REVISION OF COELOGYNE SECTION FULIGINOSAE (ORCHIDACEAE)

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SUMMARY

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

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

INTRODUCTION

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

Pfitzer & Kraenzlin (1907) included C. fimbriata Lindl., C. fuliginosa Lindl. ex Hook.f., C. longeciliata Teijsm. & Binn., C. micrantha Lindl., C. pilosissima Planch., C. ovalis Lindl., C. treutleri Hook.f. and C. triplicatula Rchb.f. in sect. Fuliginosae. Handel-Mazzetti (1936) added C. xerophyta Hand.-Mazz. Butzin (1974) included C. schilleriana Rchb.f. and C. chrysotropis Schltr. Seidenfaden (1975) suggested that C. pallens Ridl., C. leungiana S.Y. Hu and C. laotica Gagnep. (as synonyms of C. fimbriata) should be added. Barretto (1990) contributed C. primulina Barretto, and Chowdhery & Pal (1997) included C. arunachalensis H.J. Chowdhery & G.D. Pal.

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

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

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

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

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

MATERIALS AND METHODS

Pollen analysis

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

Phenetic analysis

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

Principal component analyses were performed with 29 characters (24 metric and 5 binary; see Table 1), scored from 34 collections. All data were standardized by log-transformation before calculating the correlation matrix and then analysed by an ordination of the principal components using SPSS (version 8.0).

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

Table 1. Variation of the morphological characters of the principal component analysis examined for 34 specimens of *Coelogyne* sect. *Fuliginosae* in the two main clusters of Fig. 2.

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

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

Additional data analysis

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

SPECIES DELIMITATION

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

RESULTS

Pollen analysis

The pollinaria of the four specimens studied consisted of four very sturdy pollinia connected by prominent and massive caudicles (Plate 1). The pollen grains were united in tetrads, which is in accordance with Schill & Pfeiffer (1977). The morphology of the tetrads was variable, both in the arrangement and shape of the pollen grains. Variation in tetrad morphology was high both among pollinia of different specimens and within one pollinium. The pollen grains on the surface of a pollinium were slightly more angular than those in the centre. Pollenkit kept the tetrads together but tended to dissolve during preparation. The exine ornamentation of the pollen was psilate, which was also noted by Sharma (1967). Apertures were absent, which was also observed by Zavada (1990).

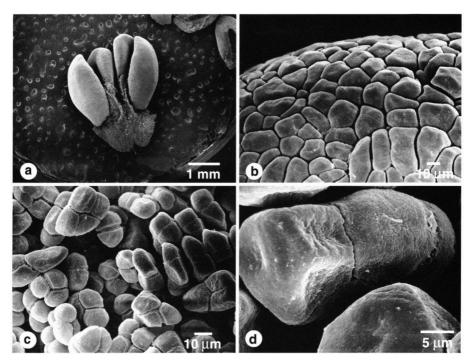


Plate 1. Coelogyne fimbriata Lindl. a. Pollinia, connected by caudicle (Leiden cult. 22704); b. pollinia surface (Leiden cult. 30759); c. tetrads (Leiden cult. 22704); d. pollen grains (Leiden cult. 30759).

Phenetic analysis

Ordination based on a principal components analysis revealed two discrete clusters of specimens (Fig. 1). The smallest cluster can be characterized by specimens of *C. triplicatula*. The largest cluster can be characterized by specimens of all other taxa studied in sect. *Fuliginosae*. The first three components explained 44%, 13% and 8% of the total variance in the data. Loading on the first component was contributed mainly by the following characters: lateral sepal length (96%), lip length (95%), median sepal length (93%), median sepal width (92%) and petal length (91%). Loading on the second component was contributed mainly by height of the lateral keels on the hypochile (68%), height of the median keel on the hypochile (67%) and length of the lateral lobes of the lip (66%). Loading on the third component was contributed mainly by length of the projections on the epichile margin (68%) and shape of the keels on the epichile (67%).

Five characters were scored in binary mode: keel shape (either bar-shaped or platelike), number of sterile bracts on the inflorescence and number of nerves on lateral sepal, median sepal and petal. These characters were fundamentally different from the others, which were all morphometric. To test whether the purely morphometric characters could distinguish *C. triplicatula* from all other specimens studied, we reran the ordinations omitting all binary characters. To test excessive weighting of flower size variation, the ordinations were also rerun with all flower measurements converted to ratios. The results were essentially the same as with binary characters or all flower measurements included (data not shown).

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

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

Scatter diagrams of the characters with the highest loadings showed continuous variation in most characters studied (Fig. 3). A diagram of lip length against lateral sepal length indicated that specimens of *C. triplicatula* tend to have relatively long lips, but they do not form a discrete group based on this character (Fig. 3A). A diagram of median sepal length against height of the lateral keels on the hypochile showed that *C. triplicatula* specimens have slightly lower keels when compared with larger specimens of all other taxa studied in sect. *Fuliginosae*, but there is some overlap in this character, too (Fig. 3B). A diagram of lip length against length of the projections on the epichile margin showed that *C. triplicatula* specimens have much shorter projections when compared with all other taxa studied (Fig. 3C). Of the key characters used by Pfitzer & Kraenzlin (1907), only the length of the projections on the epichile margin and the shape of the keels seem to show an interval in the range of variation (Fig. 1, 3C).

Additional data analysis

Data on flowering period, flower colour, habitat type and elevation of the specimens studied are summarized in Table 2. The specimens studied were collected in an area ranging from India to China to Sumatra and Borneo (Map 1). The (sub)clusters from Fig. 2 could not be characterized by an unique flowering period, flower colour, habitat, elevation or geographical distribution.

TAXONOMIC IMPLICATIONS

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

Plate 2. — Coelogyne fimbriata Lindl. a. Leiden cult. 22704, Thailand. Photograph C.G. Koops. — b. Leiden cult. 30756, India. Photograph A. Vogel. — c. Collection D.A. Clayton, Peninsular Malaysia. Photograph D.A. Clayton. — d. Collection J.B. Comber, Sumatra. Photograph J.B. Comber.



a. Coelogyne fimbriata (Thailand)



b. Coelogyne fimbriata (India)



c. Coelogyne fimbriata (Peninsular Malaysia)



d. Coelogyne fimbriata (Sumatra)

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

Table 2. Variation in additional data observed in specimens of the two main clusters of Fig. 2.

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

DISCUSSION

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

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

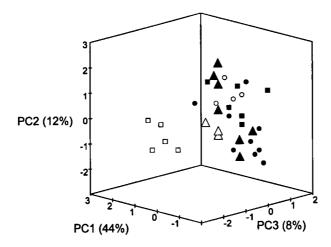


Fig. 1. Scatter diagram from ordination of the first three principal components based on 29 morphological characters (Table 1) of 34 *Coelogyne* sect. *Fuliginosae* specimens. Component 1 (PC1) separates specimens with long lips and sepals (left) from specimens with short lips and sepals (right). Component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

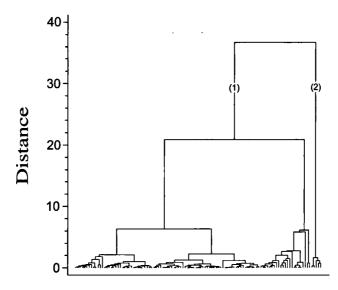


Fig. 2. Dendrogram of 111 *Coelogyne* sect. *Fuliginosae* specimens based on the six morphological characters with the highest loadings on PC1, PC2 and PC3 (see Materials & Methods for details of the clustering methods). Two main groups can be recognized, one with specimens with plate-like keels on the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

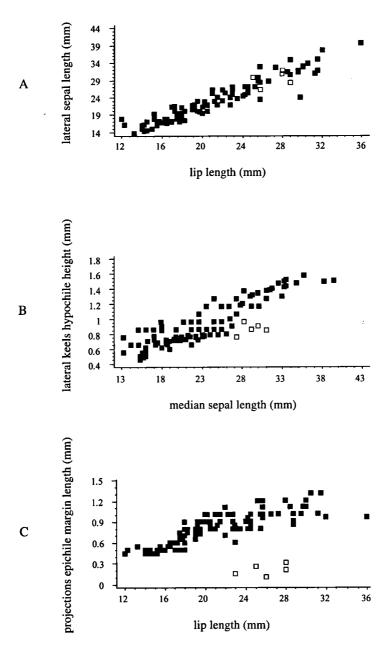
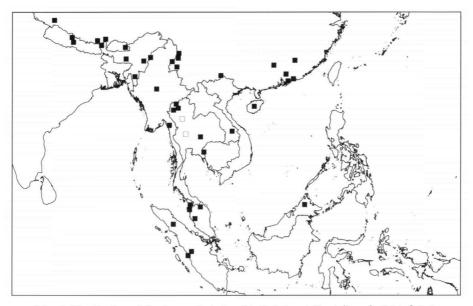


Fig. 3. Scatter diagrams of the morphological variation within 111 *Coelogyne* sect. *Fuliginosae* specimens. – A. Individuals of *C. triplicatula* do not form a discrete group based on their lip length. – B. Individuals of *C. triplicatula* have relatively low lateral keels on the hypochile, but there is some overlap in this character with *C. fimbriata*. – C. Individuals of *C. triplicatula* have much shorter projections on the epichile margin than the other specimens studied [*C. fimbriata* (\blacksquare) and *C. triplicatula* (\square)].



Map 1. Distribution of Coelogyne fimbriata Lindl. (■) and C. triplicatula Rchb.f. (□).

SYSTEMATIC TREATMENT

Coelogyne section Fuliginosae

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

Creeping, small-sized epiphytes and lithophytes. Roots attached on the rhizome at or between the nodes. Rhizome creeping; rhizome scales 5-14 between the pseudobulbs, eroding after one growth season, (slightly) imbricate, ovate to ovate-oblong; apex obtuse to acute, sometimes (slightly) mucronate; margin often dark. Pseudobulbs oblong to ovate-oblong to fusiform when fresh, oblong to ovate-oblong to terete when dried, slightly flattened, smooth to obtusely angulate and shiny when fresh, obtusely angulate when dried, 2-leafed. Leaves thin, coriaceous. Petiole orbicular to ovate in cross section, channelled, clasping the peduncle. Blade ovate-oblong, lanceolate, ovate-lanceolate to linear-lanceolate, slightly striate, smooth; apex acute to long-acuminate, sometimes mucronate; main nerves 5-9. Inflorescence suberect, hysteranthous, 1-5-flowered, glabrous. Peduncle orbicular to ovoid in cross section, broadening to the apex; sterile bracts covering the peduncle base 1-6, ovate to ovate-oblong; apex acute to mucronate. Rhachis suberect, slightly zigzag; internodes slightly curved, each with a swollen base bearing a flower. Floral bracts deciduous, ovate to ovate-oblong; apex acute, occasionally mucronate; nerves 16 to numerous. Flowers widely open, opening in succession, finely papillose. Pedicel ovate in cross section, (slightly) twisted; ovary slightly twisted, 6-ribbed. Median sepal ovate-oblong to lanceolate to ovate-lanceolate;

apex acute to slightly mucronate; nerves 5-13, midrib rounded, not prominent. Lateral sepals sometimes oblique, ovate-oblong to lanceolate; apex acute to mucronate; nerves 5-9, midrib rounded, not prominent. Petals not to slightly recurved, with (a)centric midrib, linear; apex acute to slightly obtuse; nerves 1-3, midrib not prominent. Lip immobile, boat-shaped, 3-lobed, when flattened pandurate in outline, nerves 13-22. Hypochile broadly attached, slightly saccate at the base; lateral lobes erect, in front obtuse to rounded to acute, extending in front, front margin not to very fimbriate, with shallowly to deeply rounded sinus; keels 3, starting at the base of the lip, plate-like, smooth to heavily dentate and sometimes undulating at the base, towards the apex of the epichile smooth and undulating, papillate, the lateral keels towards the apex descending, near the apex ascending, the median keel developed on the hypochile only, ending abruptly, sometimes abruptly descending. Epichile convex, when flattened ovate to ovate-oblong, with a broad, short claw; base narrow to broadly attached; apex rounded to obtuse, sometimes emarginate; tip absent to acute; margin slightly to heavily fimbriate, recurved; keels 2, a continuation of the keels on the hypochile, sometimes up to 4, plate-like and undulating (C. fimbriata) or swollen and bar-shaped (C. triplicatula), ending abruptly or sometimes descending near the apex of the epichile, papillate. Column curved to the front, when flattened spathulate; hood with winged margins, widest below the apex, gradually narrowing to the base, its apical margin irregularly dentate. Anther broadly bell-shaped in outline, near the place of attachment with an obtuse to rounded projection. Pollinia four, flattened to one side, obliquely elliptic, each with a shallow to deep ear-shaped depression, all connate at the apex by a caudicle; caudicle flattened, rectangular in outline, granular. Stigma cup-shaped, semi-orbicular with elevated, recurved margin; apex obtuse to rounded; rostellum semi-orbicular to triangular with incurved lateral margins and a longitudinal ridge. Fruit body ellipsoid, beaked by the persistent column and remnants of the perianth; valvae keeled, keels plate-like; juga band-like with a pronounced longitudinal ridge.

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

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

Cultivation — Only C. fimbriata is widely cultivated.

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

KEY TO THE SPECIES

1a.	Keels on the lip completely plate-like; projections on the lip margin longer than
	0.5 mm1. C. fimbriata
b.	Keels on the lip partly bar-shaped; projections on the lip margin shorter than 0.3
	mm

1. Coelogyne fimbriata Lindl. — Fig. 4, Map 1, Plate 2

- Coelogyne fimbriata Lindl., Bot. Reg. 11 (1827) t. 868; Hook. f., Fl. Brit. India 5 (1890) 836; Grant, Orch. Burma (1895) 172; Schltr., Orchideen (1915) 137; Seidenf. & Smitinand, Orch. Thail. 4, 2 (1965) 752, f. 81a-b; S. Y. Hu, Quart. J. Taiwan Mus. 25 (1971) 222, f. 8, 9f; Seidenf., Dansk Bot. Ark. 29 (1975) 15, f. 4; Bechtel, P.J. Cribb & Launert, Orch. Atl. (1980) 101; Seidenf. & J.J. Wood, Orchids Penins. Malaysia and Singapore (1992) 207, f. 87d-e. Pleione ovalis auct. non Lindl.: Kuntze, Rev. Gen. Pl. (1891) 680. Type: J. D. Parks (?/7/1824) (holo K; iso C, P), South China.
- Coelogyne ovalis Lindl., Bot. Reg. 24 (1838) 91; Summerh., Bot. Mag. 155 (1929) t. 9255; Seidenf. & Smitinand, Orch. Thail. 2, 1 (1959) 109, 111. Pleione fimbriata auct. non Lindl.: Kuntze, Rev. Gen. Pl. (1891) 680. Type: Wallich 1957 p.p. (holo K).
- Coelogyne fuliginosa Lindl. ex Hook.f., Bot. Mag. 75 (1849) pl. 4440; Lindl. in Lodd. Cat. 6 (1844) 146, nom. nud.; Miq., Choix Pl. Buitenzorg (1864) t. 25; Hook.f., Fl. Brit. India 5 (1890) 836; Grant, Orch. Burma (1895) 173; Cogn. & Gooss., Dict. Icon. Orch. (1903) 161; Pfitzer & Kraenzl. in Engl., Pflanzenr. 32 (1907) 34; Schltr., Orchideen (1915) 138; Backer & Bakh.f., Bekn. Fl. Java 3, 12 (1952) 128; Fl. Java 3 (1968) 280; Seidenf., Dansk Bot. Ark. 29, 4 (1975) 19, f. 5. Pleione fuliginosa (Lindl.) Kuntze, Rev. Gen. Pl. (1891) 680. Type: Loddige's collectors (???/1838) (holo K), India.
- Coelogyne pilosissima Planch., Hort. Donat. (1854) 104. Type: not designated.
- Coelogyne longeciliata Teijsm. & Binn., Nat. Tijdschr. Ned.-Indië 27 (1864) 16; Pfitzer & Kraenzl in Engl., Pflanzenr. 32 (1907) 38. Type: Lobb s.n. (holo ?, not seen).
- Coelogyne ovalis var. latifolia Hook.f., Fl. Brit. India 5 (1890) 836. Type: Clarke s.n. (holo ?, not seen), Munnipore on Kohima.
- Broughtonia linearis Wall. ex Hook.f., Fl. Brit. India 5 (1890) 836. Type: not designated.
- Coelogyne pallens Ridl., J. Straits Branch Roy. Asiat. Soc. 39 (1903) 81; Seidenf., Dansk Bot. Ark. 29, 4 (1975) 13, f. 3, pl. 1a; Seidenf. & J.J. Wood, Orchids Penins. Malaysia and Singapore (1992) 205, f. 87a-c. — Type: Curtis s.n. (holo SING?, not seen), Perak, Taiping Hills.
- Coelogyne fimbriata var. annamica Finet, Notul. Syst. (Paris) 1 (1909) 255; Gagnep., Fl. Gén. Indo-Chine 6 (1933) 309. Type: Eberhardt s.n. (holo P?, not seen).
- Coelogyne chrysotropis Schltr., Orchis 5 (1910) 58, pl. 7c; J.J. Sm., Feddes Repert. 32 (1933) 162. — Type: Schlechter s. n. (1910) (holo B⁺), Sumatra.
- Coelogyne padangensis J.J. Sm. & Schltr. in Engl., Bot. Jahrb. Syst. 104 (1911) 6; J.J. Sm., Rep Spec. Beih. 32 (1933) 166. — Type: Schlechter 15950 (holo B⁺), Sumatra, Pariaman.
- Coelogyne laotica Gagnep., Bull. Mus. Hist. Nat. (Paris) 2 (1930) 425; Fl. Gén. Indo-Chine 6 (1933) 308, 311, f. 26: 9-16; Seidenf. & Smitinand, Orch. Thail. 2, 1 (1959) 112; A.D. Kerr, Nat. Hist. Bull. Siam Soc. 23, 1-2 (1969) 189. Type: Thorel s.n. (holo P?, not seen), Laos.
- Coelogyne xerophyta Hand.-Mazz., Symb. Sin. (1936) 1346, 1353, f. 42, no. 1, 2. Type: Handel-Mazzetti 8457 (holo W), China, Yunnan.
- Coelogyne leungiana S.Y. Hu, Quart. J. Taiwan Mus. 25 (1971) 223. Type: S.Y. Hu 9089 (holo AMES, not seen), Hongkong.
- Coelogyne primulina Barretto, Orchid Rev. 98, 1156 (1990) 39. Type: G. Barretto 315 (holo K; iso HK), Hongkong.
- Coelogyne arunachalensis H.J. Chowdhery & G.D. Pal, Nord. J. Bot. 17, 4 (1997) 369. Type: G.D. Pal 1790 (holo CAL, not seen), India, Arunachal Pradesh.

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

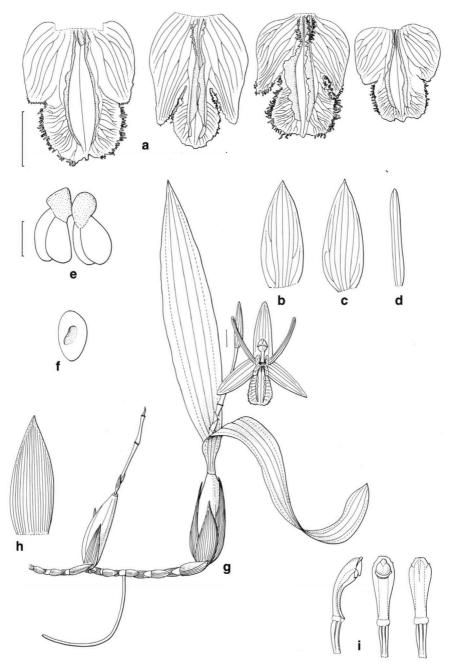


Fig. 4. Coelogyne fimbriata Lindl. a. Lip ornamentation (from left to right: Leiden cult. 30756, Comber 1069, Henry 13539, Leiden cult. 23320); b. median sepal; c. lateral sepal; d. petal (Leiden cult. 21640); e. pollinarium; f. pollinium; g. habit (Leiden cult. 30756); h. floral bract (Rock 7707); i. column, front, lateral and rear view (Leiden cult. 23320). — Scale bars: 1 cm (a-d, g-i); 1 mm (e, f).

Lip 12–36 by 12–25 mm. Hypochile when flattened 9–23 by 12–25 mm; base attached over 2–7 mm; lateral lobes in front obtuse to rounded to acute, extending 1–8 mm in front; lateral keels 0.4–1.6 mm high at the base; median keel developed on basal (and sometimes also apical) half of the hypochile, 0.3–1.8 mm high at base. Epichile 6–17 by 6–17 mm; claw 0.5–3 mm thick; base attached over 4–12 mm; margin with projections 0.5–1.3 mm long; keels plate-like, undulating, 0.5–2.5 mm high, ending 1–9 mm from the apex of the epichile. Column 10–26 by 3–7 mm. Anther 3–4 by 2–5 mm. Pollinia 1–2 by 1–1.5 mm; caudicle 1–1.5 by 1–2 mm. Stigma 1–3 by 3–5 mm; rostellum 2–3 by 2–5 mm. Fruit body 18–23 by 7–10 mm; valvae keels 3.5 mm high; juga with a pronounced longitudinal ridge 2 mm high.

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

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

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

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

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

2. Coelogyne triplicatula Rchb.f. — Fig. 5, Map 1, Plate 2

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

Roots 0.5-2.5 mm diam. Rhizome 2-5 mm thick; rhizome scales 5-8 between the pseudobulbs. *Pseudobulbs* 1.5-3.5 cm apart, 2.8-6.3 by 1-1.7 cm. Petiole 5-8 mm

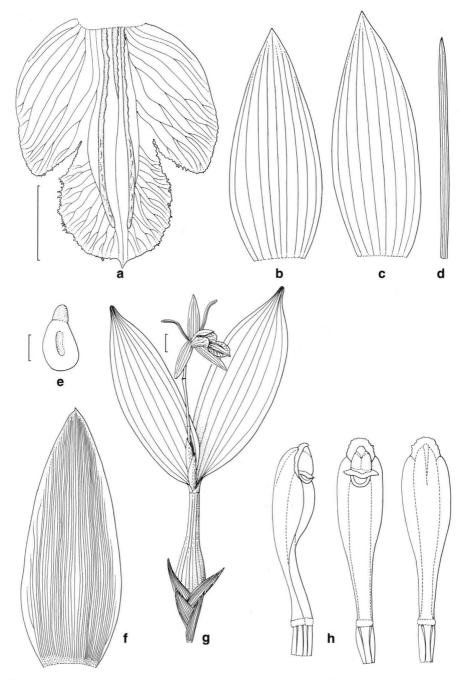


Fig. 5. Coelogyne triplicatula Rchb.f. a. Lip ornamentation; b. median sepal; c. lateral sepal; d. petal; e. pollinium [Van Imschoot s.n. (1889)]; f. floral bract [Glasnevin s.n. (8/11/1904)]; g. habit; h. column, front, lateral and rear view [Van Imschoot s.n. (1889)]. — Scale bars: 1 cm (a-d, f-h); 1 mm (e).

long. Blade 6.4–11.4 by 1.4–3.8 cm. *Inflorescence* 3-flowered. Peduncle 33-47 mm long; sterile bracts 1 or 2, covering 3/4 of peduncle. Rhachis up to 7.4 cm long; internodes 25–30 by 1–1.5 mm. *Floral bracts* c. 40 by 15 mm. *Pedicel* 13–18 by 1–1.5 mm; ovary 7–8 by 2–3 mm. *Median sepal* ovate-oblong, 27–31 by 9–17 mm; nerves 9–11. *Lateral sepals* ovate-oblong, 26–32 by 9–11 mm. *Petals* slightly recurved, 25–34 by 1–3 mm. *Lip* 25–29 by 19–29 mm. *Hypochile* when flattened 15–21 by 19–29 mm; base attached over 3–5 mm; lateral lobes in front obtuse; extending 4–9 mm in front; lateral keels 0.7–1 mm high at the base, median keel developed on the basal half of the hypochile, 1–1.3 mm high at the base. *Epichile* 13–17 by 11–18 mm; claw 2–3 mm thick; base attached over 7–11 mm; margin with projections 0.1–0.3 mm long; keels swollen and bar-shaped, sometimes slightly longitudinally channelled, 0.8–1.3 mm high, ending 2–4 mm from the apex of the epichile. *Column* 19–21 by 5–6 mm. *Anther* 4–4.5 by 3–4.5 mm. *Pollinia* c. 3 by 2 mm; caudicle not seen. *Stigma* 2–3 by 2–2.5 mm; rostellum 2–3 by 3–4 mm. *Fruit* not seen.

Distribution — Burma (Moulmein).

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

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

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

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

INSUFFICIENTLY KNOWN VARIETY

3. Coelogyne fimbriata var. acuminata Regel

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

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

EXCLUDED SPECIES

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

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

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

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

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

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

ACKNOWLEDGEMENTS

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IDENTIFICATION LIST

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

- 1. C. fimbriata 2. C. triplicatula
- Abraham cult. 3160: 1 Allen 27/1/1957: 1 Anonymous 39961: 1; 40130: 1; 305480: 1; ?/?/ 1872: 1; 17/12/1915: 1; ?/1/1920: 1.
- Balston 1/10/1912: 1 Barretto 221: 1; 222: 1; 315: 1; 413: 1; 48782: 1 Barriger 785: 1 Berkeley 25/11/1882: 1 — Berlin cult. 7778: 1; 9326: 1; 9346: 1; 10899: 1; 16951: 1; 17044: 1; 17045: 1; 17046: 1; 23590: 1; 24114: 1; 24258: 1; (Prag) 27506: 1; (Cubr.) 28714: 1 — Bogor cult. B146: 1; 203: 1; F203: 1; (Smith) 209: 1; (Piepers) 485: 1 — Bor 6608: 1 — Burkidge cult. 26/1/1886: 1 — Burkill & Haniff 12708: 1 — Butterfield cult. 42194: 1 — Buxbaum cult. 284: 1.
- Carr 16/11/1934: 1 Champion 527: 1 Charoenphol, Larsen & Warncke 4294: 1 Clarke 25145: 1; 41382: 1 Clayton ?/1/1997: 1 Cogniaux 20/8/1897: 1 Comber 1069: 1.
- Dullupchan 113: 1.
- Ehrendorf 9/10/1954: 1.

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

- Gamble 4017A: 1; **9981: 1**; 23142: 1 Glasgow cult. 29/10/1920: 1 Glasnevin cult. 26/11/ 1894: 1; 8/11/1904: 2 — Godefroy cult. ?/12/1891: 2 — Gravendeel cult. 16/10/1996: 1 — Griffith 5158: 1 — Groeneveldt cult. 595: 1.
- Hallier 3/11/1892: 1 Hance 401: 1; (Lamont) 401A: 1; 401B: 1; (Faber) ?/9/1883: 1 Handel-Mazzetti 8457: 1; 9789: 1 — Haniff 9057: 1 — Haniff & Nur 2324: 1 — Hegel ?/11/1848: 1 — Henry 13539: 1; 13598: 1 — Hooker 127: 1 — How 73235: 1 — Hu 6065: 1; 6176: 1; 11094: 1; 12454: 1.

Inayat 24100: 1.

- Kadoorie cult. (Barretto 301) 53014: 1; (Barretto 315) 55624: 1 Keke 1143: 1 Kerr 200A: 1; 200B: 1; 200C: 1; 0755: 1; 0762: 1 Kew cult. ?/11/1886: 1; ?/11/1887: 1; ?/11/1888: 1; (Warre) ?/10/1897: 1; ?/2/1920: 1; (Elwes) 247-1922: 1; 14/10/1926: 1; (Hinde) 175-1926: 1; 3-1928: 1; 215-29: 1; 12/10/1931: 1; 310-1948: 1; 636-1954: 1; 638-54.63802: 1; (Matthews 170) 705-6: 1; 705-63.70538: 1; (Rittershauser) 58234: 1 Kienast cult. ?/12/1895: 1; ?/11/1889: 1 King ?/5/1874: 1.
- Lamont 755: 1 Latif 6: 1 Lau 2486: 1; 4667: 1 Lindley 55: 1 Leiden cult. (hortus VU Amsterdam) 21405: 1; 21464: 1; 21640: 1; 21764: 1; 21786: 1; (van Vliet) 21789: 1; 22704: 1 (p); 22725: 1 (p); 22767: 1; 23320: 1; 27294: 1; (de Vogel) 27675b: 1; 30723: 1; 30729: 1 (p); 30756: 1; 30759: 1 (p); 30767: 1; 920836: 1; (Barretto) 970702: 1; (Barretto) 970703: 1; 970704: 1 — Loddige's collectors ?/?/1838: 1 — Low cult. ?/10/1894: 1 — Ludlow & Sherriff **1048: 1**. Macpherson 6/9/1909: 1 — Meise cult. 1907-3824: 1; 30/8/1912: 1; 3/10/1912: 1; 1974-0170: 1
- Metcalf 18045: 1; 18328: 1 Moore ?/12/1885: 1.
- Pal 1790: 1 Pantling 19: 1 Parish 118: 1; ?/?/1863: 2 Parkinson 6404: 2 Parks (?/7/ 1824): 1 — Parry 423: 1; 435: 1 — Peradeniya cult. (Jayaweera) 1167: 1 — Polunin, Sykes & Williams 5735: 1 — Prain's collector 117: 1; 173: 1.
- Ridley ?/12/1892: 1 Robinson & Kloss 6085: 1 Rock 7158: 1; 7707: 1.
- Schlechter 15950: 1 Shi 15116: 1 Smith 29: 1 Stainton 8480: 1; 8775: 1 Stainton, Sykes & Williams 8962: 1 Swinhoe 90: 1.
- Taam 1750: 1 Ting & Shih 1046: 1 Tsai 54159: 1; 58531: 1; 58732: 1 Tsang 24274: 1; 25681: 1; 25910: 1.
- Van Beusekom & Phengklai 2466: 1 Van Imschoot ?/10/1889: 2; ?/11/1890: 1; 29/6/1893: 1; ?/?/1896: 2 Vienna cult. 18/8/1958: 1.
- Wai Tak 8737: 1 Wallich 1957: 1 Wang 34701: 1; 36128: 1; 36496: 1; 40130: 1 Wilford 101: 1 Wilson 101: 1 Wood 862: 1.

INDEX

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

Broughtonia	(Coelogyne)
<i>linearis</i> Wall. ex Hook.f. 1 Coelogyne Lindl.	ovalis Lindl. 1 var. latifolia Hook.f. 1
sect. Fuliginosae Pfitzer & Kraenzl. [p. 264]	padangensis J.J. Sm. & Schltr. 1
arunachalensis H.J. Chowdhery &	pallens Ridl. 1
G.D. Pal 1	pilosissima Planch. 1
chrysotropis Schltr. 1	primulina Barretto 1
fimbriata Lindl. 1	schilleriana Rchb.f. 5
var. acuminata Regel 3	treutleri Hook.f. 6
var. annamica Finet 1	triplicatula Rchb.f. 2
fuliginosa Lindl. ex Hook.f. 1	xerophyta HandMazz. 1
laotica Gagnep. 1	Pleione
leungiana S.Y. Hu 1	fimbriata auct.1
longeciliata Teijsm. & Binn. 1	fuliginosa (Lindl.) Kuntze 1
micrantha Lindl. 4	ovalis auct. 1