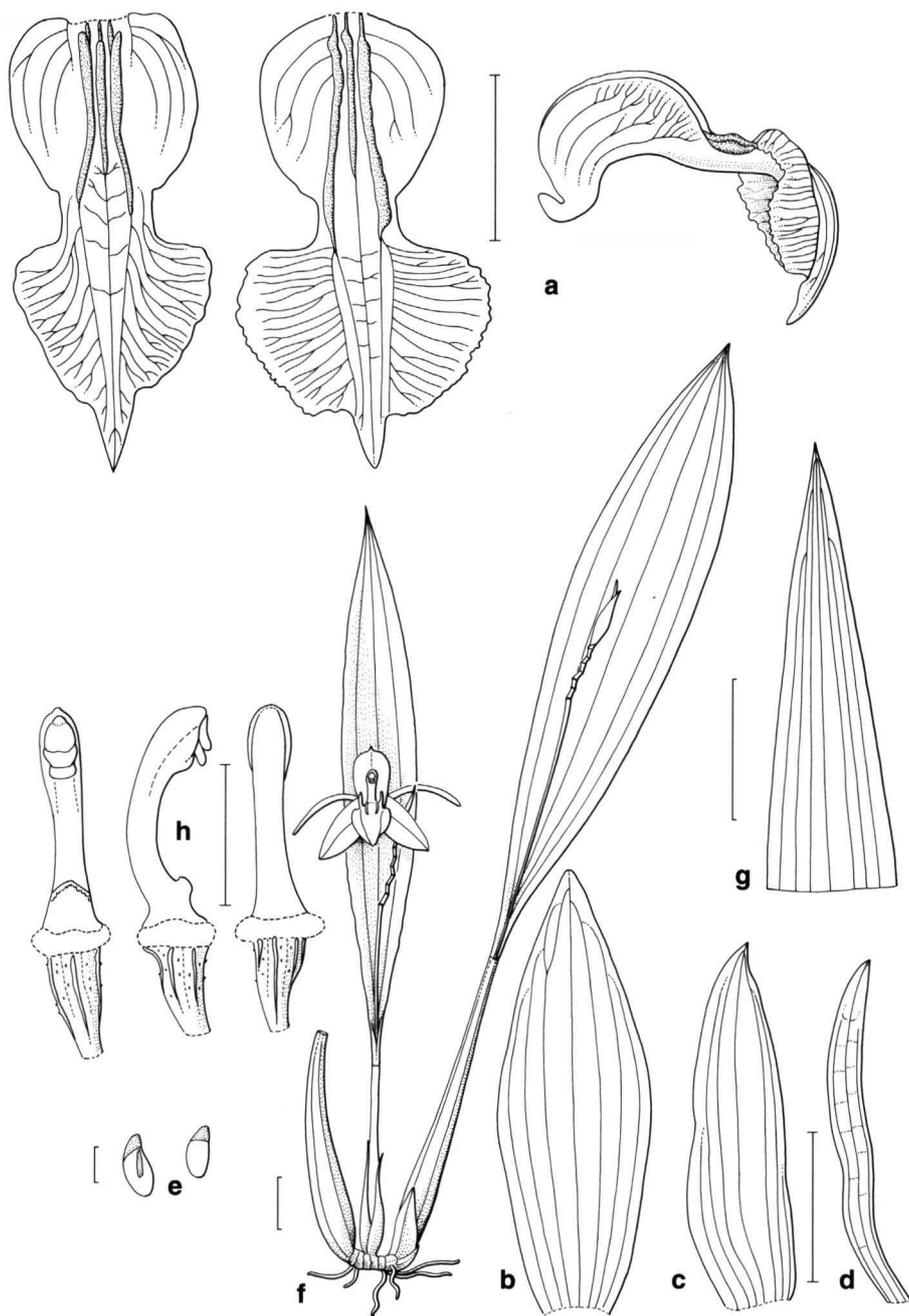


Fig. 5. *Coelogyne gibbifera* J.J. Sm. a. Lip, front view (from left to right: Bacon 54, Wood 627) and lateral view (Bacon 54); b. median sepal; c. lateral sepal; d. petal (Bacon 54); e. pollinia (Wood 627); f. habit (De Vogel 8291, Leiden cult. 23176); g. floral bract (Bacon 54); h. column, front, lateral and rear view (Wood 627). — Scale bars: 1 cm (a–d, f, h); 1 mm (e); 5 mm (g).

3.3–3.5 by 2.8–3.1 mm, apex emarginate. *Pollinia* ovoid, 1.1–1.3 by 0.7–0.9 mm. *Stigma* 2–2.2 by 2.1–2.3 mm, with emarginate margin; rostellum broadly ovate, 2.8–3.2 by 2.3–2.5 mm, with entire margin. *Fruit* 2.9–3.2 by 1.4–1.6 cm. *Seeds* 0.9–1.4 mm long.

Distribution — Borneo (Kalimantan, Sarawak, Sabah).

Habitat & Ecology — Epiphyte on tree trunks in primary forest. Recorded from low, open montane *Agathis–Lithocarpus–Dacrydium*, riverine and kerangas forest on sand, rock or clay. Elevation 1000–2900 m. Flowering: April to January.

Notes — 1. Pseudobulbs and leaves dark green tinged red. Inflorescence and bracts brownish green. Pedicel, ovary and sepals salmon to white tinged ochre to green tinged brown. Petals creamy white, with a dark brown mark along basal half of midnerve. Hypochile brown orange, cream coloured towards the centre, keels yellow. Epichile white, lobules separated by a red-brown to orange band, apex cream. Column pink to cream to salmon, with brown spot in front on base of swelling, anther brown to cream to yellow. Not fragrant.

2. The epithet *gibbifera* (Latin for hump-bearing) refers to the swelling on the base of the column.

3. The dimensions are based on herbarium, living and spirit collections.

4. The species can be recognised by its relatively large, successively opening, light salmon to whitish coloured flowers with a large white epichile with acute apex and a column with a swollen base.

5. The variation in size and shape of the midlobe of the lip of the specimens studied appears to be continuous, hence it is concluded that *C. macroloba* is synonymous with *C. gibbifera*.

6. *Coelogyne gibbifera* is very similar to *C. vermicularis* (see note 4 under description of this species).

3. *Coelogyne harana* J.J. Sm. — Fig. 6, Map 1, Plate 1a

Coelogyne harana J.J. Sm. (1927a) 27, t. 4, f. 17; J.J. Wood & P.J. Cribb (1994) 154. — Type: Winkler 346 (holo HBG), Borneo, Lebang Hara.

Roots 1.1–1.5 mm diameter. *Rhizome* 4.5–9.5 mm thick, the portion between two pseudobulbs with 3–6 internodes; scales soon disintegrating. *Pseudobulbs* 9–11 mm apart, 7.5–16 by 1–1.8 cm. *Leaf* petiole 11–14 mm long; blade oblong to (obovate-) lanceolate, 21–32 by 4.7–8 cm, margin slightly undulating, apex acute to cuspidate, main nerves 5–7. *Inflorescence* 9–35-flowered. Peduncle incrassate, 8–22 cm long. Rachis pendulous, constricted at the nodes, 3–8 cm long; internodes short, rectangular, quadrangular in cross section and with rounded edges, with distinct pedicel scars, 3–4.5 by 3–3.5 mm; floral bracts triangular, sparsely covered with scattered minute brown scale-like hairs, 12–14 by 7–8 mm. *Flowers* opening in successive clusters of

Plate 1. — a. *Coelogyne harana* J.J. Sm. (*Leiden cult.* 932547, Sarawak). Photograph B. Kieft. — b. *C. longpasiaensis* J.J. Wood & C.L. Chan (*Leiden cult.* 913542, Kalimantan). Photograph B. Kieft. — c. *C. monilrachis* Carr (*Leiden cult.* 980037, Sarawak). Photograph C.G. Koops. — d. *C. naja* J.J. Sm. (*Leiden cult.* 990122, Sarawak). Photograph C.G. Koops.



a. *Coelogyne harana*



b. *Coelogyne longpasiaensis*



c. *Coelogyne monilirachis*



d. *Coelogyne naja*

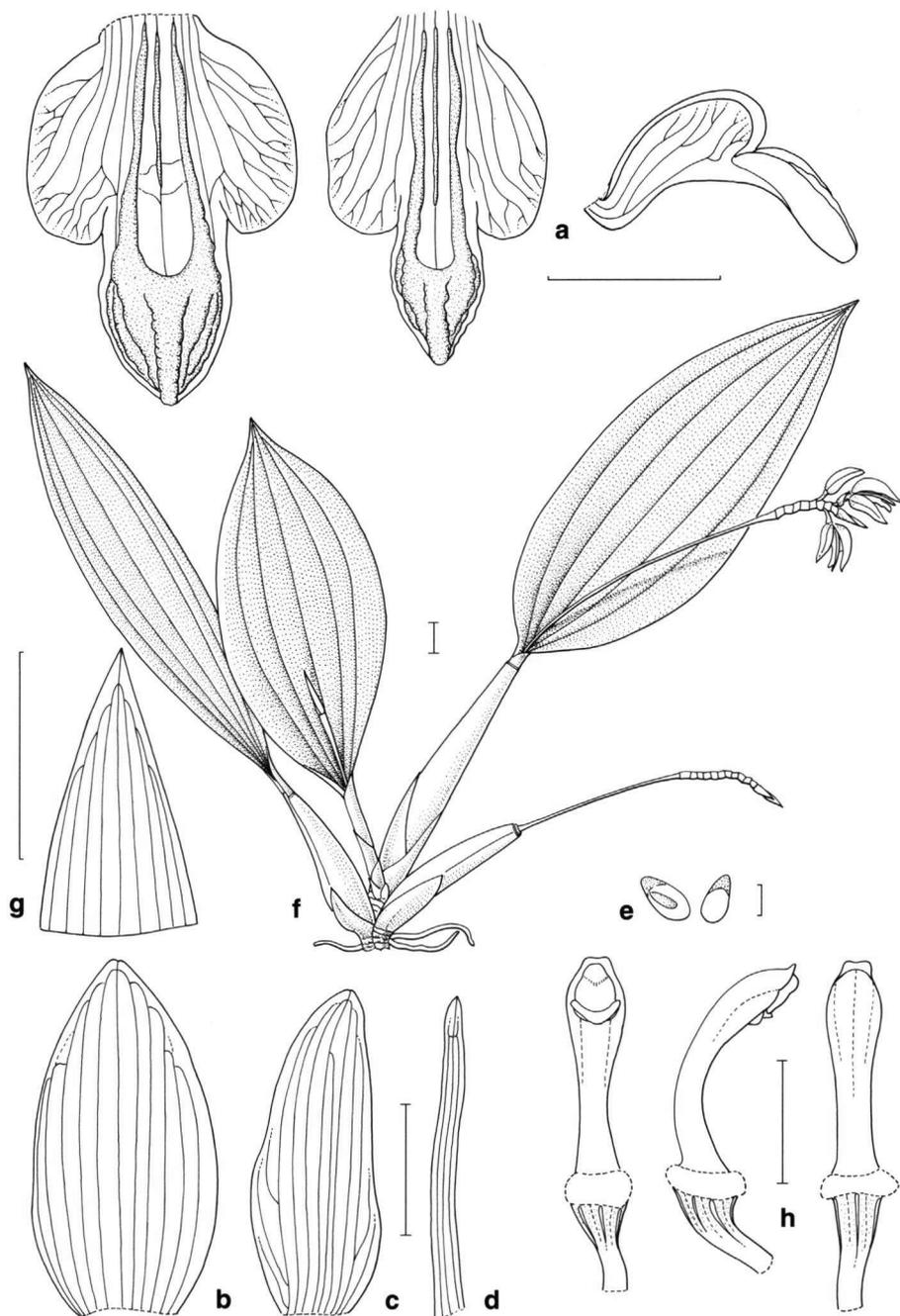


Fig. 6. *Coelogyne harana* J.J. Sm. a. Lip, front view (from left to right: *Leiden cult.* 980559, *Leiden cult.* 932547) and lateral view (*Leiden cult.* 932548); b. median sepal; c. lateral sepal; d. petal; e. pollinia; f. habit (*Leiden cult.* 980559); g. floral bract; h. column, front, lateral and rear view (*Leiden cult.* 932548). — Scale bars: 1 cm (a–d, f, h); 1 mm (e); 5 mm (g).

three or more. Pedicel 1–1.3 by 4–5 mm; ovary 2–3.5 by 2.5–3 mm. *Median sepal* ovate, sparsely covered with scattered minute brown scale-like hairs, 23–29 by 9–13 mm, nerves 9–11. *Lateral sepals* ovate-oblong, sparsely covered with scattered minute brown scale-like hairs, 22–27 by 7–9 mm, nerves 9–11. *Petals* 22–27 by 1–1.5 mm, sparsely covered with scattered minute brown scale-like hairs, nerves 3. *Hypochile* 12–13 by 12–15 mm, base slightly saccate, lateral lobes 22–27 by 3.5–5.5 mm, with broadly rounded to truncate apex, sinus 1.5–2 mm deep, keels 3, not connected, low at the base, gradually ascending on the basal half of the hypochile, descending on the apical third of the hypochile, ascending again towards the apex of the hypochile, the median keel occurring on the hypochile only, the lateral keels much higher than the median keel, without triangular hook at the base. *Epichile* spatulate, 7–10 by 6–8 mm, slightly recurved, claw 2.5–3 by 5–7 mm, keels running some distance from the margin, ascending towards the apex, blade when flattened broadly ovate, 6–7.5 by 6–8 mm, warty, slightly recurved, with slightly undulating margins, sides not pronounced as lobules, top acute, ornamentation consisting of 5–7 swollen, completely fused warty keels, forming a broadly ovate patch, covering nearly the entire apex. *Column* spatulate in outline, 15–16 by 2–3 mm, base without swelling, hood with slightly distinct wings, apex emarginate, not curved to the front. *Anther* broadly ovate, 2.5–4 by 2–3 mm, apex slightly emarginate. *Pollinia* ovoid, 1–1.2 by 0.9–1.2 mm. *Stigma* 1.9–2.2 by 2–3 mm, with emarginate margin; rostellum broadly ovate, 3–4 by 2.9–3.8 mm, with slightly emarginate margin. *Fruit* and *seeds* not seen.

Distribution — Borneo (Sabah, Sarawak, Kalimantan).

Habitat & Ecology — Epiphyte in primary hill and montane forest. Recorded from Fagaceae–Dipterocarpaceae–*Agathis* forest on clay soil. Elevation 150–1700 m. Flowering: the whole year round.

Notes — 1. Pseudobulbs dark green tinged red. Leaves dark olive-green above, paler beneath, oldest tinged reddish brown. Sepals and petals translucent salmon orange to light salmon. Lip salmon orange to opaque, base and apex pale orange, lateral lobes with pale brown apex, midlobe with transverse brown blotch in centre. Column pale salmon to white, deep salmon on the back and towards the apex. Anther light yellow to cream coloured with a longitudinal orange salmon coloured line. Pollinia light yellow. Not fragrant.

2. The epithet *harana* refers to the Indonesian village Lebang Hara, where the type specimen was collected.

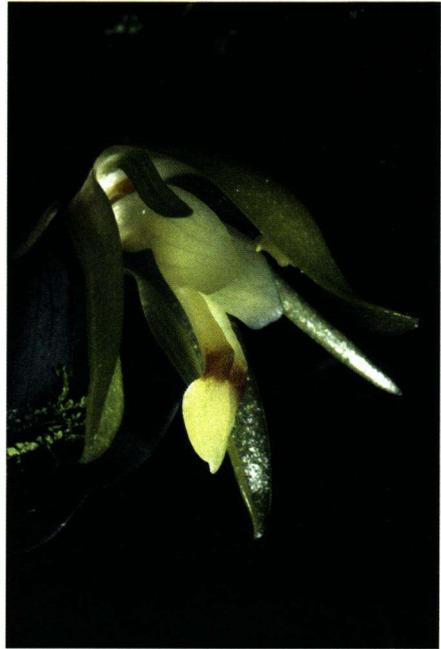
3. The dimensions are based on living and spirit collections.

4. The species can be recognised by its intermediate-sized, in periodic clusters of 3 or more simultaneously opening salmon coloured flowers with a hypochile with lateral lobes with broadly rounded to truncate apex and an epichile with thickened apex.

Plate 2. — a. *Coelogyne incrassata* (Blume) Lindl. var. *incrassata* (Leiden cult. 913485, Kalimantan). Photograph B. Kieft. — b. *C. incrassata* (Blume) Lindl. var. *valida* J.J. Sm. (Beaman 10275, Sabah). Photograph J.H. Beaman. — c. *C. incrassata* (Blume) Lindl. var. *sumatrana* J.J. Sm. (Leiden cult. 932928, Sarawak). Photograph C.G. Koops. — d. *C. chanii* Gravendeel & de Vogel (Poring Hot Springs cult. (Lohok) B 156-920103, Sabah). Photograph C.G. Koops.



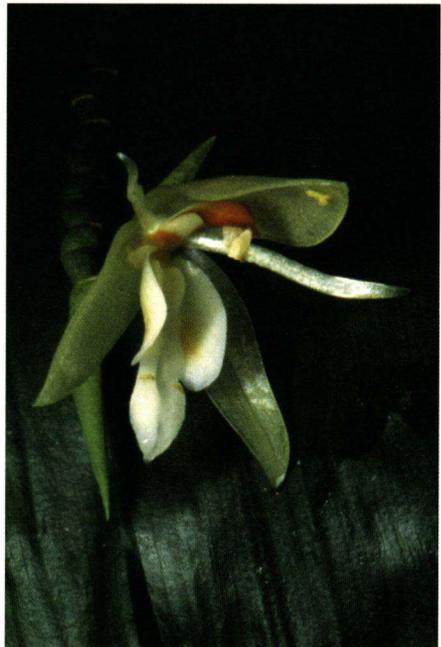
a. *Coelogyne incrassata* var. *incrassata*



b. *Coelogyne incrassata* var. *valida*



c. *Coelogyne incrassata* var. *sumatrana*



d. *Coelogyne chanii*

5. Smith (1927a) states that the flowers of *C. harana* open in succession. The type collection, however, has only one mature inflorescence and several, fully opened flowers in an attached envelope. As the flowers of all living collections studied of this species open nearly simultaneously Smith may have made a mistake in the description of the type.

4. *Coelogyne incrassata* (Blume) Lindl.

Literature: see under the varieties.

Rhizome scales soon disintegrating. Peduncle slender. Rachis pendulous, constricted at the nodes; internodes short, rectangular, quadrangular in cross section and with rounded edges, with distinct pedicel scars; floral bracts glabrous. *Flowers* opening nearly simultaneously. *Median sepal* glabrous. *Lateral sepals* glabrous. *Petals* glabrous, nerves 1–3. *Hypochile* base saccate, keels 3, not connected, low at the base, the median keel occurring on the entire hypochile, the lateral keels slightly higher than the median keel, without triangular hook at the base. *Epichile* recurved, keels on claw running completely along the margins of the epichile, ascending towards the apex, blade when flattened orbicular, warty, sides not pronounced as lobules, top acute, ornamentation consisting of 4–7 swollen completely fused warty keels, forming a broadly ovate patch, covering nearly the entire apex. *Column* spatulate in outline, base without swelling, apex curved to the front. *Anther* ovate; apex emarginate. *Pollinia* ovoid. *Stigma* with emarginate margin; rostellum ovate, emarginate.

Notes — 1. Leaves, inflorescences and bracts greenish red to brown. Sepals and petals yellowish green to cream-coloured tinged salmon. Lip cream-coloured to white to salmon with a transverse orange-red to brown bar and salmon base; lateral lobes of hypochile light reddish brown to ochrish yellow. Column cream-coloured to white to pale salmon, with brown margin and pale salmon to reddish brown hood; apex dull orange at the back. Anther brown to light yellow to pale dull orange. Rostellum cream-coloured. Ovary dull salmon tinged brown. Not fragrant.

2. Three different varieties can be recognised, based on the height of the keels and depth of the sinus of the lateral lobes of the hypochile. The rank of variety is maintained because the infraspecific taxa of *C. incrassata* do not seem to occupy distinct distribution areas. However, many of the collections studied lack precise locality indications.

3. The species is easily recognised by the epichile with 2 plate-like keels, running along the margins, transverse orange-red to brown bar and apex with swollen patch.

KEY TO THE VARIETIES

- 1a. Hypochile with lateral keels only slightly higher at the basal half than towards the apex 2
- b. Hypochile with lateral keels distinctly higher at the basal half than towards the apex c. var. **valida**
- 2a. Hypochile with lateral lobes with sinus up to 2 mm deep ... a. var. **incrassata**
- b. Hypochile with lateral lobes with sinus deeper than 3 mm . b. var. **sumatrana**

a. var. *incrassata* — Fig. 7a, Map 2, Plate 2a

Coelogyne incrassata (Blume) Lindl. var. *incrassata* Lindl. (1830) 40; (1854b) 11; Miq. (1859) 667; Rchb.f. (1861b) 231; Pfitzer & Kraenzl. (1907b) 23; Backer & Bakh.f. (1968) 279; J.B. Comber (1990) 111; J.J. Wood & P.J. Cribb (1994) 154; T.E. Beaman, J.J. Wood, R.S. Beaman & J.H. Beaman (2001) 216, pl. 11C; O'Byrne (2001) 45. — *Chelonanthera incrassata* Blume (1825) 384. — *Pleione incrassata* (Blume) Kuntze (1891) 680. — Type: *Blume s.n.* (holo L), Java, Pantjar.

Roots 1–1.5 mm diameter. *Rhizome* 3–5 mm thick, the portion between two pseudobulbs with 4–6 internodes. *Pseudobulbs* 4–8 mm apart, 5–8 by 0.9–1.4 cm. *Leaf* petiole 5–9 mm long; blade lanceolate, 14–18.5 by 3.5–4.7 cm, margin slightly undulating, apex cuspidate, main nerves 3–5. *Inflorescence* 18–35-flowered. Peduncle 5.5–9 cm long. Rachis 3–6 cm long; internodes 1.5–3 by 1–1.5 mm; floral bracts ovate, 5–6 by 2.5–3 mm. Pedicel 2–2.5 by 1–1.5 mm; ovary 2.5–3 by 1–2 mm. *Median sepal* oblong, 17–18 by 4–6 mm, nerves 7–9. *Lateral sepals* ovate-lanceolate, 14–16 by 3.5–4 mm, nerves 5–7. *Petals* 13–16 by 0.9–1.1 mm. *Hypochile* 0.7–1.3 by 0.7–1.2 mm, lateral lobes 8–11 by 2.5–3.5 mm, with acute apex, sinus 1–2 mm deep, keels gradually ascending on the basal half of the hypochile and then descending again towards the apex of the hypochile. *Epichile* spatulate, 5–11 by 2–4 mm, claw 3.5–5 by 2–3.5 mm, blade 2.9–5 by 2.7–3.9 mm, slightly recurved, with distinctly undulating margins. *Column* 11–12 by 2.5–3 mm, hood with distinct wings, apex emarginate. *Anther* 1.5–1.6 by 1.4–1.7 mm. *Pollinia* 6–8 by 0.6–0.8 mm. *Stigma* 0.9–1.1 by 1.2–1.3 mm; rostellum 1.3–1.5 by 1.4–1.6 mm. *Fruit* 2–2.5 by 1–1.2 cm. *Seeds* 0.6–0.8 mm long.

Distribution — Java, Borneo (Kalimantan, Sarawak).

Habitat & Ecology — Epiphyte in montane or riverine forest. Elevation 800–1400 m. Flowering: the whole year round.

Notes — 1. The epithet *incrassata* (Latin for swollen) refers to the swollen apex of the epichile.

2. The dimensions are based on herbarium and spirit material.

3. The variety can be recognised by the hypochile with shallow sinus.

b. var. *sumatrana* J.J. Sm. — Fig. 7b, Map 2, Plate 2c

Coelogyne incrassata (Blume) Lindl. var. *sumatrana* J.J. Sm. (1914) 1; J.B. Comber (2001) 323 (excluding the photograph on p. 324 below, which is *C. renae*). — Type: *Bogor cult.* (*Jacobson. leg. Ajoeb*) 775, 863 (syntypes BO, not seen), Sumatra, Bukit Kaba.

Coelogyne vermicularis auct. non. J.J. Sm.: Ridl. (1925) 91; J.J. Sm. (1933) 171.

Roots 1.5–2 mm diameter. *Rhizome* 4–5.5 mm thick, the portion between two pseudobulbs with 3 or 4 internodes. *Pseudobulbs* 9–13 mm apart, 5–10 by 0.5–0.7 cm. *Leaf* petiole 7–9 mm long; blade (obovate-)lanceolate, 16–24 by 3.2–5 cm, margin finely

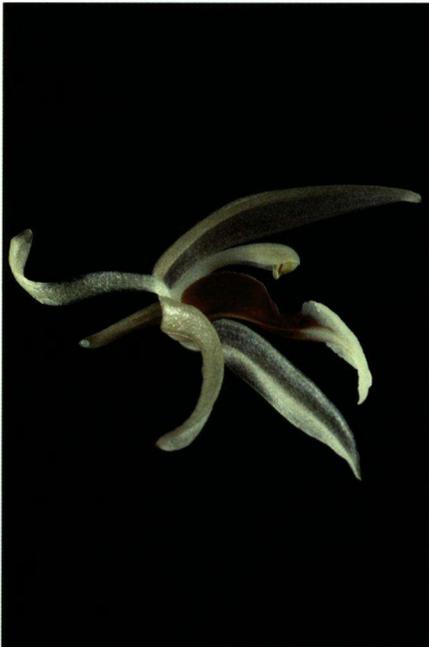
Plate 3. — a. *Coelogyne kelamensis* J.J. Sm. (*Leiden cult.* 930568, unknown locality). Photograph J. Meijvogel. — b. *C. renae* Gravendeel & de Vogel (*Leiden cult.* 970290, Sarawak). Photograph C.G. Koops. — c. *C. gibbifera* J.J. Sm. (*Leiden cult.* 22074, Sabah). Photograph B. Kieft. — d. *C. vermicularis* J.J. Sm. (*Leiden cult.* 914400, Sarawak). Photograph J. Meijvogel.



a. *Coelogyne kelamensis*



b. *Coelogyne renae*



c. *Coelogyne gibbifera*



d. *Coelogyne vermicularis*

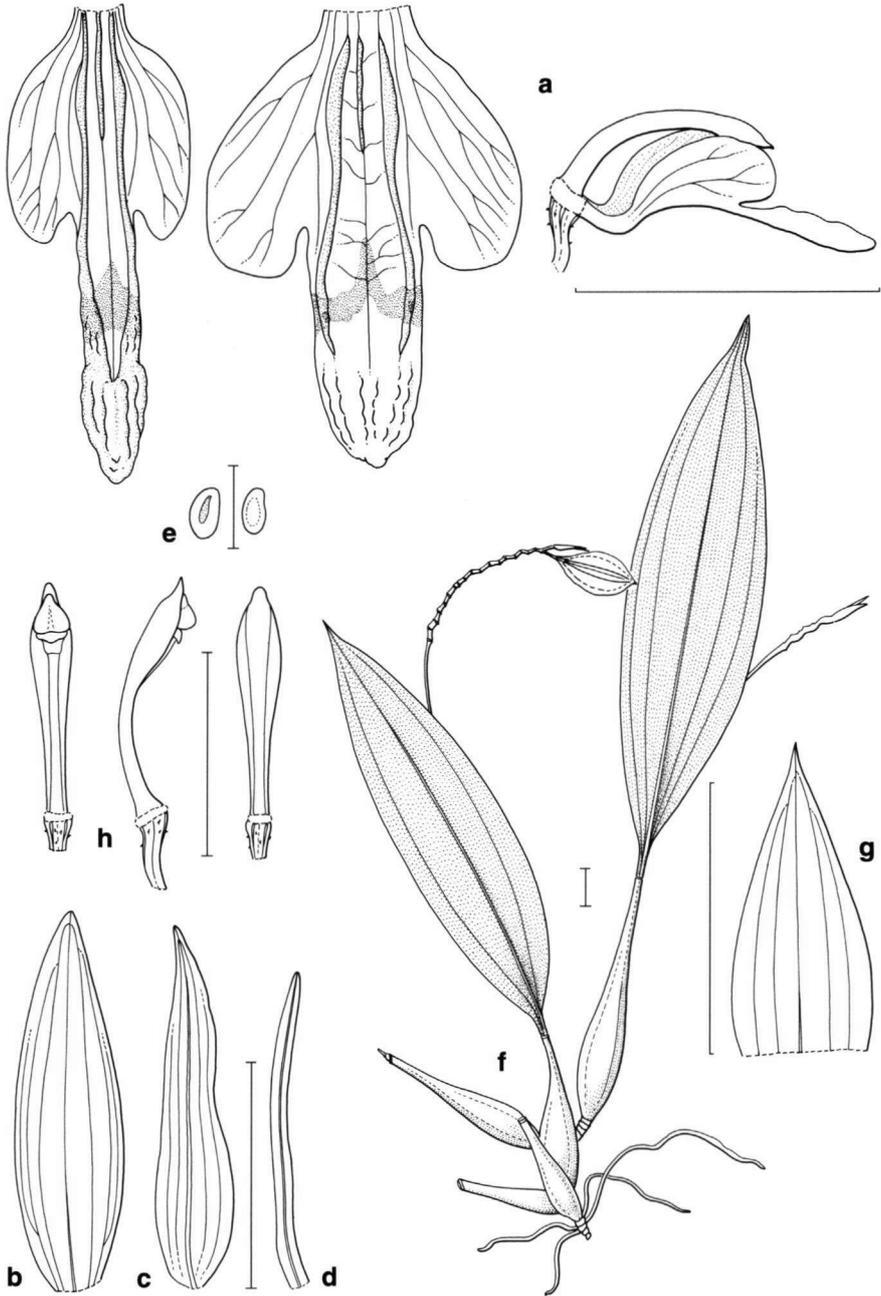


Fig. 7a. *Coelogyne incrassata* (Blume) Lindl. var. *incrassata*. a. Lip, front view (from left to right: Bogor cult. 38, Leiden cult. 980362, Leiden cult. 933127) and lateral view (Leiden cult. 933127); b. median sepal; c. lateral sepal; d. petal; e. pollinia (Bogor cult. 38); f. habit (Blume s.n.); g. floral bract; h. column, front, lateral and rear view (Bogor cult. 38). — Scale bars: 1 cm (a–d, f, h); 1 mm (e); 5 mm (g).

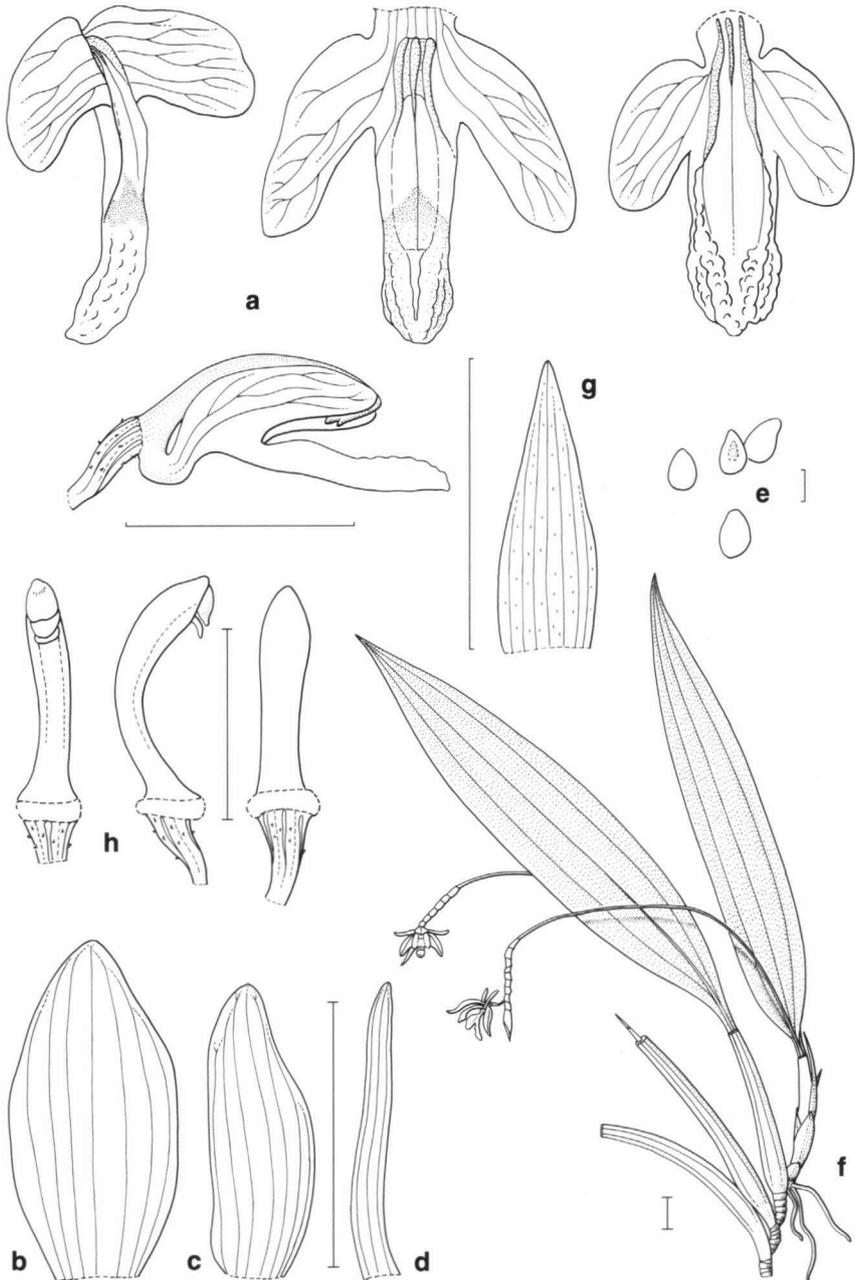


Fig. 7b. *Coelogyne incrassata* (Blume) Lindl. var. *sumatrana* J.J. Sm. a. Lip, front view (from left to right: *De Wilde & De Wilde-Duyffjes 12414*, *Leiden cult. 911184*, *Leiden cult. 932928*) and lateral view (*Leiden cult. 911184*); b. median sepal; c. lateral sepal; d. petal; e. pollinia (*Leiden cult. 911184*); f. habit (*Leiden cult. 932928*); g. floral bract (*Jacobs 8406*); h. column, front, lateral and rear view (*Leiden cult. 911184*). — Scale bars: 1 cm (a–d, f, h); 1 mm (e); 5 mm (g).

undulating, apex acuminate, main nerves 3–5. *Inflorescence* 15–22-flowered. Peduncle 8–18 cm long. Rachis 2–5 cm long; internodes 2–2.5 by 1.3–1.7 mm; floral bracts triangular, 6–8 by 3–4 mm. Pedicel 1.7–2 by 1–1.2 mm; ovary 2.7–3 by 2.3–2.6 mm. *Median sepal* elliptic, 16–18 by 6–8 mm, nerves 7–9. *Lateral sepals* ovate, 13–14 by 5–6 mm, nerves 7–9. *Petals* 14–16 by 1.3–1.6 mm. *Hypochile* 5–10 by 7.5–10 mm, lateral lobes 5.5–8 by 2.3–3 mm, with acute to broadly rounded apex, sinus 3–5 mm deep, keels abruptly ascending on the basal half of the hypochile and then descending again towards the apex of the hypochile. *Epichile* oblong to spatulate, 5–8.5 by 2–3.5 mm, claw 2–6 by 2–3 mm, blade 2.3–3 by 2–3.5 mm, not recurved, with slightly undulating margins. *Column* 12–14 by 1.5–2 mm, hood with slightly distinct wings, apex emarginate. *Anther* 1.4–1.6 by 1.2–1.3 mm. *Pollinia* 0.8–1 by 0.6–0.7 mm. *Stigma* 0.5–0.7 by 0.9–1.1 mm; rostellum 1.8–2 by 1.2–1.4 mm. *Fruit* 2.3–2.7 by 1.3–1.7 cm. *Seeds* 0.8–1.3 mm long.

Distribution — Sumatra, Borneo (Brunei, Sabah, Sarawak, Kalimantan).

Habitat & Ecology — Epiphyte in montane and lowland rain forest. Elevation 150–800 m. Flowering: the whole year round.

Notes — 1. The epithet *sumatrana* refers to the island of Sumatra, where the type collections were made by *Jacobson* (leg. *Ajoeb*) in 1916.

2. The dimensions are based on herbarium and spirit collections.

3. The variety can be recognised by the hypochile with lateral lobes with a deep sinus.

4. The variety is rather variable. The length of the lateral lobes of the hypochile varies from large (Sumatra) to intermediate (Borneo) and the hypochile can be oblong to spatulate. Additional varieties may be recognised when more collections become available.

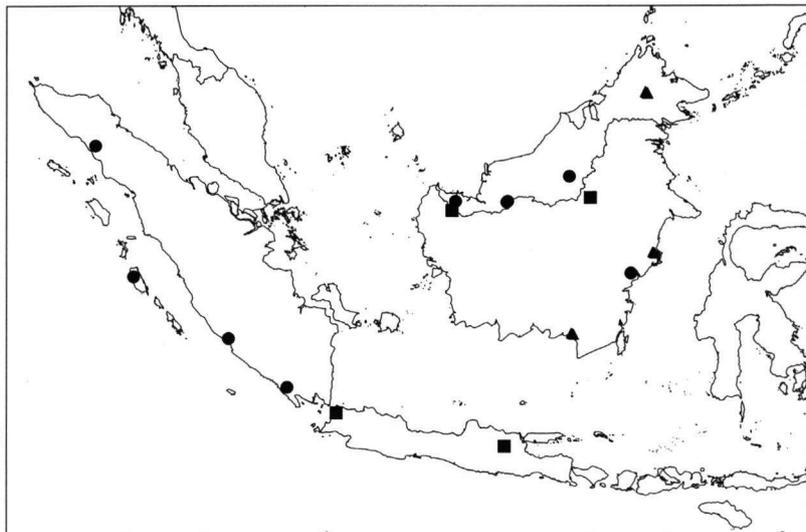
c. var. *valida* J.J. Sm. — Fig. 7c, Map 2, Plate 2b

Coelogyne incrassata (Blume) Lindl. var. *valida* J.J. Sm. (1931b) 92; J.J. Wood & P.J. Cribb (1994) 154. — Type: *Hallier 3054* (holo L; iso BO), Borneo, Liang Gagang.

Roots 0.5–2 mm diameter. *Rhizome* 3.5–6.5 mm thick, the portion between two pseudobulbs with 3–5 internodes. *Pseudobulbs* 5–11 mm apart, 4–12 by 0.5–0.9 cm. *Leaf* petiole 3–4 mm long; blade (obovate-)oblong, 13–26 by 4.5–7.5, margin roughly undulating, apex acuminate, main nerves 5–7. *Inflorescence* 8–56-flowered. Peduncle 8–15 cm long. Rachis 3–19 cm long; internodes 4–5 by 1–2 mm; floral bracts triangular, 8–8.5 by 3.9–4.5 mm. Pedicel 2–3 by 1.3–1.5 mm; ovary 1.5–2 by 0.5–0.9 mm. *Median sepal* oblong, 19–21 by 4–6 mm, nerves 5–7. *Lateral sepals* ovate-oblong, 17–19 by 3–4 mm, nerves 3–5. *Petals* 14–16 by 0.5–0.9 mm. *Hypochile* 7–9 by 6–8 mm, lateral lobes 7–9 by 3–3.5 mm, with acute apex, sinus 1.5–2 mm deep, keels abruptly ascending on the basal half of the hypochile and then descending again towards the apex of the hypochile. *Epichile* oblong, 6–8 by 3–4 mm, claw 1–1.5 by 3–4 mm, blade 2.7–3.2 by 2.9–3.3 mm, slightly recurved, with slightly undulating margins. *Column* 0.9–1.2 by 3–3.5 mm, hood with slightly distinct wings, apex with entire margin. *Anther* 1.9–2.1 by 2–2.2 mm. *Pollinia* not seen. *Stigma* 0.9–1.2 by 0.8–1.1 mm; rostellum 1.9–2.1 by 1.5–1.8 mm. *Fruit* 18–28 by 11–20 mm. *Seeds* 1–1.2 mm long.



Fig. 7c. *Coelogyne incrassata* (Blume) Lindl. var. *valida* J.J. Sm. a. Lip, front view (Endert 4038) and lateral view (Hallier 3054); b. median sepal; c. lateral sepal; d. petal; e. anther; f. habit; g. column, front, lateral and rear view (Endert 4038). — Scale bars: 1 cm (a–d, f, g); 1 mm (e).



Map 2. Distribution of *Coelogyne incassata* (Blume) Lindl. var. *incassata* (■), var. *sumatrana* J.J. Sm. (●) and var. *valida* J.J. Sm. (▲).

Distribution — Borneo (Kalimantan, Sabah).

Habitat & Ecology — Epiphyte in primary hill and lowland forest. Elevation 400–800 m. Flowering: June, September, November.

Notes — 1. The epithet *valida* (Latin for robust) refers to the large size of the type specimen.

2. The dimensions are based on herbarium collections only.

3. Specimens collected on ultrabasic rock have a much smaller habit.

4. The variety can be recognised by its high keels on the hypochile and shallow sinus.

5. *Coelogyne kelamensis* J.J. Sm. — Fig. 8, Map 3, Plate 3a

Coelogyne kelamensis J.J. Sm. (1910) 5, t. 302; Ames (1921b) 144; J.J. Wood & P.J. Cribb (1994) 156; de Vogel, Schuit., FelÛs & A. Vogel (1999) pl. 69. — Type: *Hallier 2489* (holo BO, not seen), Borneo, Mount Kelam.

Roots 1–1.5 mm diameter. *Rhizome* 4–6 mm thick, the portion between two pseudobulbs with 6–8 internodes; scales not disintegrating. *Pseudobulbs* 15–40 mm apart, 7–8 by 0.5–0.8 cm. *Leaf* petiole 20–30 mm long; blade obovate-oblong, 10.5–16.5 by 2.7–5 cm, margin slightly undulating, apex acute, main nerves 3–5. *Inflorescence* 10–19-flowered. Peduncle slender, 4.5–8.5 cm long. Rachis pendulous, not constricted at the nodes, 3–6 cm long; internodes elongated, quadrangular in cross section and with rounded edges, with distinct pedicel scars, 4.5–5 by 0.8–1.1 mm; floral bracts ovate, glabrous, 8.5–9 by 4.5–5.5 mm. *Flowers* opening in succession. Pedicel 4–5 by 0.9–1.1 mm; ovary 1.5–2 by 3–4 mm. *Median sepal* oblong, covered with scattered minute brown scale-like hairs, 13–15 by 5–6 mm, nerves 7–9. *Lateral sepals* ovate-oblong, covered with scattered minute brown scale-like hairs, 15–16 by 4.5–5.5 mm,

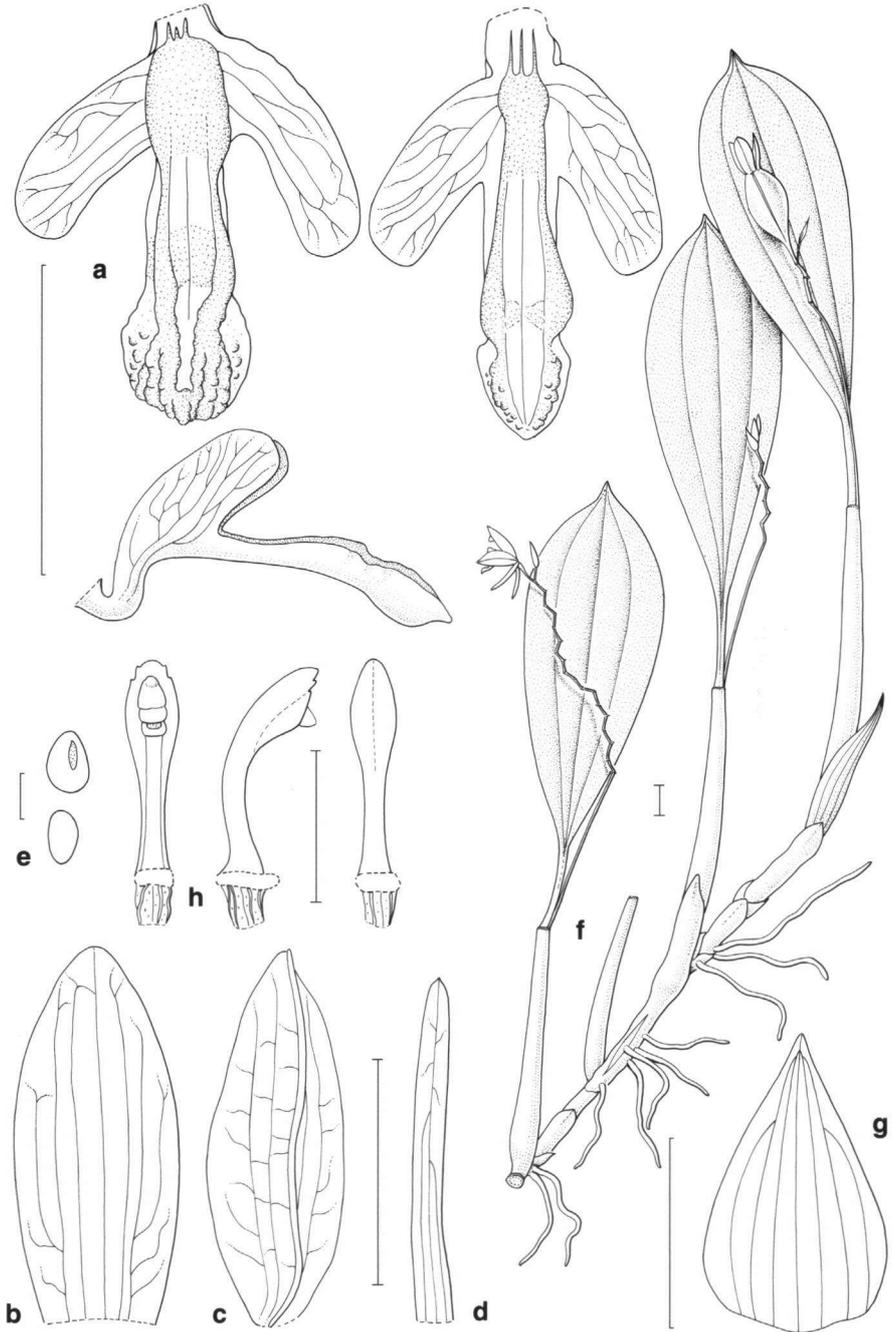
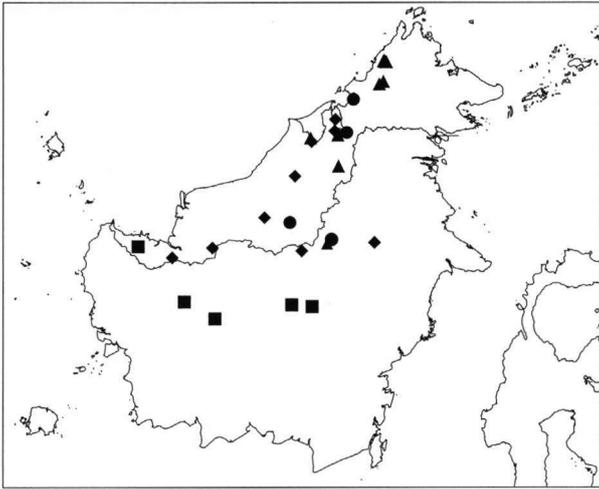


Fig. 8. *Coelogyne kelamensis* J.J. Sm. a. Lip, front view (from left to right: *Ridsdale 476*, *Keßler 2558*) and lateral view (*Ridsdale 476*); b. median sepal; c. lateral sepal; d. petal; e. pollinia; f. habit (*Keßler 258*); g. floral bract; h. column, front, lateral and rear view (*Ridsdale 476*). — Scale bars: 1 cm (a–d, f, h); 1 mm (e); 5 mm (g).



Map 3. Distribution of *Coelogyne kelamensis* J.J. Sm. (■), *C. longpasiaensis* J.J. Wood & C.L. Chan (●), *C. monilirachis* Carr (▲) and *C. naja* J.J. Sm. (◆).

nerves 5–7. *Petals* covered with scattered minute brown scale-like hairs, 13–14 by 0.8–1.1 mm, nerves 3. *Hypochile* 6–7 by 2.3–2.8 mm, base saccate, lateral lobes 6–7 by 2–2.5 mm, with broadly rounded apex, sinus 3–3.5 mm deep, keels 3, basally connected, low at the base, abruptly ascending on the basal half of the hypochile and then descending again towards the apex of the hypochile, the median keel occurring on the basal third of the hypochile only, the lateral keels much higher than the median keel, without triangular hook at the base. *Epichile* spatulate, 8–9 by 2.6–3 mm, slightly recurved, claw 5.5–6 by 2.4–2.6 mm, keels running some distance from the margin, ascending towards the apex, descending abruptly in the median rows of warts covering the apex, blade when flattened orbicular to broadly ovate, 2.8–3.2 by 2.9–3.3 mm, warty, slightly recurved, with entire margins, sides not pronounced as lobules, top broadly rounded, ornamentation consisting of 6–8 swollen, completely fused warty keels, forming a broadly ovate patch, covering the entire apex. *Column* spatulate in outline, 12–14 by 2.4–2.6 mm, base without swelling, hood with distinct wings, apex emarginate, curved to the front. *Anther* broadly ovate, 1.8–2.3 by 1.7–2.2 mm, apex emarginate. *Pollinia* ovoid, 1–1.2 by 0.7–0.8 mm. *Stigma* 1.5–1.8 by 1.8–2.2 mm, with entire margin; rostellum broadly ovate, 1.9–2.2 by 2.3–2.5 mm, with entire margin. *Fruit* c. 2.3 by 1.1 cm. *Seeds* not seen.

Distribution — Borneo (Kalimantan, Sarawak).

Habitat & Ecology — Epiphyte or terrestrial in primary swamp forest and kerangas on sandstone. Elevation 15–290 m. Flowering: March to June.

Notes — 1. Sepals and petals yellow to yellowish green, lip with white tip and orange brown transverse marking near base of epichile.

2. The epithet *kelamensis* refers to mount Kelam in Kalimantan, where the type specimen was collected.

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

4. The species can be recognised by the widely spaced pseudobulbs, creeping rhizome with persistent scales, obovate-oblong leaves with relatively long petiole, and small yellowish green flowers with a hypochile with long lateral lobes and broadly rounded apices.

5. Despite several deviating characters (persistent rhizome scales, widely spaced pseudobulbs and slender rachis without constricted internodes), phylogenetic analyses using morphological and molecular characters suggest that *C. kelamensis* belongs in sect. *Moniliformes*.

6. *Coelogyne longpasiaensis* J.J. Wood & C.L. Chan — Fig. 9, Map 3, Plate 1b

Coelogyne longpasiaensis J.J. Wood & C.L. Chan (1990) 87; J.J. Wood & P.J. Cribb (1994) 155; de Vogel, Schuit., Felëus & A. Vogel (1999) pl. 71. — Type: *Vermeulen & Duistermaat 946* (holo K; iso L), Borneo, Sabah, Long Pa Sia.

Roots 0.9–1.4 mm diameter. *Rhizome* 5–7 mm thick, the portion between two pseudobulbs with 3–5 internodes; scales soon disintegrating. *Pseudobulbs* 5–8 mm apart, 6–13 by 0.8–1.1 cm. *Leaf* petiole 12–15 mm long; blade (obovate) lanceolate, 13–22 by 2.3–4.7 cm, margin finely undulating, apex acuminate; main nerves 5–7. *Inflorescence* 3–37-flowered. Peduncle slender, 6.5–10.5 cm long. Rachis pendulous, constricted at the nodes, 4.5–6 cm long; internodes short, rectangular, quadrangular in cross section and with rounded edges, with indistinct pedicel scars, 1.5–2.5 by 1.1–1.4 mm; floral bracts triangular, glabrous, 10–11 by 5–6 mm. *Flowers* opening nearly simultaneously. Pedicel 3.5–4 by 1.3–1.4 mm; ovary 4.5–5 by 1.9–2.2 mm. *Median sepal* oblong, 16–17 by 6–7 mm; nerves 5–7. *Lateral sepals* ovate-lanceolate, 15–16 by 3.5–4 mm, nerves 5–7. *Petals* 16–17 by 1.9–2.2 mm, nerves 1 or 2. *Hypochile* 8–9 by 8.5–9.5 mm, base slightly saccate, lateral lobes 8–9 by 2.5–3 mm, with acute apex, sinus 0–1 mm deep, keels 3, not connected, low at the base, gradually ascending towards the apex of the hypochile, the median keel occurring on the basal half of the hypochile only, the lateral keels slightly higher than the median keel, without triangular hook at the base. *Epichile* slightly spatulate, 4.5–5.5 by 3.5–4.5 mm, slightly recurved, claw 2–2.5 by 3.5–4 mm, keels running some distance from the margin, ascending towards and ending in a patch of small warts on the apex, blade when flattened orbicular, 0.3–0.35 by 0.35–0.45 mm, warty, slightly recurved, with distinctly undulating margins, sides pronounced as lobules, top slightly acute, ornamentation consisting of 4–6 swollen, completely fused warty keels, forming a triangular patch, covering nearly the entire apex. *Column* spatulate in outline, 9–11 by 2.3–2.4 mm, base without swelling, hood with slightly distinct wings, apex emarginate, not curved to the front. *Anther* broadly ovate, 1.9–2.2 by 1.1–1.3 mm, apex slightly emarginate. *Pollinia* ovoid, 1–1.2 by 0.6–0.8 mm. *Stigma* 1.2–1.3 by 1.2–1.3 mm, with emarginate margin; rostellum broadly ovate, 1.7–1.9 by 1.9–2.1 mm, with entire margin. *Fruit* 1.9–2.5 by 0.8–1.1 cm. *Seeds* 0.9–1.2 mm long.

Distribution — Borneo (Kalimantan, Sarawak, Sabah).

Habitat & Ecology — Epiphyte in primary forest. Recorded from moist riverine and dry montane Fagaceae–Dipterocarpaceae–*Agathis* forest on loamy and sandstone soil. Elevation 800–1700 m. Flowering: the whole year round.

Notes — 1. Leaves, inflorescence and bracts green to red. Sepals and petals pale green to light salmon coloured. Lip cream to light yellow to light salmon coloured.

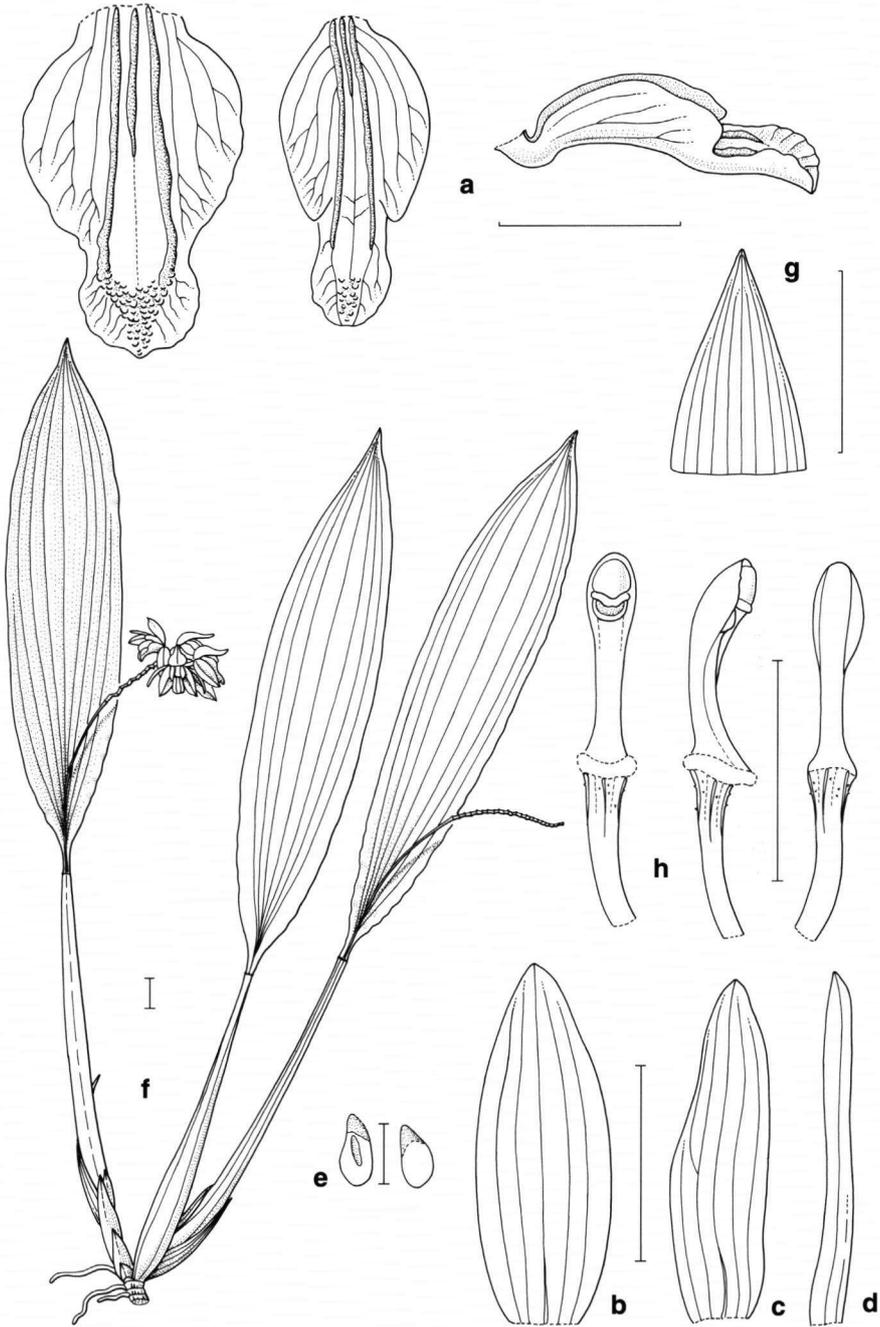


Fig. 9. *Coelogyne longpasiaensis* J.J. Wood & C.L. Chan. a. Lip, front view (from left to right: *Leiden cult. 913480*, *Leiden cult. 913542*) and lateral view (*Leiden cult. 913542*); b. median sepal; c. lateral sepal; d. petal; e. pollinia; f. habit; g. floral bract; h. column, front, lateral and rear view (*Leiden cult. 913542*). — Scale bars: 1 cm (a–d, f, h); 1 mm (e); 5 mm (g).

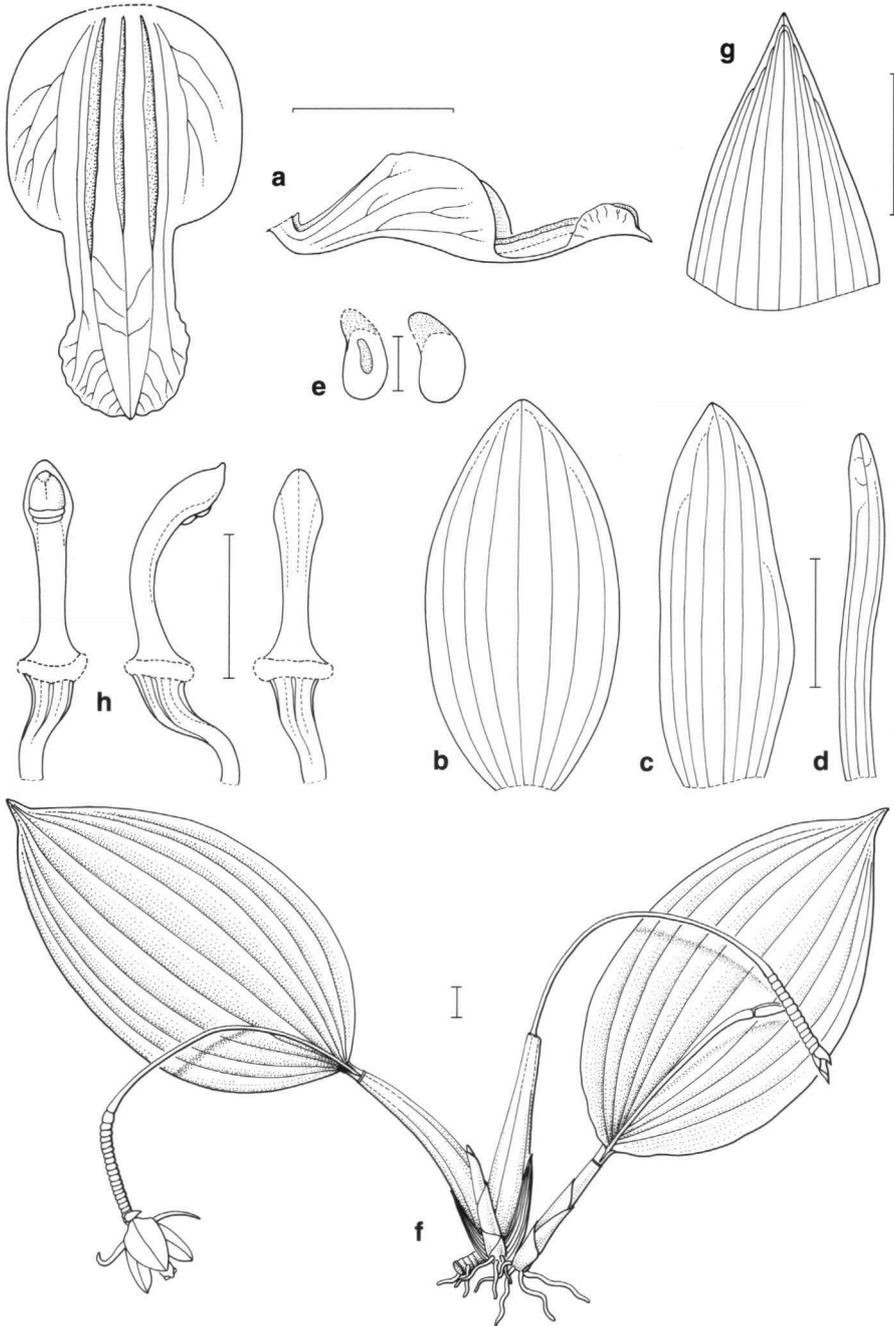


Fig. 10. *Coelogyne monilirachis* Carr. a. Lip, front view (*Leiden cult. 980222*) and lateral view (*Leiden cult. 980037*); b. median sepal; c. lateral sepal; d. petal; e. pollinia; f. habit; g. floral bract; h. column, front, lateral and rear view (*Leiden cult. 980037*). — Scale bars: 1 cm (a–d, f, h); 1 mm (e); 5 mm (g).

Column cream to yellow coloured, with brown to orange margin, its base with an orange to somewhat ochre brown band, hood brown, anther light yellow. Slightly scented.

2. The epithet *longpasiaensis* refers to the Malay village Long Pa Sia, near where the type specimen was collected.

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

4. The species can be recognised by its leaves with finely undulating margins and flowers with a lip with hypochile with shallow to absent sinus and epichile with a triangular patch of small warts on the apex.

7. *Coelogyne monilirachis* Carr — Fig. 10, Map 3, Plate 1c

Coelogyne monilirachis Carr (1935) 208; A.L. Lamb & C.L. Chan (1978) 238; J.J. Wood, R.S. Beaman & J.H. Beaman (1993) 144; pl. 25B; J.J. Wood & P.J. Cribb (1994) 157; T.E. Beaman, J.J. Wood, R.S. Beaman & J.H. Beaman (2001) 218, pl. 12B, 12C. — Type: *SFN* (Carr) 27230 (holo SING; iso K, L, P), Borneo, Mount Kinabalu, Tenompok.

Roots 2–2.3 mm diameter. *Rhizome* 4.5–8.5 mm thick, the portion between two pseudobulbs with 5–7 internodes; scales soon disintegrating. *Pseudobulbs* 7–12 mm apart, 7–11 by 1–1.8 cm. *Leaf* petiole 7–15 mm long; blade oblong, 23–25 by 6–11 cm; margin slightly undulating, apex acuminate, main nerves 7–9. *Inflorescence* 22–45-flowered. Peduncle slender, 8.7–15 cm long. Rachis pendulous, constricted at the nodes, 6–10 cm long; internodes short, disc-shaped, round in cross section, with indistinct pedicel scars, 2–3 by 2–4 mm; floral bracts triangular, glabrous, 12–14 by 6–8 mm. *Flowers* opening in succession. Pedicel 3–5 by 2–2.3 mm; ovary 5–7 by 3–4 mm. *Median sepal* elliptic, 30–32 by 15–18 mm, nerves 7–9. *Lateral sepals* ovate-oblong, 33–35 by 11–13 mm, nerves 7–9. *Petals* 30–32 by 2.8–3.2 mm, nerves 3. *Hypochile* 12–14 by 13–14 mm, base slightly saccate, lateral lobes 12–14 by 5–6 mm, with broadly rounded apex, sinus 0–1 mm deep, keels 3, not connected, low at the base, gradually ascending on the basal half of the hypochile, gradually descending towards the base of the epichile, the median keel occurring on the entire hypochile, the lateral keels higher than the median keel, without triangular hook at the base. *Epichile* spatulate, 10–12 by 5–7 mm, slightly recurved, claw 5–6 by 5–7 mm, keels running some distance from the margin, ending abruptly in the median raised nerves of the upper quarter of the claw, blade when flattened orbicular, 4.5–5.5 by 5–7 mm, glabrous, slightly recurved, with slightly undulating margins, sides pronounced as lobules, top slightly acute, ornamentation absent. *Column* narrowly spatulate in outline, 14–16 by 3.5–4.5 mm, base without swelling, hood with slightly distinct wings, apex with entire margin, curved to the front. *Anther* broadly ovate, 2.8–3.5 by 3–3.3 mm, apex slightly emarginate. *Pollinia* ovoid, 1.7–1.8 by 1.4–1.5 mm. *Stigma* 2.5–2.8 by 2.9–3 mm, with emarginate margin; rostellum broadly ovate, 3–3.2 by 3.3–3.5 mm, with entire margin. *Fruit* 4–4.3 by 1.5–2.5 cm. *Seeds* 1.2–1.5 mm long.

Distribution — Borneo (Kalimantan, Brunei, Sarawak, Sabah).

Habitat & Ecology — Epiphyte on tree branches and trunks in the shade in montane, swamp or ridge forest. Recorded from oak-laurel or oak-chestnut forest on sandstone or rocks. Elevation 1125–1800 m. Flowering: the whole year round.

Notes — 1. Leaves, bracts and rachis reddish liver coloured. Sepals and petals pale salmon. Lip pale salmon in the centre, creamy salmon at the base, along the margins

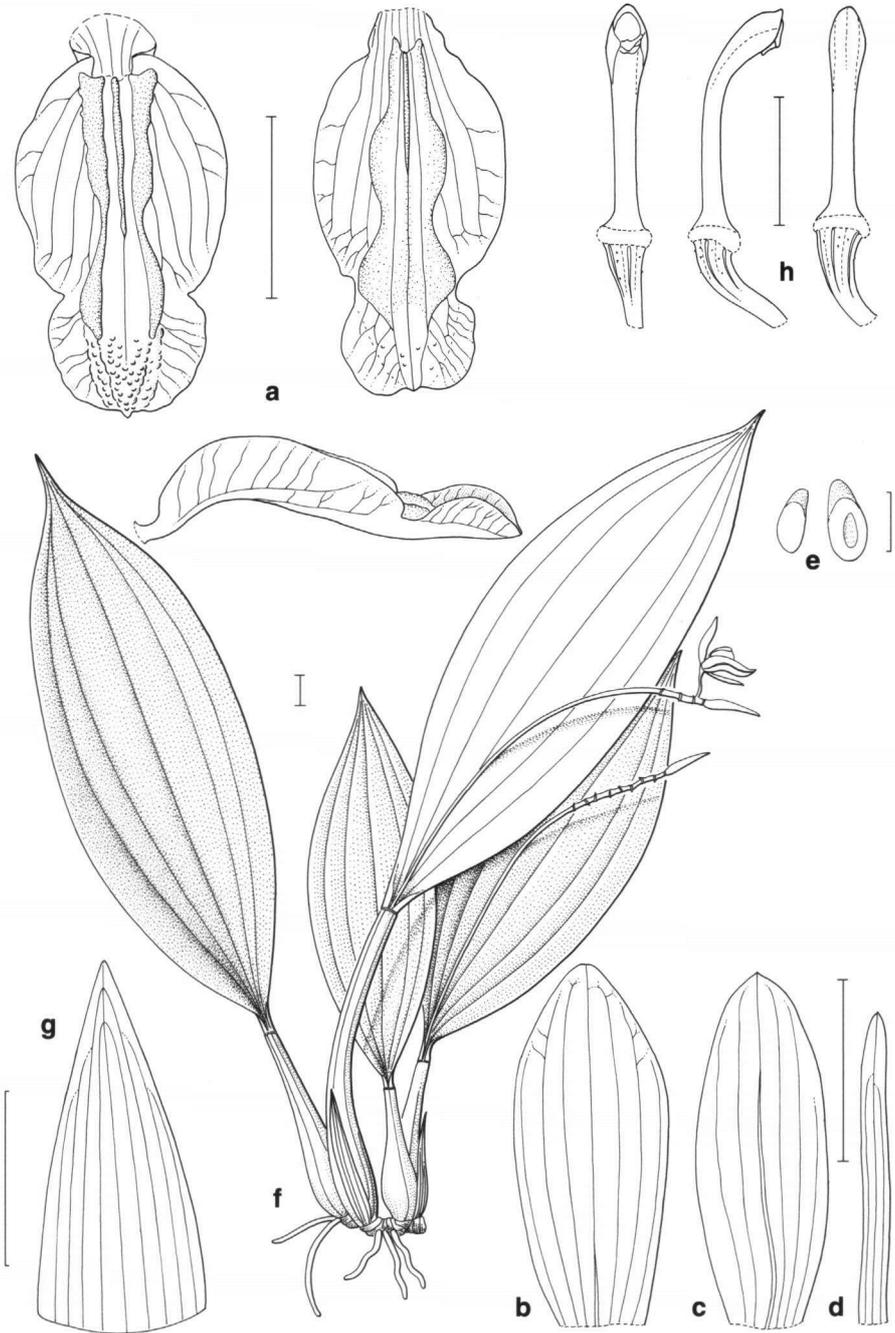


Fig. 11. *Coelogyne naja* J.J. Sm. a. Lip, front view (from left to right: *Leiden cult. 911114*, *Leiden cult. 914193*) and lateral view (*Leiden cult. 914193*); b. median sepal; c. lateral sepal; d. petal; e. pollinia; f. habit (*Leiden cult. 30238*); g. floral bract; h. column, front, lateral and rear view (*Leiden cult. 914193*). — Scale bars: 1 cm (a–d, f, h); 1 mm (e); 5 mm (g).

and at the top, midlobe creamy salmon. Column cream coloured grading to salmon at the top, anther creamy yellow, pollinia bright yellow. Nutmeg smell.

2. The epithet *monilirachis* (from the Latin *monile*, a necklace) refers to the rachis, which resembles a string of beads.

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

4. The species can be recognised by its drooping inflorescence with intermediately sized pale salmon pink flowers and rachis with short, disc-shaped internodes, which are round in cross section.

5. The type collection *SFN (Carr) 27230* is the same as *Carr 3366*.

8. *Coelogyne naja* J.J. Sm. — Fig. 11, Map 3, Plate 1d

Coelogyne naja J.J. Sm. (1931c) 93; (1949) t. 157, f. 1; J.J. Wood & P.J. Cribb (1994) 157; de Vogel, Schuit., Felĳus & A. Vogel (1999) pl. 73. — Type: *Endert 3708* (holo L), Borneo, Mount Kemul.

Roots 0.9–1.5 mm diameter. *Rhizome* 5–7 mm thick, the portion between two pseudobulbs with 3–6 internodes; scales soon disintegrating. *Pseudobulbs* 3–8 mm apart, 5.5–11 by 0.8–1.5 cm. *Leaf* petiole 5–9 mm long; blade (obovate-)oblong, 15–29 by 3.5–5.5 cm, margin slightly undulating, apex cuspidate, main nerves 3–5. *Inflorescence* 4–25-flowered. Peduncle slender, 6–10 cm long. Rachis pendulous, constricted at the internodes, 3–7 cm long; internodes short, rectangular, quadrangular in cross section and with rounded edges, with distinct pedicel scars, 2.5–4 by 1.5–2 mm; floral bracts narrowly triangular, glabrous, 10–16 by 5–7 mm. *Flowers* opening in succession. Pedicel 3–5 by 1.1–1.4 mm; ovary 5–7 by 3–5 mm. *Median sepal* obovate-oblong, glabrous, 21–23 by 7–9 mm; nerves 5–7. *Lateral sepals* ovate-oblong, glabrous, 20–22 by 6–7 mm, nerves 6 or 7. *Petals* 18–20 by 1.2–1.4 mm, glabrous, nerves 3. *Hypochile* 12–14 by 9–11 mm, base slightly saccate, lateral lobes 12–14 by 2.5–3 mm, with acute apex, sinus 0–1 mm deep, keels 3, basally connected on the upper third of the hypochile, low at the base, abruptly ascending at the basal half of the hypochile and then abruptly descending again on the apical third of the hypochile, the median keel occurring on the basal half of the hypochile only, the lateral keels much higher than the median keel, erect, without triangular hook at the base. *Epichile* slightly spatulate, 6–8 by 6–7 mm, slightly recurved, claw 1.5–2 by 4–5 mm, keels running some distance from the margin, patent, ascending towards the middle of the claw, descending abruptly in the median raised nerves of the base of the apex, blade when flattened broadly ovate, 4.5–5.5 by 5–6 mm, warty, slightly recurved, with entire margins, sides pronounced as lobules, top slightly acute, ornamentation consisting of few to many small warts. *Column* spatulate in outline, 15–17 by 2–3 mm, base without swelling, hood with distinct wings, apex emarginate, not curved to the front. *Anther* broadly ovate, 1.5–1.8 by 1.8–2 mm, apex emarginate. *Pollinia* ovoid, 0.7–1 by 0.5–0.7 mm. *Stigma* 1.4–1.7 by 1.4–1.6 mm, with emarginate margin; rostellum deltoid, 1.3–1.4 by 1.9–2.2 mm, with entire margin. *Fruit* 2.5–3 by 1.4–1.6 cm. *Seeds* 0.9–1.1 mm long.

Distribution — Borneo (Brunei, Sarawak, Kalimantan).

Habitat & Ecology — Epiphyte in primary forest. Recorded from hill and montane Dipterocarp forest and kerangas with *Agathis* on clay, rocky and sandy soils. Elevation 600–1500 m. Flowering: the whole year round.

Notes — 1. Leaves and pseudobulbs shining red-brown tinged green, leaves dark green with brownish margin above, brownish green below. Sepals and petals yellowish green to bright green to cream coloured to pale salmon, tinged brown to ochre near base and median part, translucent. Lip cream coloured tinged green to yellowish green, with a pale brown longitudinal forking band between the keels, or with brown keels on the epichile, lateral lobes with scattered minute brown spots. Column dull yellow to light pinkish ventrally, brownish dorsally, hood brownish orange to reddish brown, wings cream coloured. Anther dull yellow, median with a light reddish brown line. Pollinia bright yellow. Fruits purple. Very sweet smell.

2. The epithet *naja* (Latin name of the cobra) refers to the resemblance of the keels on the epichile with the hood of this snake species.

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

4. The species can be recognised by its relatively small, successively opening flowers with two times ascending and descending keels on the hypochile and epichile, which are very broad and patent on the midlobe of the epichile, and rachis with elongated internodes with distinct pedicel scars.

9. *Coelogyne renae* Gravendeel & de Vogel, *spec. nov.* — Fig. 12, Map 4, Plate 3b

Flores intervallate tri- vel plures aggregatae simultanee aperientes. Labium loborum lateralium apicibus late rotundatis, epichilium valde recurvatum vitta transversa dilute brunnea. — Typus: *Leiden cult. (George) 914563* (holo L), Sarawak.

Coelogyne incrassata auct. non (Blume) Lindl.: J.B. Comber (2001), photograph on p. 324 below (excl. the description).

Roots 0.5–1.5 mm diameter. *Rhizome* 4.5–6 mm thick, the portion between two pseudobulbs with 4 or 5 internodes; scales soon disintegrating. *Pseudobulbs* 5–9 mm apart, 9–15 by 1.1–1.9 cm. *Leaf* petiole 13–15 mm long; blade oblong, 19–22 by 4–6.5 cm, margin slightly undulating, apex acute, main nerves 5–7. *Inflorescence* 42–78-flowered. Peduncle slender, 11–13 cm long. Rachis pendulous, constricted at the internodes, 7.5–15 cm long; internodes short, rectangular, quadrangular in cross section and with rounded edges, with distinct pedicel scars, 3–4 by 2–3 mm; floral bracts triangular, sparsely covered with scattered minute brown scale-like hairs, 9–11 by 5–7 mm. *Flowers* opening in successive clusters of three or more. Pedicel 1.3–1.6 by 1.2–1.4 mm; ovary 1.5–1.6 by 0.9–1.1 mm. *Median sepal* ovate, 15–17 by 7–9 mm, glabrous, nerves 7–9. *Lateral sepals* oblong, glabrous, 16–17 by 5–6 mm, nerves 5 or 6. *Petals* glabrous, 15–16 by 1.5–2 mm, nerves 1. *Hypochile* 8–10 by 11–12 mm, base slightly saccate, lateral lobes 8–10 by 3–4.5 mm, with broadly rounded apex, sinus 0–1 mm deep, keels 3, not connected at the base, low over the entire lip, the median keel sometimes occurring on the basal half of the hypochile only, the lateral keels without triangular hook at the base. *Epichile* ovate, 4–5 by 3.5–4 mm, strongly recurved to reflexed, claw 1–1.5 by 3.5–4 mm, keels running some distance from the margin, descending towards the apex, blade when flattened broadly ovate, 2.8–3.2 by 3.8–4.2 mm, warty, distinctly recurved, with slightly undulating margins, sides not pronounced as lobules, top acute, ornamentation consisting of 7–9 swollen, completely fused warty keels, forming a swollen patch, covering the entire apex. *Column* spathulate in outline, 11–13 by 2.5–3.2 mm, base without swelling, hood with distinct wings, apex with

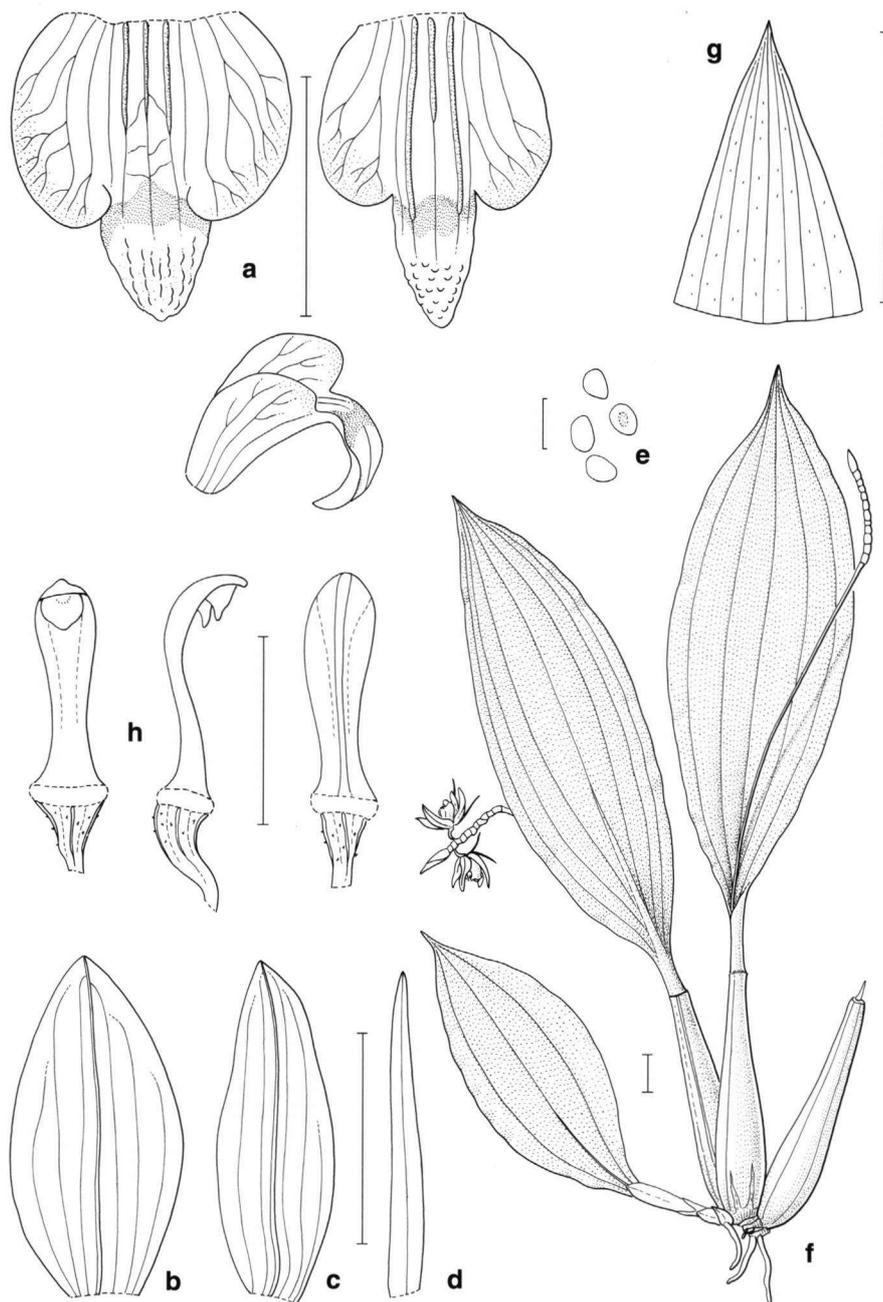
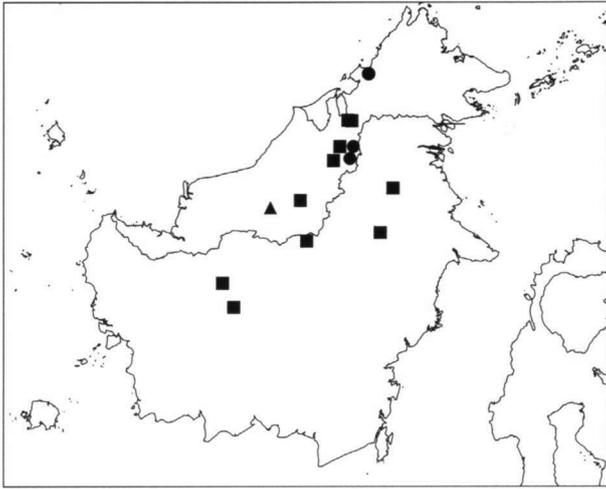


Fig. 12. *Coelogyne renae* Gravendeel & de Vogel. a. Lip, front view (from left to right: *Leiden cult.* 970768, *Leiden cult.* 970183) and lateral view (*Leiden cult.* 970290); b. median sepal; c. lateral sepal; d. petal; e. pollinia (*Leiden cult.* 914563); f. habit (*Kinabalu Park cult.* G. G. 6102-34/200); g. floral bract; h. column, front, lateral and rear view (*Leiden cult.* 914563). — Scale bars: 1 cm (a–d, f, h); 1 mm (e); 5 mm (g).



Map 4. Distribution of *Coelogyne gibbifera* J.J. Sm. (■), *C. renae* Gravendeel & de Vogel (●) and *C. vermicularis* J.J. Sm. (▲).

entire margin, not curved to the front. *Anther* broadly ovate, 1.8–2.1 by 2.2–2.4 mm, apex emarginate. *Pollinia* broadly ovoid, 0.8–0.9 by 0.6–0.7 mm. *Stigma* 1.3–1.4 by 1.5–2 mm, with emarginate margin; rostellum broadly ovate, 1.8–1.9 by 2–2.2 mm, with emarginate margin. *Fruit* and *seeds* not seen.

Distribution — Borneo (Sabah, Sarawak).

Habitat & Ecology — Epiphyte in lower montane forest and kerangas. Elevation 600–1200 m. Flowering: the whole year round.

Notes — 1. Leaves and pseudobulbs liver coloured. Sepals and petals translucent pale salmon to dull light green. Lip pale orange salmon to somewhat ochre to cream, lateral lobes honey brown. Midlobe with honey brown base and a transverse light brown band. Column orange to somewhat ochre to light green, margin and hood darker orange. Anther yellowish cream.

2. The epithet *renae* refers to the late Ms. Rena George, who collected the type specimen in Sarawak for the Semenggoh orchid collections.

3. The dimensions are based on spirit collections.

4. The species can be recognised by the flowers, opening in successive clusters of three or more, the hypochile with lateral lobes with a broadly rounded apex, and a strongly recurved epichile with a transverse light brown band.

10. *Coelogyne tenuis* Rolfe — Fig. 13, Map 1

Coelogyne tenuis Rolfe (1893) 171; J.J. Wood & P.J. Cribb (1994) 162. — Type: *Linden s. n.* (holo K), Borneo.

Coelogyne bihamata J.J. Sm. (1927c) 29, t. 4, f. 19. — Type: *Winkler 517* (holo HBG?, not found), Borneo, Mount Mulu.

Roots 1–1.8 mm diameter. *Rhizome* 6–7 mm thick, the portion between two pseudobulbs with 3 or 4 internodes; scales soon disintegrating. *Pseudobulbs* 5–9 mm apart,

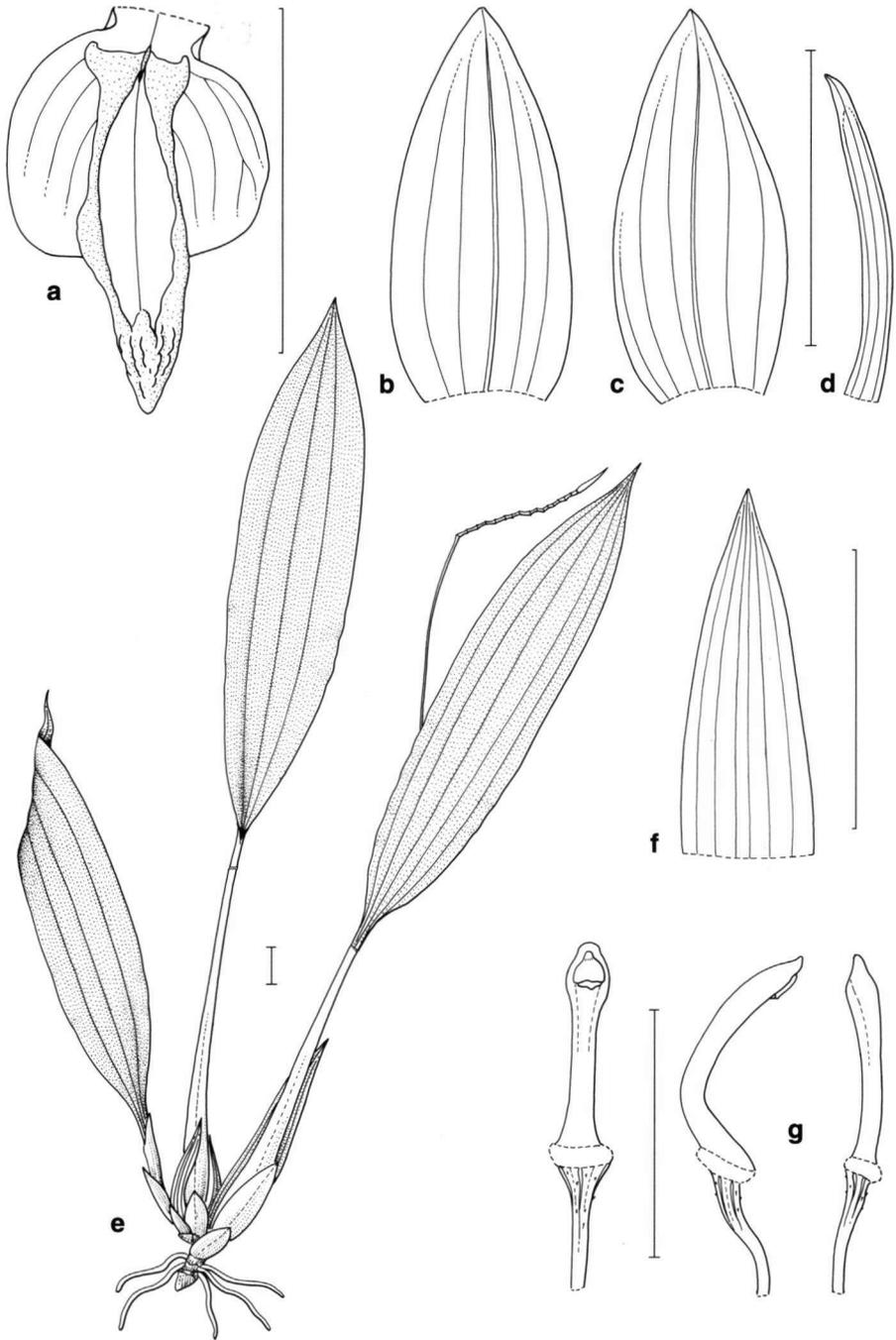


Fig. 13. *Coelogyne tenuis* Rolfe. a. Lip, front view; b. median sepal; c. lateral sepal; d. petal; e. habit; f. floral bract (*Mogea* 3783); g. column, front, lateral and rear view (*Linden s.n.* (?/8/1892)). — Scale bars: 1 cm (a–d, g); 1 mm (e); 5 mm (f).

13–14 by 0.4–0.6 cm. *Leaf* petiole 10–15 mm long; blade obovate-lanceolate, 20–21 by 4.3–4.7 cm, margin finely undulating, apex acute, main nerves 3–5. *Inflorescence* 6–18-flowered. Peduncle slender, 16–17.5 cm long. Rachis erect, constricted at the nodes, 1.5–6 cm long; internodes short, rectangular, quadrangular in cross section and with rounded edges, with distinct pedicel scars, 4–5 by 1–1.5 mm; floral bracts triangular, glabrous, 12–14 by 5–7 mm. *Flowers* opening in succession. Pedicel 5–7 by 0.5–1 mm; ovary 2–3 by 2.5–3.5 mm. *Median sepal* ovate, glabrous, 12–14 by 5–6 mm; nerves 5–7. *Lateral sepals* ovate-oblong, glabrous, 11–13 by 3–5 mm, nerves 5–7. *Petals* glabrous, 9–11 by 0.8–1.1 mm, nerves 3. *Hypochile* 6–8 by 8–9 mm, base slightly saccate, lateral lobes 6–7 by 2.5–3 mm, with broadly rounded apex, sinus 1.5–2 mm deep, keels 3, basally connected, low at the base, abruptly ascending towards the apical third of the hypochile, slightly descending towards the apex of the hypochile, the median keel occurring on the basal half of the hypochile only, the lateral keels much higher than the median keel, abruptly elevated into a triangular hook with recurved, acute top at the base. *Epichile* spatulate, 4.5–5 by 3–3.5 mm, slightly recurved, claw 1–1.5 by 2.5–3 mm, keels running completely along the margin and ascending towards the apex, blade when flattened broadly ovate, 2.5–3.5 by 2–3 mm, warty, slightly recurved, with distinctly undulating margins, sides not pronounced as lobules, top acute, ornamentation consisting of 5–7 swollen, completely fused warty keels, forming a broadly ovate patch, covering nearly the entire apex. *Column* spatulate in outline, 7–8 by 2–2.5 mm; base without swelling; hood with distinct wings; apex with entire margin, curved to the front. *Anther* broadly ovate, 2–2.5 by 2.5–3 mm, apex entire. *Pollinia* not seen. *Stigma* 1.8–2 by 2.1–2.3 mm, with entire margin; rostellum deltoid, 1.5–1.7 by 2–2.3 mm, with entire margin. *Fruit* 2–2.5 by 1–1.5 cm. *Seeds* not seen.

Distribution — Borneo (Sarawak, Kalimantan).

Habitat & Ecology — Epiphyte in primary lower montane ridge forest. Elevation 500–1200 m. Flowering: August, October, November.

Notes — 1. Leaves pinkish green beneath. Tepals pale salmon to light brown. Lip yellow inside.

2. The epithet *tenuis* (Latin for delicate) refers to the slender peduncle.

3. The dimensions are based on herbarium material only.

4. The species can be recognised by the hooked projections of the lateral keels on the base of the hypochile, which is referred to by the epithet *bihamata* (Latin for double hooked).

5. Only four collections of this species were encountered. It is probably extremely rare.

11. *Coelogyne vermicularis* J.J. Sm. — Fig. 14, Map 4, Plate 3d

Coelogyne vermicularis J.J. Sm. (1906) 9, t. 204; Ames (1921c) 146; J.J. Wood, R. S. Beaman & J.H. Beaman (1993) 152; J.J. Wood & P.J. Cribb (1994) 162; de Vogel, Schuit., Felëus & A. Vogel (1999) pl. 77. — *Chelonistele vermicularis* (J.J. Sm.) Kraenzl. (1907) 163. — Type: *Nieuwenhuis s.n.* (holo BO, not seen), Borneo.

Roots 1.2–1.8 mm diameter. *Rhizome* 5–8 mm thick, the portion between two pseudobulbs with 3–5 internodes; scales soon disintegrating. *Pseudobulbs* 7–10 mm apart, 12.5–14.5 by 9.5–12 cm. *Leaf* petiole 5–8 mm long; blade (ovate-)oblong, 23–29 by

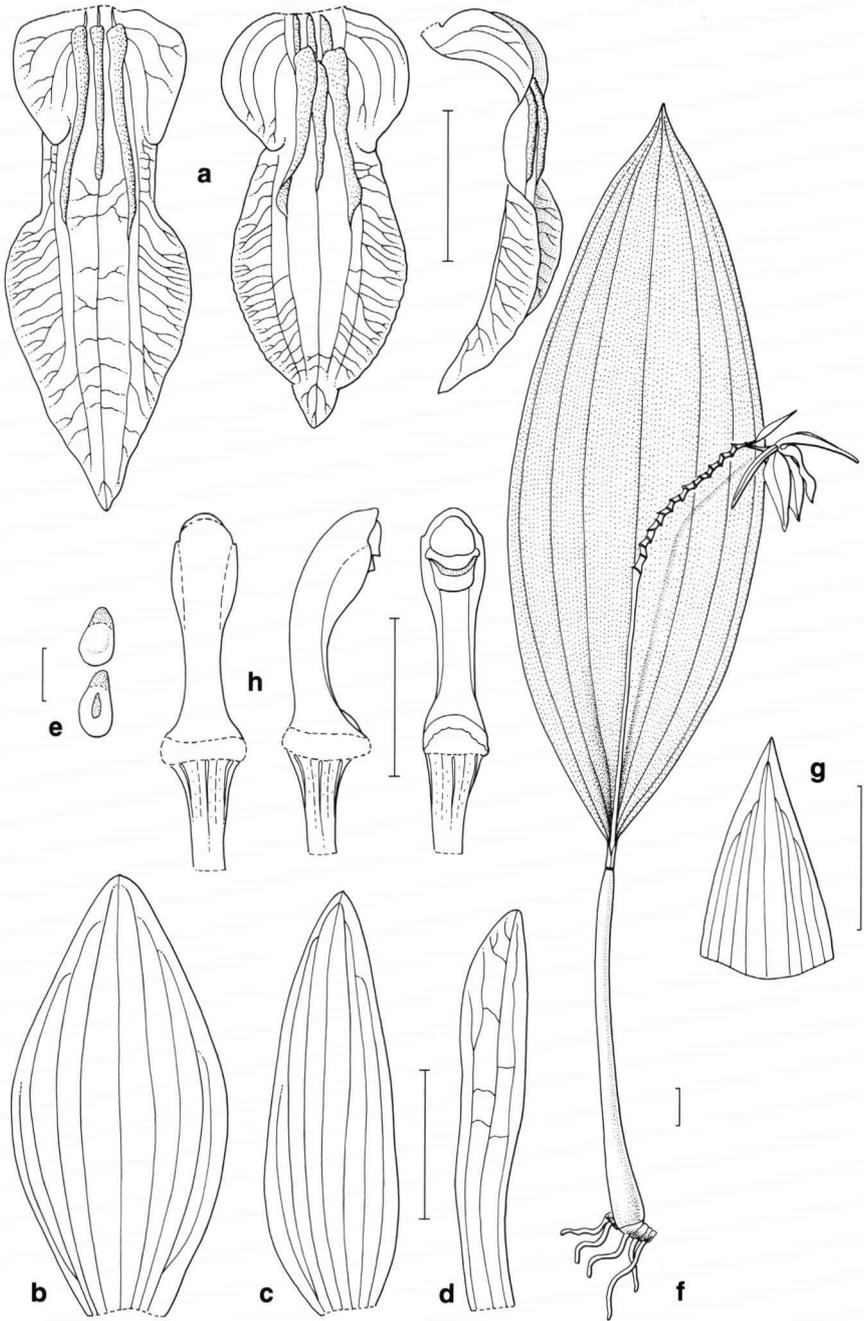


Fig. 14. *Coelogyne vermicularis* J.J. Sm. a. Lip, front view (from left to right: *de Vogel* 9267, *Leiden cult.* 914400) and lateral view (*Leiden cult.* 914400); b. median sepal; c. lateral sepal; d. petal; e. pollinia; f. habit (*De Vogel* 9267); g. floral bract; h. column, front, lateral and rear view (*Leiden cult.* 914400). — Scale bars: 1 cm (a–d, f, h); 1 mm (e); 5 mm (g).

6.5–10.5 cm, margin slightly undulating, apex acuminate to cuspidate, main nerves 5–7. *Inflorescence* 4–17-flowered. Peduncle slender, 13–15.5 cm long. Rachis erect, constricted at the nodes, 1.5–6 cm long; internodes short, rectangular, quadrangular in cross section and with rounded edges, with distinct pedicel scars, 3.5–5 by 2–3 mm; floral bracts triangular, glabrous, 15–18 by 6–7 mm. *Flowers* opening in succession. Pedicel 9–12 by 1.4–1.9 mm; ovary 4–6 by 2–3 mm. *Median sepal* oblong, 33–41 by 14–16 mm; nerves 7–9. *Lateral sepals* ovate-oblong, 31–33 by 10–12 mm, nerves 5–7. *Petals* 29–33 by 4–5 mm, nerves 3. *Hypochile* 8–9 by 11–12 mm, base slightly saccate, lateral lobes 8–9 by 2.5–3 mm, with decurrent apex, sinus 0–1 mm deep, keels 3, not connected, low at the base, abruptly ascending on the basal third of the hypochile, slightly descending towards the apex of the hypochile, the median keel occurring on the entire hypochile, the lateral keels higher than the median keel and without triangular hook at the base. *Epichile* oblong to elliptic, 19–23 by 11–12 mm, slightly recurved, claw 4–5 by 7–9 mm, keels running some distance from the margin, the median keel ending abruptly on the basal half of the claw, the lateral keels descending towards the apex of the claw, ending abruptly in the median raised nerves of the base of the apex, blade when flattened obovate, 13–18 by 11–12 mm, warty, slightly recurved, with slightly undulating margins, sides pronounced as lobules, top distinctly acute, ornamentation absent. *Column* spatulate in outline, 12–13 by 2.8–3.2 mm, base with a triangular, apically warted swelling, 1.8–2.2 by 2.1–2.4 mm, hood with distinct wings, apex emarginate, not curved to the front. *Anther* broadly ovate, 1.8–2.2 by 2.1–2.3 mm, apex slightly emarginate. *Pollinia* ovoid, 1.1–1.4 by 0.8–1.1 mm. *Stigma* 2.1–2.3 by 1.9–2.2 mm, with entire margin; rostellum broadly ovate, 2.2–2.4 by 2.3–2.4 mm, with entire margin. *Fruit* and *seeds* not seen.

Distribution — Borneo (Sarawak).

Habitat & Ecology — Epiphyte in lower montane forest. Recorded from mossy forest on sandstone and clay soil. Elevation 800–1200 m. Flowering: June to December.

Notes — 1. Pseudobulbs and leaves green tinged red. Sepals and petals pale yellowish to salmon, the base more orange yellow. Lip at base dark brownish red, keels dark yellow, epichile bright yellow to cream-coloured. Column cream-coloured, reddish brown at the top and below the stigma, in front brownish red. Anther light yellow. No scent recorded.

2. The epithet *vermicularis* (from the Latin *vermiculus*, which means worm) refers to the rachis with its swollen internodes.

3. The dimensions are based on spirit and herbarium collections.

4. The species is very similar to *C. gibbifera*, but can be distinguished by the shorter lateral lobes of the hypochile and epichile with obovate instead of broadly ovate blade.

DOUBTFUL SPECIES

12. *Coelogyne crassiloba* J.J. Sm.

Coelogyne crassiloba J.J. Sm. (1927b) 28, t. 4, f. 18. — Type: *Winkler 481* (holo HBG, not found), Borneo, Mount Mulu.

Note — According to the type description (Smith, 1927b) this species differs from *C. harana* and *C. incrassata* by the successively opening flowers and much longer epichile. It is questionable whether *C. crassiloba* really is a distinct species, but only

a study of the type specimen, which was not found in HBG, can provide a definitive answer to this.

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IDENTIFICATION LIST

The number after each collection refers to the corresponding species in the text. If the number of a collection is unknown, the collecting date is added between brackets.

<i>Coelogyne</i>	5. <i>C. kelamensis</i>
1. <i>C. chanii</i>	6. <i>C. longpasiaensis</i>
2. <i>C. gibbifera</i>	7. <i>C. monilirachis</i>
3. <i>C. harana</i>	8. <i>C. naja</i>
4a. <i>C. incrassata</i> var. <i>incrassata</i>	9. <i>C. renae</i>
4b. <i>C. incrassata</i> var. <i>sumatrana</i>	10. <i>C. tenuis</i>
4c. <i>C. incrassata</i> var. <i>valida</i>	11. <i>C. vermicularis</i>

Afriastini 2705: 4b — Anderson 140: 5.

Bacon 54: 2 — Bailes & Cribb 867: 7 — Beaman et al. 7311: 7; 7377: 7; 8997: 7; 10275: 4c; 10772: 7 — Blume s.n. (1833): 4a — Bogor cult. 30: 4c; 38: 4a; 67: 4a; 202: 4b; IZ 285: 4a; 991.XII.424: 4a; 993.X.578: 4a; 995.IX.324: 5; 996.X.1019: 4a — Brooks s.n. (1902): 4b — Burt & Martin 4937: 6; 5055: 11.

Chan 31: 7 — Church, Ismail & Ruskandi 2564: 10 — Church & Mahyar: 10 — Clemens & Clemens 26127: 7; 27166: 7; 28294: 7; 28316: 7; 28454: 7; 28951: 7; 29293: 7; 30993: 7; 33665: 7; 34055: 7; 50366: 7; s.n. (1/1/1932): 7 — Collenette A109: 7; 47/79: 7.

Darnton s.n. (1954): 6; s.n. (1954) A: 7 — De Vogel 8189: 6; 8291: 2; 8303: 6; 8378: 2; 8793: 3; 9134: 8; 9139: 8; 9166: 6; 9213: 6; 9267: 11; 9375: 8; 9383: 8; 9476: 7 — De Wilde & De Wilde-Duyfjes 12414: 4b.

Edinburgh cult. (Kerby) 773361: 3; (Kerby) 773362: 3; (Argent) 852172: 2 — Endert 2609: 4c; 3708: 8; 4038: 4c; 4354: 2.

Forbes 438: 4a.

Hallier 3054: 4c — Hansen 1079: 8 — Haviland 41: 4b — Hewitt 442: 3 — Holten 7: 4b.

Iboet 232: 4b; 286: 4b.

Jacobs 8406: 4b — Jarvie & Ruskandi 5185: 4a.

Keßler 2558: 5 — Kidman Cox 911: 7; 971: 7; 1011: 7 — Kinabalu Park cult. G.G. 6102-34/200: 9 — Kuhl & Van Hasselt 24: 4a.

Lamb 223/85: 2 — Langlassé 94: 5 — Leiden cult. (Franken & Roos) 21213: 4b; (Bacon) 22074: 2; (Nootboom) 23176: 2; (Vermeulen) 26416: 4b; (De Vogel) 27199: 8; (De Vogel) 27532: 3; (De Vogel) 30238: 8; (De Vogel) 30247: 8; (De Vogel) 911114: 8; (De Vogel) 911151: 8; (De Vogel) 911184: 4b; (De Vogel) 911305: 8; (De Vogel) 913406A: 6; (De Vogel) 913421: 7; (De Vogel) 913470: 8; (De Vogel) 913480: 6; (De Vogel) 913485: 4a; (De Vogel) 913486: 4b; (De Vogel) 913542: 6; (De Vogel) 914049: 8; (De Vogel) 914193: 8; (De Vogel) 914400: 11; (George) 914563: 9; (De Vogel) 930568: 5; (Schuiteman, Mulder & Vogel) 932547: 3; (Schuiteman, Mulder & Vogel) 932548: 3; (Schuiteman, Mulder & Vogel) 932553: 3; (Schuiteman, Mulder & Vogel) 932701: 4b; (Schuiteman, Mulder & Vogel) 932804: 4b; (Vogel, Schuiteman & Mulder) 932849: 8; (Schuiteman, Mulder & Vogel) 932928: 4b; (Schuiteman, Mulder & Vogel) 933127: 4a; (Schuiteman, Roelfsema & Vogel) 970183: 9; (Schuiteman, Roelfsema & Vogel) 970290: 9; (Schuiteman, Roelfsema & Vogel) 970768: 9; (Schuiteman, Roelfsema & Vogel) 980002: 7;

- (Schuiteman, Roelfsema & Vogel) 980037: 7; (Schuiteman, Roelfsema & Vogel) 980045: 7; (Schuiteman, Roelfsema & Vogel) 980053: 7; (Schuiteman, Roelfsema & Vogel) 980222: 7; (Schuiteman, Roelfsema & Vogel) 980362: 4a; (Schuiteman, Roelfsema & Vogel) 980438: 8; (Schuiteman, Roelfsema & Vogel) 980559: 3; (Schuiteman, Roelfsema & Vogel) 990122: 4a — Linden s.n. (?/8/1892): 10.
- Mogea 3783: 10; 3812: 2 — Moulton 12: 2.
- Nootboom 1867: 3; 4645: 2 — Nootboom & Chai 2226: 2.
- Poring Hot Springs cult. (Lohok) B156-920103: 1 — Puasa 3108: 3.
- Reinwardt 281: 4a — Ridsdale 476: 5 — RSNB (Chew & Corner) 6007: 7.
- S series: (Yii Puan Ching) 42244: 5; (Lee) 45463: 4b; (Mohtar) 48260: 2; (Awa & Lee) 50697: 8; (Yii et al.) 51632: 2; (Yii et al.) 52300: 8; (Lee) 52473: 8; (Yii Puan Ching) 56565: 3 — SAN series: (Madani) 132737: 7 — Sands 3882: 7 — Sarawak Museum series: (Kitit) 747: 5 — SBGO 2016: 2 — SFN series: (native collector) 539: 8; (Moulton) 6682: 8; (Moulton) 6682A: 2; (Carr) 27230: 7 — Stevens 650: 7.
- Tenom Agricultural Park cult. 96: 1.
- Vermeulen 947: 6; 1023: 2; 1093: 6; 1097: 3; 1160: 5 — Vermeulen & Chan 373: 7 — Vermeulen & Duistermaat 946: 6 — Vermeulen & Lamb 752: 4c.
- Winkler 346: 3; 860: 2 — Wood 626: 2; 627: 2; 687: 6; 807: 3.

INDEX

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

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|---|---|
| <i>Chelonanthera incrassata</i> Blume 4a | (Coelogyne) |
| <i>Chelonistele vermicularis</i> (J.J. Sm.) Kraenzl. 11 | <i>incrassata</i> auct. 9 |
| Coelogyne Lindl. | kelamensis J.J. Sm. 5 |
| sect. Moniliformes Carr [p. 421] | longpasiaensis J.J. Wood & C.L. Chan 6 |
| <i>bihamata</i> J.J. Sm. 10 | <i>macroloba</i> J.J. Sm. 2 |
| chanii Gravendeel & de Vogel 1 | monilirachis Carr 7 |
| <i>crassiloba</i> J.J. Sm. 12 | naja J.J. Sm. 8 |
| <i>gibbifera</i> J.J. Sm. 2 | renae Gravendeel & de Vogel 9 |
| <i>harana</i> J.J. Sm. 3 | tenuis Rolfe 10 |
| <i>incrassata</i> (Blume) Lindl. 4 | vermicularis J.J. Sm. 11 |
| var. <i>incrassata</i> 4a | <i>vermicularis</i> auct. 4b |
| var. <i>sumatrana</i> J.J. Sm. 4b | <i>Pleione incrassata</i> (Blume) Kuntze 4a |
| var. <i>valida</i> J.J. Sm. 4c | |