Molecular phylogenetic systematics in the Dendrobiinae (Orchidaceae), with emphasis on *Dendrobium* section *Pedilonum*

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Abstract

Clements, M.A. (*Centre for Plant Biodiversity Research, Australian National Herbarium, G.P.O. Box 1600, Canberra, A.C.T. 2601, Australia*) *2003. Molecular phylogenetic systematics of the Dendrobiinae (Orchidaceae), with emphasis on* Dendrobium *section* Pedilonum. Telopea *10(1): 247–298*. Molecular systematic research using the internal transcribed spacer (ITS) region of the 18–26S nuclear ribosomal DNA repeat unit, on representatives of most taxonomic units within the Dendrobiinae has provided independent support, in addition to morphological and biological data, for the phylogenetic reassessment of the taxon. At a broad level, the Dendrobiinae is polyphyletic with *Epigeneium* forming an independent clade; *Dendrobium* section *Oxystophyllum* is deeply embedded within one of the outgroups, subtribe Eriinae: Podochileae; and the remaining taxa isolated into two major groups, viz the Asian and Australasian clades. A detailed study of part of the Asian clade, with emphasis on representatives of the morphologically based *Dendrobium* section *Pedilonum,* groups species into seven major clades. *Dendrobium* section *Pedilonum* is shown to be non-monophyletic with most species previously interpreted as belonging to it being well isolated from *D. secundum,* the designated type of that taxon, and interspersed amongst representatives of *D.* section *Calcarifera, Calyptrochilus, Cuthbertsonia, Dendrobium, Dolichocentrum, Oxyglossum* and *Platycaulon*. *Dendrobium* section *Rhopalanthe,* which separates the two major clades containing representatives of *D.* section *Pedilonum*, is itself paraphyletic with representatives of sections *Aporum* and *Bolbidium* embedded within it. These molecular results, combined with morphological data, provide a strong basis for a reassessment of the phylogeny of part of the study taxon. A reclassification of this part of the Dendrobieae and Podochileae is provided in Appendix 2, including: re-instatement of the genus *Oxystophyllum* (Eriinae: Podochileae); the recognition and description of subtribes Epigeneiinae and Grastidiinae (Dendrobieae); recognition or re-instatement of the genera *Aporum, Callista, Ceraia, Coelandria, Eurycaulis, Distichorchis, Pedilonum* as distinct from *Dendrobium*; the elevation of *Anisopetala* to generic status; and where necessary the transfer of the appropriate species from *Dendrobium* to these genera.

Introduction

The Dendrobiinae Lindl. comprises a diverse group of epiphytic, lithophytic and terrestrial herbs classified in six genera in current usage containing approximately 1150 species (Dressler 1993). Species within these genera are distributed predominantly throughout paleotropical regions with extensions to temperate Asia (Seidenfaden 1985, 1992, Seidenfaden & Woods 1992), the Philippines (Ames 1908, Quisumbing 1934), the Malay archipelago (Smith 1905, Comber 1990, Wood et al. 1993), New Guinea (Schlechter 1912, van Royen 1979), Australia (Rupp 1947, Dockrill 1969, Jones 1999), New Caledonia (Hallé 1997), south-west pacific islands (Lewis & Cribb 1989, 1992, Kores 1991, Cribb & Whistler 1996), and New Zealand (Moore 1972). Members of the Dendrobiinae vary considerably in their floral and vegetative morphology, especially in the southern part of their range, making them prime candidates for studies of character evolution. The subtribe has already been the focus of a broad taxonomic study (Brieger 1981) and phylogenetic studies based on analysis

of chloroplast DNA restriction sites (Yukawa et al. 1993, 1996) and chloroplast DNA sequences (Yukawa et al. 2000).

The subtribe Dendrobiinae was created in 1829, as a section within the tribe Malaxideae Lindl., accompanying the description and illustration of *Dendrobium secundum* (Blume) Lindl. in the Botanical Magazine (Lindley 1829). Thereafter Lindley enumerated his concept of Dendrobiinae, embracing 20 genera and grouping them together on the possession of two, four or eight pollinia (Lindley 1830). *Dendrobium* Sw. was grouped together with ten other genera including *Aporum* Blume, *Macrostomium* Blume, *Bulbophyllum* Thouars and *Polystachya* Hook. on account of the possession of four naked pollinia. Most subsequent authors including Lindley (1851), Reichenbach (1861), Bentham (1881), Bentham and Hooker (1883), Pfitzer (1882, 1889), Schlechter (1905, 1912, 1926), Dressler and Dodson (1960) and Dressler (1972, 1979, 1981), have progressively narrowed the interpretation of the Dendrobiinae so that Dressler (1993), in his most recent classification of the family, recognised only six genera with approximately 1150 species within the subtribe, viz *Cadetia* Gaudich. (67 spp.), *Dendrobium* (c. 900 spp.), *Diplocaulobium* Kraenzl. (94 spp.), *Epigeneium* Gagnep. (12 spp.), *Flickingeria* A. Hawkes (70 spp.) and *Pseuderia* Schltr. (4 spp.).

However, the systematic position and presumed monophyly of the Dendrobiinae *sensu* Schlechter (1926) was questioned when Brieger (1981) published an account of the group as part of a revised classification of the family. He noted that Lindley had united a great number of taxa into two huge collective genera, *Dendrobium* and *Eria*. Thereafter, with the description of many additional species, it became necessary to create a sometimes complex, infra-generic structure to accommodate the various forms being described within each of these large genera, e.g. Bentham and Hooker (1880), Pfitzer (1889), Kraenzlin (1910), Schlechter (1912). However, in Kraenzlin's complex, and confusing thesis on the Dendrobiinae, he proposed the re-instatement and recognition of several segregate genera within the subtribe, *viz*. *Callista* Lour., *Inobulbum* (Schltr.) Schltr. et Kraenzl. [as *Inobulbon*], *Sarcopodium* Lindl., *Diplocaulobium* (Rchb.f.) Kraenzl. and *Desmotrichum* Blume. Thereafter, the situation changed slightly with a push towards the acceptance or recognition of several of these segregate genera, so that by 1980 typically in the scientific literature six genera were recognised within the Dendrobiinae and eight in the Eriinae (Dressler 1981). Brieger (1981) took the classification of the subtribes Dendrobiinae and Eriinae to new levels of confusion, combining them into one large subtribe containing six informal categories that he termed 'Genera-Series' based on overall perceived similarities of vegetative and floral morphology. He also reinstated, recognised and described many new genera within this framework. The systematic position of the Dendrobiinae also came under scrutiny as a result of studies of embryological development, from representatives of the Orchidaceae including the Dendrobiinae (Clements 1995, 1996, 1999, unpublished). These studies provided independent evidence that the Dendrobiinae, and more particularly *Dendrobium*, was polyphyletic with respect to the Eriinae (Podochileae), where different embryo types were identified within these taxa. Results from phylogenetic analyses of *rbc*L and *mat*K plastid sequences and cpDNA restriction sites in the Dendrobiinae (Yukawa et al. 1993, 1996, 2000, Yukawa & Uehara 1996) also supported similar conclusions. These authors concluded that the Dendrobiinae is polyphyletic and comprises four major clades: (i) *Pseuderia* which was shown to belong to the Podochilinae [?](Yukawa et al. 1996); (ii) *Epigeneium*; (iii) *Dendrobium* Clade 1 containing species predominantly inhabiting mainland Asia, including the type of the genus; and (iv) *Dendrobium* Clade 2 containing taxa including *Cadetia, Diplocaulobium* and *Flickingeria* widespread mostly in Australasia and the Pacific Islands. It was on the basis of these results and some unpublished data that genera such as *Dockrillia* Brieger (Clements & Jones 1996), *Grastidium* Blume (Clements & Jones 1997), *Inobulbum* (Schltr.) Schltr. et Kraenzl. (Clements & Jones 1998a), *Tetrodon*

(Kraenzl.) M.A.Clem. et D.L.Jones (Clements and Jones 1998a), *Winika* M.A.Clem., D.L.Jones et Molloy (Clements et al. 1997), and *Cannaeorchis* M.A.Clem. et D.L.Jones (Clements & Jones 1998b) from the Malesian and Australasian regions have been recognised, reinstated or described.

Dendrobium section *Pedilonum*

One characteristic group of species in *Dendrobium*, often with extremely colourful flowers, and frequently encountered throughout the Malesian region, which as yet has received little attention at the molecular level, is *Dendrobium* section *Pedilonum* and its associated sections *Calyptrochilus*, *Cuthbertsonia* and *Oxyglossum*. Brieger (1981) treated these taxa in genus series *Dendrobia*, all as part of the genus *Pedilonum*, and he added two further sections formerly treated as part of *Dendrobium*, section *Sanguinolenta* and section *Platycaulon*. *Dendrobium* section *Pedilonum* was described by Blume in 1825 but then, almost immediately, he treated it at generic rank (Blume 1825). Blume considered *Pedilonum* distinct from *Dendrobium* by the absence of an articulate, slipper shaped labellum and included six species in the genus. He divided *Pedilonum* into two unnamed sections: one, containing *P. kuhlii* and *P. hasseltii*, was distinguished by possession of an elongate, laterally compressed sack formed by fusion of the lateral sepals not adnate to the labellum claw; the second, containing *P. secundum*, *P. undulatum*, *P. biflorum* and *P. erosum*, was distinguished by lateral sepals forming an elongate spur often adnate to the labellum claw. Over 140 species have since been assigned to *Pedilonum* all as *Dendrobium,* mainly by Miquel (1859), Pfitzer (1888), Hooker (1890), Ridley (1896), Bailey (1902), Kraenzlin (1910), Schlechter (1905, 1912), and Seidenfaden (1985).

Kraenzlin (1910) in his monograph of *Dendrobium* divided the genus into ten subgenera, including subgenus *Pedilonum,* all roughly equivalent to the sections of earlier authors. He treated 137 species within subgenus *Pedilonum* and further divided it into five sections, viz. *Secunda*, *Glomerata*, *Capitata*, *Ceratobium* and *Brevisaccata*. Of these five sections only the first three contain species closely related to *Pedilonum* as considered by authors such as Schlechter (1910, 1911a & b, 1912, 1914, 1921, 1923a & b, 1925), Smith (1908b, 1909, 1910a,b & c, 1911a, b & c, 1912, 1913, 1916, 1917, 1918, 1919, 1020, 1922, 1924, 1925, 1926, 1927a & b, 1928a,b & c, 1929, 1930, 1933a & b, 1934a ,b & c) and van Royen (1979).

Schlechter (1912), in his account of *Dendrobium* in the Orchids of German New Guinea, considered section *Pedilonum* to be part of subgenus '*Eu-Dendrobium*', which he distinguished as those taxa possessing: leaves upon distinct sheaths; stems pseudobulbous or fleshy for their whole length; and the absence of any longitudinal splitting of the labellum into well defined lobes. He also considered that section *Pedilonum* shared these characteristics with sections *Dendrobium*, *Platycaulon*, *Calyptrochilus*, *Cuthbertsonia* and *Oxyglossum*. He further characterised section *Dendrobium* as having the habit of two- to multi-flowered lateral inflorescences with spreading flowers, and an undivided, rotund labellum in most cases internally finely papillate. Section *Platycaulon* was characterised by the much-flattened, compressed pseudobulbs and the labellum veins thickened frequently into ridges. Section *Calyptrochilus* was characterised by the labellum, which at the apex is turned inwards and cucullate, and with finely serrate margins, an elongated column-foot adnate with the margins of the labellum forming a spur. Section *Cuthbertsonia* included species with short pseudobulbs but with a peculiar papillose covering of the leaves and outside of the flowers, particularly the ovaries; the flowers werecharacteristic of those found in the previous section minus the serrate inward facing labellum apices. Section *Oxyglossum* was also characterised by the short pseudobulbs, two but occasionally

multi-flowered inflorescence, an ovary with three to ten, sharp wings, and an attenuate labellum with a brightly coloured, sharp apex.

By comparison, Brieger (1981) recognised *Pedilonum* at generic rank with six sections, viz. *Pedilonum*, *Calyptrochilus*, *Cuthbertsonia*, *Oxyglossum*, *Sanguinolenta (Calcarifera)* and *Platycaulon*. Section *Sanguinolenta* was created by Brieger (1981) to account for a group of species typified by *D. sanguinolentum*, possessing 'stem axes uniformly cylindrical, with numerous leaves, rarely non-uniformly thickened, not flattened; labellum narrow at base, broadening and with erect margins, indistinct, rarely distinctly trilobed'. The section is more or less equivalent to Smith's *D.* section *Calcarifera* which he characterised as differing from section *Pedilonum* by the labellum which is larger, broader, and usually more or less lobed and has a tooth protruding into the mentum. Based upon Brieger's interpretation of the subtribe, Rauschert (1983) made hundreds of automatic transfers to various genera including *Pedilonum* although authors such as Seidenfaden (1985) and Cribb et al. (1985) criticised these taxonomic changes.

Since there is obviously much confusion surrounding the status and circumscription of *Pedilonum* and associated taxa, I decided to investigate furthur the relationships of such a prominent member of the Dendrobiinae in the Malesian region. The main purpose of this study was therefore to: (i) contribute to our understanding of the phylogenetic relationships in the Dendrobiinae; (ii) determine if *Pedilonum* and associated taxa are monophyletic, based on analyses of the internal transcribed spacer (ITS) region of 18-26S nuclear ribosomal DNA, an independent data set; and (iii) clarify the status of *Pedilonum* and allied taxa. This study also offers the opportunity to further unravel the confusion that currently surrounds the status of *Dendrobium* sens. lat., and subtribe Dendrobiinae and tribe Dendrobieae of which it is a part.

Methods

Plant material. Material of 75 species representative of genera in the Dendrobiinae and sections within *Dendrobium*, but in particular those associated with section *Pedilonum,* were used in this study. Outgroups were chosen on the basis of previous studies and are roughly equivalent to those used by Yukawa et al. (1996, 2000) and comprised species of *Bryobium*, *Eria* (Eriinae: Podochileae), *Adelopetalum, Bulbophyllum, Oxysepala* (Bulbophyllinae: Dendrobieae), *Liparis* (Malaxideae) and *Drymoanthus* (Aeridinae: Vandeae) (Appendix 1). Species used in this study were carefully chosen from amongst representatives of the c. 290 species in the study group for which sequences were available. Fresh leaf samples were collected either in the field or from cultivated plants of known provenance. All collections are vouchered and deposited at the Australian National Herbarium (CANB) (Appendix 1).

DNA extraction and PCR and sequencing procedures. Genomic DNA extraction and sequencing procedures used are the same as those described in the preparation of material for the analyses of the Diurideae (Clements et al. 2002). The complete sequence of the ITS1–5.8S–ITS2 region for each sample was edited and assembled from the sequencing chromatograms using Sequencher 3.0 software (Gene Codes Corporation). The sequences have been submitted to GenBank and given accession numbers as shown in Appendix 1.

Method of alignment and sequence analysis. Sequences were first aligned using the EclustalW program supplied by the Australian National Genomic Information Service (ANGIS) Multiple alignment parameters were set at the default values; a gap opening penalty of 10 (range 1–100), a gap extension penalty of 5 (range 0.10–100) and gap separation penalty of 8 (range 1–50). Sequences were manually re-aligned, using

BioEdit version 4.7.8. The re-aligned files were converted to PAUP/NEXUS format, exported to MacClade and analysed using PAUP version 4.0b4a. The most parsimonious trees were determined using a heuristic search algorithm with 100 replicates of random taxon entry, TBR branch swapping and the 'Multrees' option. Successive weighting (Farris 1969) was applied through recalculation of the rescaled consistency indices until a stable position was attained. Bootstrap analyses were done for both unweighted and weighted trees to determine the relative support for the resultant clades (Felsenstein 1985), and all minimal length trees saved. These equally parsimonious trees were summarised by generating a consensus tree.

Results

An overall assessment of the Dendrobieae, centered on the Dendrobiinae, was first undertaken through a sequence analysis of 23 species, representative of most major taxonomic groups used in previous studies of the group (Yukawa et al. 1993) including seven outgroup species, viz. *Bryobium*, *Eria* (Eriinae: Podochileae), *Adelopetalum*, *Bulbophyllum* and *Oxysepala* (Bulbophyllinae: Dendrodieae), *Liparis* (Malaxideae) and *Drymoanthus* (Aeridinae: Vandeae). The alignment used contained 786 nucleotide sites of which 324 were potentially parsimony-informative. Analysis of this computer based alignment produced 3 equally parsimonious trees; tree length = 1440; consistency index (CI) = 0.5743; retention index (RI) = 0.4853; and rescaled consistency index (RC) = 0.2787. One of these trees is shown in Figure 1.

These results show a polyphyletic Dendrobiinae with: (i) *Dendrobium* section *Oxystophyllum* deeply embedded within the strongly supported (100% bootstrap support) Eriinae (Podochileae), (ii) a strongly supported (96% bootstrap support) monophyletic *Epigeneium* sister to the remainder of the Dendrobiinae, and (iii) the remaining representatives of the Dendrobiinae separated into two major groups, the Australasian and Asian clades. Excluding *Dendrobium* section *Oxystophyllum* these results reveal only weak support (<50% bootstrap support) for the monophyly of the remainder of the ingroup including *Epigeneium*. Conversely there is moderately strong support for monophyly of *Epigeneium*, the Australasian (85% bootstrap support) and Asian (91% bootstrap support) clades. These results also show that the Dendrobieae is polyphyletic when the Bulbophyllinae is included, with the Eriinae (Podochileae) deeply embedded within it.

A more comprehensive molecular phylogenetic analysis was then undertaken based on the inclusion of an additional 52 species, mostly representative of the Asian clade from within the Malesian and Australasian regions, and in particular those attributed in the literature to *Dendrobium* section *Pedilonum* and associated taxa *viz*. sections *Aporum, Calcarifera, Cuthbertsonia, Calyptrochilus, Dendrobium, Dolichocentrum, Oxyglossum and Rhopalanthe*. This analysis, based on an alignment of 768 nucleotide sites of which 444 were potentially parsimony-informative, produced 122 equally parsimonious trees; tree length = 2726; consistency index (CI) = 0.3899; retention index (RI) = 0.6719; and rescaled consistency index (RC) = 0.2620. Successive weighting was then applied resulting in three trees, all with the same general topography. One randomly selected tree is shown as a phylogram in Fig. 2. These results again show the polyphyletic condition of the Dendrobiinae and its fragmentation into two separate component groups, the larger of which is only weakly supported by both nuclear and plastid molecular analyses but contains three major, well-supported clades. *Dendrobium* section *Oxystophyllum* with *Epigeneium* remain isolated from the main body of the Dendrobiinae. Some of the species that were added in the more comprehensive analyses (*Winika cunninghamii*, *Cannaeorchis fractiflexa*, *Dendrobium*

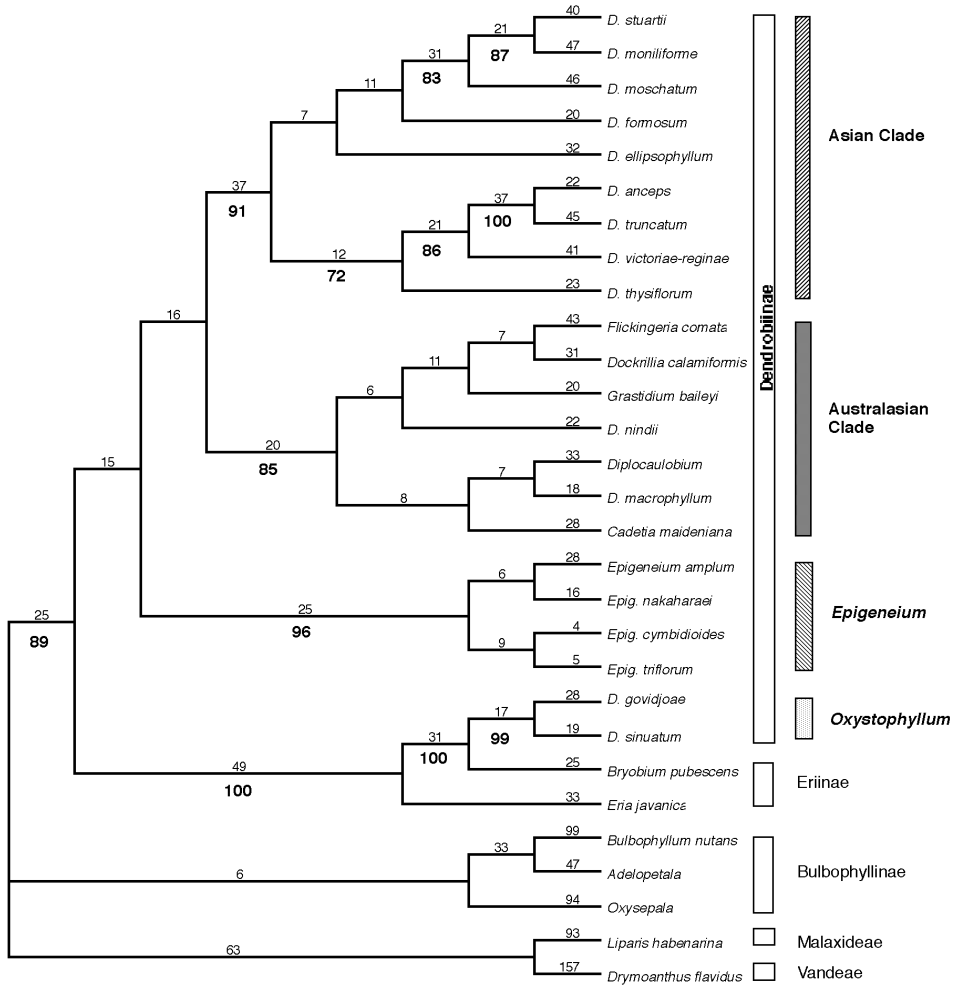

Fig. 1. One of three most parsimonious trees generated from the broad based data matrix based on nuclear ITS sequences, showing the composition of the Dendrobiinae with *Oxystophyllum*, *Epigeneium* and Australasian and Asian clades identified relative to 7 outgroup species: L. = 1440, CI = 0.5743, RI = 0.4853. Numbers above branches are branch length estimates (ACCTRAN optimalization); bootstrap percentages greater than 50% are given below in bold.

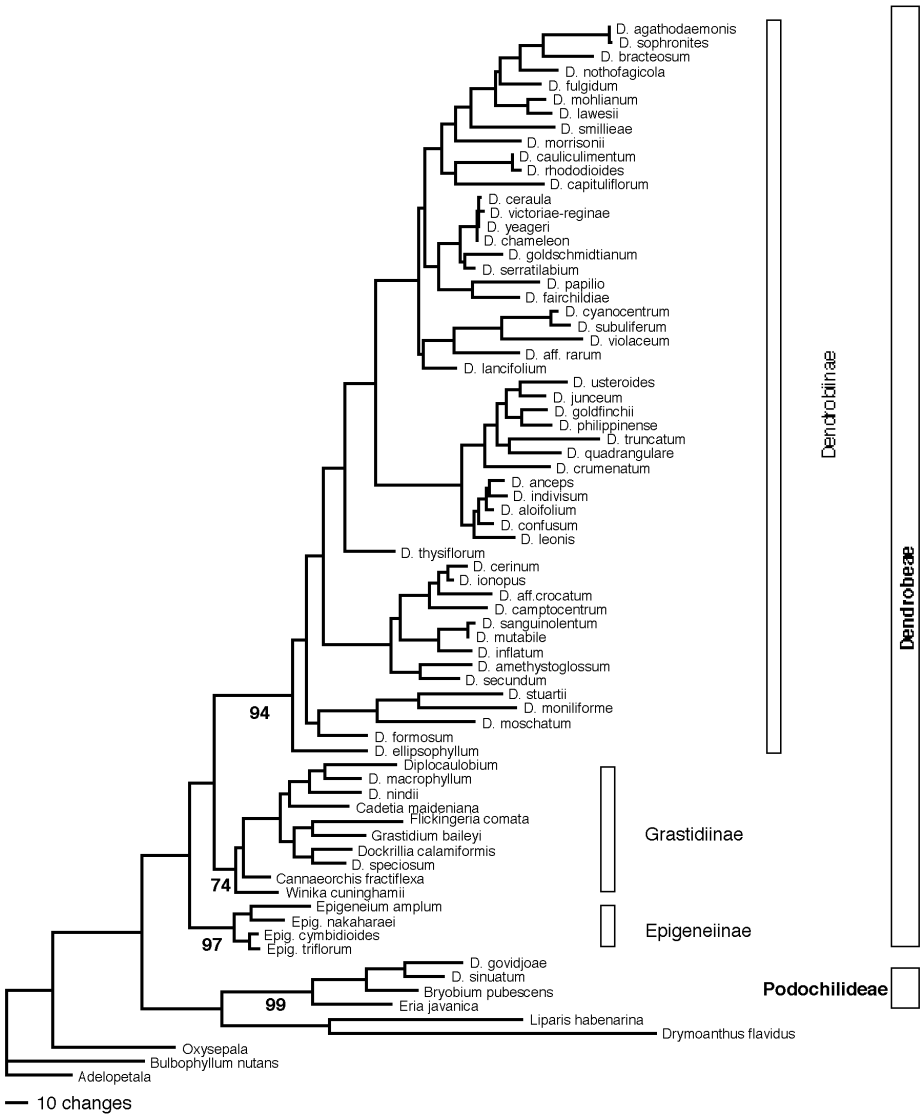

Fig. 2. A phylogram of one of the three most parsimonious successively weighted trees from the ITS analysis of a study of the Dendrobiinae and outgroup taxa based on 75 species: L = 2728, CI = 0.3897, RI = 0.6715, showing the relationships between groups when all study species are included. Bootstrap percentages (50% or more) for the four main taxa containing elements of the Dendrobiinae are in bold.

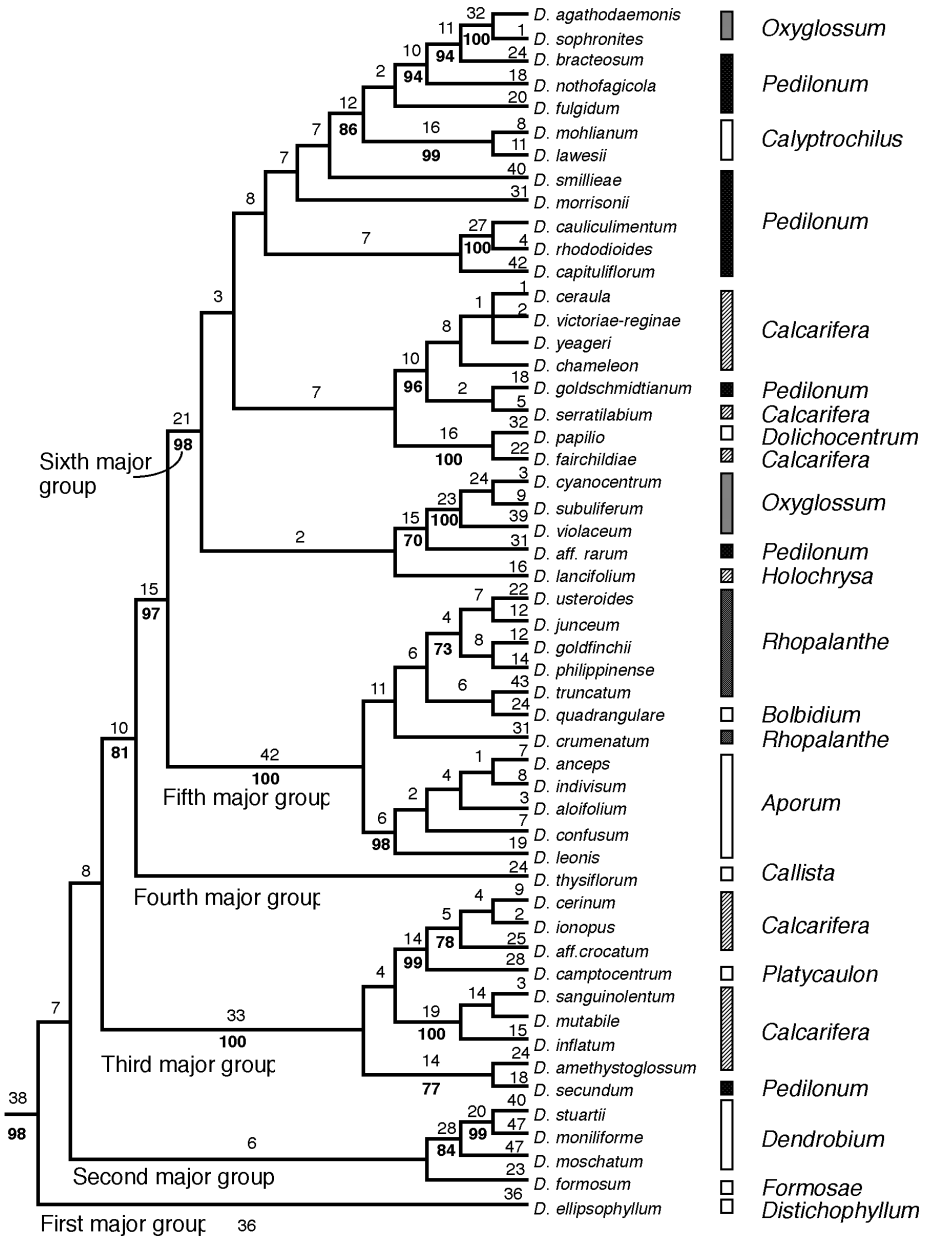

Fig. 3. Details of the Asian clade portion of Fig. 2 showing one of the 3 most parsimonious successively weighted trees from the ITS analysis of the Dendrobiinae, and proposed arrangement of the six major groups within: L = 2728, CI = 0.3897, RI = 0.6715. Sections in which species have historically or are currently placed are shown on the right hand side column. Numbers above branches are branch length estimates (ACCTRAN optimalization); bootstrap percentages greater than 50% are given below in bold.

nindii, *D. macrophyllum* and *D. speciosum*), group with *Cadetia*, *Diplocaulobium*, *Dockrillia*, *Flickingeria* and *Grastidium* into the moderately supported Australasian clade (74% bootstrap support) thus rendering *Dendrobium* in its current interpretation, polyphyletic. All remaining species cluster into a strongly supported monophyletic Asian clade (94% bootstrap support) also shown in Figure 3. Within the Asian clade there are six major groupings. The first contains a single species *Dendrobium ellipsophyllum* representative of section *Distichophyllum*. The second major group contains representatives of section *Formosa* and section *Dendrobium* including *D. moniliforme*, the designated type of the genus. All four remaining major groups are all clearly isolated and strongly supported (81–100% bootstrap values) from each other. The third major group contains representatives of sections *Pedilonum*, *Calcarifera* and *Platycaulon* while the fourth major group contains a single species *D. thysiflorum* representative of section *Callista.* The fifth and sixth major groupings are grouped together with strong support (97% bootstrap value). Representatives of sections *Aporum, Bolbidium* and *Rhopalanthe* comprise the fifth major group. The sixth major group comprises a large assemblage of species, most of which have been assigned to section *Pedilonum* or the allied sections *Calyptrochilus*, *Calcarifera* and *Oxyglossum*, in addition to representatives of section *Dolichocentrum*. These results reveal the non-monophyletic nature of many sections within this part of the Dendrobiinae but in particular, sections *Calcarifera* and *Pedilonum.* Additionally, section *Rhopalanthe* is paraphyletic with a representative of section *Bolbidium* embedded within it. Section *Oxyglossum* is polyphyletic whereas section *Aporum* represents a monophyletic group.

Discussion

These current analyses, based on ITS nrDNA sequence data, provide an insight into the phylogeny and overall structure in the Dendrobieae including a significant portion of the Dendrobiinae, in particular the Malesian elements of the Asian clade. At the broader level, using a similar range of species to that used in previous molecular systematic studies (Yukawa et al. 1993, 1996a, 1996b, 2000), the present results strongly corroborate the overall phylogeny of the Dendrobiinae based on analyses of plastid DNA data (restriction sites and *rbc*L and *mat*K sequences). Both sets of results show representatives of *Epigeneium* grouped together in a strongly supported clade (96–100% bootstrap support) and sister to the remainder of the Dendrobiinae. They also show the remainder of the Dendrobiinae split into the same two major groupings, the Australasian and Asian clades. The strong correlation between both sets of results suggests the taxonomic status of this group needs reconsideration. On the basis of both independent sets of results the continued recognition of *Epigeneium* in a separate genus would seem appropriate.

Dendrobium section *Oxystophyllum*

Of particular note in these ITS sequence analyses is the grouping of *Dendrobium govidjoae* and *D. sinuatum* with *Eria javanica* and *Bryobium pubescens*, two representatives of the Eriinae (Podochileae). D*endrobium govidjoae* and *D. sinuatum* are members of the taxon *Dendrobium* section *Oxystophyllum* and this group historically has been treated either as a separate genus *Oxystophyllum* (Blume 1825, Lindley 1830), as a section of *Dendrobium* (Miquel 1859, Smith 1908, Kraenzlin 1910, Schlechter 1912), or as a section of the genus *Aporum* (Reichenbach 1861, Hooker 1890, Brieger 1981) all within the tribe Dendrobieae, subtribe Dendrobiinae. When treated within *Dendrobium*, section *Oxystophyllum* has been interpreted as allied to sections *Aporum* and *Rhopalanthe* (Schlechter 1912) on account of similarities of vegetative features most

notably the equitant leaves and the abbreviated, lateral inflorescences formed in the axils of the leaf-sheaths along the leafy part of the stem. The position of *Oxystophyllum* outside the Dendrobieae renders that tribe polyphyletic unless the Eriinae is included within it. Additionally, inclusion of *Oxystophyllum* within the Eriinae contradicts the interpretation that possession of eight pollinia can be used as a defining character for that subtribe (Dressler 1993). Careful examination of *Dendrobium govidjoae* and *D. sinuatum* plus other species in the group, both as living or herbarium specimens, reveals the existence of key morphological characters that correlate with, and support, the proposed alignment with the Eriinae rather than with the Dendrobiinae. Characters possessed by *D.* section *Oxystophyllum* include: pensile habit; roots wiry, hirsute, rusty brown, with a purplish growing apex; leaves equitant, rigid, falcate to lanceolate, with abscission layer towards base, apex sharply acute and with vascular traces confined to adaxial surface; inflorescences compressed, simple or compound, indeterminate, lateral or terminal, racemes, covered with persistent equitant, imbricate bracts, the solitary flowers arising intermittently; flowers sombre coloured, with short, acute, thick, rigid tepals, lateral sepals contiguous and adnate to column-foot, saccate; labellum ligulate, on a short hinge, thick, fleshy and secreting sticky fluids at base; pollinia four, in two separate sets of two, small, irregularly shaped, pinkish cream, and with prominent caudicles. Two of these characters in particular (the roots, wiry, hirsute, rusty brown, with a purplish growing apex; and the pollinia, with prominent caudicles) are more consistent with those present in various members of the Eriinae than with those in the Dendrobiinae. Although unusual in the Eriinae, the equitant leaf habit is present in *Eria* section *Aporodes* (Schlechter 1912, Cootes 2001), another example of convergent evolution within the Orchidaceae. Aside from the obvious similarities of habit and vegetative morphology, characters possessed by species in *D.* section *Aporum* are: roots white or green, thin, glabrous; vascular traces scattered randomly throughout the leaf tissue; compressed simple or compound inflorescence lacking; bracts equitant, imbricate, persistent; flowers with a well defined column-foot; labellum non-articulate, lacking any secretory processes; pollinia yellow, four in two tightly appressed hemi-pollinia lacking caudicles. On the basis of these ITS sequence analyses and the cited morphological characters, it is proposed that *Oxystophyllum* as originally interpreted by Blume (1825), should again be recognized at generic rank within the subtribe Eriinae (Podochilideae) rather than in the Dendrobieae (see below). Additionally, the definition of the Eriinae should be adjusted to include: pollinia, eight (rarely four) in two sets of four (two), with caudicles.

Epigeneium

Although there is strong support for the monophyly of *Epigeneium* (96% bootstrap support) in the present ITS analyses, there is only weak support for its position as sister group to the remaining members of the Dendrobiinae, a result that was also found in analyses of *rbc*L and *mat*K sequences and cpDNA restriction sites (Yukawa et al. 1993, 1996a, 2000). Treatment of the group as part of, but sister to, the bulk of the Dendrobiinae is not unreasonable (see below). Many species in this group were first treated under the epithet *Sarcopodium* Lindl. (Lindley 1850, Rolfe 1910, Kraenzlin 1910) or as a section of *Dendrobium* (Hooker 1890, Schlechter 1912), based on *Dendrobium amplum*. However, none of these authors was apparently aware that the name *Sarcopodium* was a later homonym of a fungal genus. Later Gagnepain (1932) described *Epigeneium* to accommodate a small group of morphologically distinct *Dendrobium* species typified by *D. fargesii*, because of their *Bulbophyllum*-like habit but having flowers reminiscent of a *Coelogyne*. Because of the unavailability of the name *Sarcopodium*, Hawkes (1956) proposed the alternative name *Katherinea,* overlooking, or not making the connection to, the earlier published legitimate name *Epigeneium.* The name *Epigeneium* has since been taken up and applied, using a broader

circumscription, to all species in the group (Summerhayes 1957, Seidenfaden 1980, Garay & Romero-Gonzalez 1999) although some authors prefer to maintain the distinction between *Epigeneium* and *Katherinea* (Balakrishnan & Chowdhury 1966). Based on detailed morphological study of both living and herbarium material, species in the *Epigeneium* clade can be circumscribed by the following combination of characters: plants epiphytic or lithophytic; stems rhizomatous terminating in a single internode pseudobulb; leaves conduplicate, coriaceous, 1–3, terminal; inflorescence subterminal, determinate, single or multi-flowered, erect or pedant, arising from a prominent erect, imbricate bract; flowers long-lasting, with spreading segments, non-articulate labellum, a prominent long column-foot, petals obliquely attached for greater part or not, glabrous elongate column, with prominent apical often ornate anther attachment (see below).

In addition, there are three well-supported, morphologically distinct groups within the *Epigeneium* clade. These three taxa, represented in Figure 1 by (a) *E. nakaharaei*, (b) *E. amplum,* and (c) *E. cymbidioides* and *E. triflorum*, more or less correspond to those identified as sections by Garay and Romero-Gonzalez (1999), *viz E.* section *Epigeneium*, *E.* section *Katherinea* and *E.* section *Racemosum*. Briefly these are characterised as follows:

(a) section *Epigeneium*: epiphytic herb with reptant habit; stems pseudobulbous, pseudomoniliform, terminated by solitary leaf; inflorescence one-flowered, arising from new growth, shorter than leaves; dorsal and lateral sepals well separated and petals obliquely attached for greater part along a prominent long column-foot that is 2–3 times longer than the broadly concave column.

(b) section *Katherinea*: epiphytic herb with *Coelogyne*-like habit; stems rhizomatous terminating in erect, pseudobulbs; leaves erect, two to three per pseudobulb; inflorescence one-flowered, arising only from old growth, shorter than leaves; flowers large, *Coelogyne*-like; column approximately equal to the column-foot; column-foot porrect, narrow.

(c) section *Racemosum*: epiphytic herb often in large clumps; stems rhizomatous, often markedly so, terminating in suberect to ascending, pseudobulbs; leaves two or three per pseudobulb erect or spreading; inflorescence racemose, terminal to subterminal, multi-flowered, erect to pendulous, commonly much exceeding the leaves; flowers stellate, the lateral sepals not joined at base and labellum contiguous with column-foot; column narrowly concave approximately equal to the column-foot; a porrect, narrow column-foot.

In addition to highlighting the isolation of the *Epigeneium* clade as distinct from the remainder of the Dendrobiinae, results from these ITS analyses also provide a basis for alternative interpretations on the taxonomic status of the three identified groups within the clade. Since the whole group is monophyletic, one option is to maintain all three groups as a single genus under the name *Epigeneium* in line with the proposal of Garay and Romero-Gonzalez (1999). Another equally plausible and tempting option is to recognise all three sections at generic rank. There is, however, a problem with this option. *Epigeneium* section *Racemosa* is typified by *E. acuminatum* for which no material was available for sequencing. Without ITS sequence data it would be presumptive to suggest that *Epigeneium* section *Racemosa,* based only on study of *E. cymbidioides* and *E. triflorum,* represents a monophyletic taxon. One unacceptable option, based on these ITS sequence analysis results, is the recognition of just two genera in the group, as proposed by Balakrishnan and Chowdhury (1966), because acceptance of section *Katherinea* at generic rank would render *Epigeneium* paraphyletic. On the basis of all available evidence (and recognising that further research is require) for the present it is proposed to recognise only *Epigeneium* within the Epigeneiinae.

This leaves the remainder of the Dendrobiinae spread amongst the relatively strongly supported Australasian and Asian clades, a situation consistent with the results based on *rbc*L and *mat*K sequence and plastid restriction site analyses (Yukawa et al. 1996, 2000). Several taxonomic options are apparent; the *status quo*.unfortunately is not one of them.

Australasian clade

Focusing firstly on the Australasian clade in results from the present ITS analyses, the presence of the long-accepted, established genera *Cadetia*, *Diplocaulobium* and *Flickingeria*, deep within the well-supported Australian clade (85% bootstrap support), renders the current concept of the genus *Dendrobium* polyphyletic.

Cadetia was first described by Gaudichaud (1826) but it was Schlechter (1912) who finally established its status as distinct from *Dendrobium*. He characterised *Cadetia* by the possession of: the *Pleurothallis*-like habit; formation of a spur through cohesion anteriorly in the lower half of the lateral sepals; papillae in front of the column and labellum.

Since its proposal as a genus *Diplocaulobium* (Kraenzlin 1910) has gradually gained acceptance as separate from *Dendrobium* based on possession of the following characters: closely spaced single internode pseudobulbs; flowers mostly solitary, pedicellate, arising from a conspicuous bract at base of single terminal leaf, stellate, flowers lasting one day (rarely longer), with distinct mentum and articulate labellum (Lavarack et al. 2000)

Flickingeria, which was originally described under the illegitimate name *Desmotrichum* (Blume 1825), has similarly regained acceptance as a separate genus having in the interim been treated as a section of *Dendrobium* (Schlechter 1912) and under the generic name *Ephemerantha* (Hunt & Summerhayes 1961). The genus *Flickingeria* is characterised by: rhizomes irregularly branched, creeping, terminating in an erect pseudobulbous internode with a terminal non-sheathing leaf; inflorescences single or multi-flowered, terminal or subterminal to pseudobulb, both adaxial and abaxial to leaf, and covered by persistent sheathing bracts; flowers ephemeral; labellum midlobe fimbriate plicate, or bilobate (Seidenfaden 1980) Since the type species for *Dendrobium* is embedded within the Asian clade, one option is to accept that all species in the Australasian clade are representatives of genera other than *Dendrobium*. A second option is to re-include *Cadetia*, *Diplocaulobium* and *Flickingeria* in a broadly defined *Dendrobium* that includes both the Australian and Asian clades. However, there is only very weak support from the present analyses for treating the Australasian and Asian clades together as one large monophyletic group, and including these well-established, morphologically well-defined genera in an extremely broad concept of the genus *Dendrobium* would lead to much confusion and be unpopular with users. It would also leave Dendrobium as a huge (c. 1800 spp) unwieldy genus. A third option, to treat the Australasian and Asian clades as two separate genera, is likewise unhelpful. Such a proposal requires, in the case of the Australasian clade, the reduction of *Cadetia*, *Diplocaulobium* and *Flickingeria,* as well as all other members of this clade, to synonyms of the morphologically disparate and distinct *Grastidium* (Blume, 1825), as it represents the oldest named genus in the clade.

As shown previously, *Grastidium* is easily separated from other Dendrobiinae by the possession of: laterally flattened stems of pseudo-indeterminate growth; synchronous flowering; lateral inflorescences emerging from a node opposite a leaf lamina and breaking through its subtending sheath; inflorescences emerging with the protection of two indurated, laterally compressed sheathing bracts; inflorescence a much reduced, geminate raceme with terminal, inward-facing flowers; flowers ephemeral (Clements & Jones 1997). These characters, or combinations thereof, are also absent

from the remaining species in the Australasian clade and the aggregation of all species into a single genus under the name *Grastidium* would create more confusion and uncertainty than presently exist. Yukawa et al. (1993) arrived at similar conclusions with respect to the integrity and maintenance of representatives within the Australasian clade (including the genera *Cadetia*, *Diplocaulobium* and *Flickingeria*) although they refrained from formally recognising any other genera in the clade. Taxonomic and systematics treatments of most taxa within the Australasian clade are already well-advanced with the recognition of 35 genera:

> *Abaxianthus* M.A.Clem. et D.L.Jones (Clements & Jones 2002), *Australorchis* Brieger (Brieger 1981), *Bouletia* M.A.Clem. et D.L.Jones (Clements & Jones 2002), *Cadetia* Gaud. (Schlechter 1912), *Cannaeorchis* M.A.Clem. et D.L.Jones (Clements & Jones 1998b); *Cepobaculum* M.A.Clem. et D.L.Jones, *Ceratobium* (Lindl.) M.A.Clem. et D.L.Jones, *Davejonesia* M.A.Clem, *Dendrobates* M.A.Clem. et D.L.Jones (Clements & Jones 2002), *Dichopus* Blume, *Diplocaulobium* (Rchb.f.) Kraenzl. (Kraenzlin 1910), *Dockrillia* Brieger (Clements & Jones 1996), *Durabaculum* M.A.Clem. et D.L.Jones, *Eleutheroglossum* (Schltr.) M.A.Clem. et D.L.Jones (Clements & Jones 2002), *Eriopexis* (Schltr.) Brieger (Brieger 1981, Clements & Jones 1997), *Euphlebium* (Kraenzl.) Brieger (Brieger 1981), *Exochanthus* M.A.Clem. et D.L.Jones (Clements & Jones 2002), *Flickingeria* A.Hawkes (Seidenfaden 1980), *Grastidium* Blume (Clements & Jones 1997), *Herpethophytum* (Schltr.) Brieger (Brieger 1981), *Inobulbum* (Schltr.) Schltr. et Kraenzl. (Clements & Jones 1998a), *Kinetochilus* (Schltr.) Brieger (Brieger 1981), *Leioanthum* M.A.Clem. et D.L.Jones (Clements & Jones 2002), *Microphytanthe* (Schltr.) Brieger (Brieger 1981), *Monanthos* (Schltr.) Brieger (Brieger 1981), *Sarcocadetia* (Schltr.) M.A.Clem. et D.L.Jones (Clements and Jones 2002), *Sayeria* Kraenzl. (Rauschert 1983), *Stelbophyllum* M.A.Clem. et D.L.Jones, *Tetrabaculum* M.A.Clem. et D.L.Jones (Clements and Jones 2002), *Tetrodon* (Kraenzl.) M.A.Clem. et D.L.Jones (Clements & Jones 1998a), *Thelychiton* Endl. (Clements and Jones 2002), *Trachyrhizum* (Schltr.) Breig. (Brieger 1981), *Tropilis* Raf. (Rauschert 1983, Clements and Jones 2002), *Vappodes* M.A.Clem. et D.L.Jones (Clements and Jones 2002) and *Winika* M.A.Clem., D.L.Jones et Molloy (Clements et al. 1997).

A full account of the phylogeny of these taxa based on the results of molecular analyses is in preparation. The present ITS sequence analyses, and the plastid DNA analyses of Yukawa et al. (1996, 2000), also provide a basis for the recognition of both the Australasian and Asian clades at higher taxonomic rank within the Dendrobieae (examined below).

Asian clade

The remaining element of the Dendrobiinae, the Asian clade, forms a strongly supported monophyletic group (94% bootstrap support value), which strongly correlates with the results of Yukawa et al. (1996, 2000). Presence of *Dendrobium moniliforme*, the designated type species for the genus *Dendrobium* (Holttum et al. 1982) automatically means that in any classification system this clade must be included within the Dendrobiinae. Focussing on the elements of this clade, there are three strongly supported major groupings, all with 98–100% bootstrap support values, as well as two isolated species and another major group that contains *D. moniliforme*. Once again, although the species used in this study are not fully representative of all the groups considered to make up the Asian clade, they nevertheless provide an insight into the phylogeny of the group as a whole and in particular many of the Malesian elements of the Dendrobiinae with emphasis on representatives of *Dendrobium* section *Pedilonum*.

First major group: The first major group comprises a single species *Dendrobium ellipsophyllum*, that historically has been treated as: part of *Dendrobium* subgenus *Dendrobium* (Lindley 1851, Smith 1905); in section *Chrysantha* (Reichenbach, 1861); in section *Revoluta*; in subgenus *Grastidium* (Kraenzlin 1910); but more typically in section *Distichophyllum* (Hooker 1890, Schlechter 1912, Seidenfaden 1985, Brieger 1981). Hooker (1890) established section *Distichophyllum* to accommodate those species with

the habit of the genus *Appendicula* and flowers solitary or in short leaf-opposed racemes, a short, spur-like mentum as long as, or longer than, the lateral sepals and with broad recurved side lobes. Despite the taxon being represented by a single species in the present ITS sequence analyses (in order to keep a direct compatability with the species used by Yukawa et al. (1993)), the isolation of *D. ellipsophyllum* from the other major groups supports it recognition as a distinct from *Dendrobium sens. str*. Sequence analyses of other species from within the group, *D. austrcaledonicum*, *D. revolutum*, and *D.* aff. *sculptum*, are in progress. Examination of fresh and herbarium material of *D.* section *Distichophyllum,* including many type collections, has revealed additional key characters to those cited above present in all species in this taxon. Key characters for the taxon are: stems slender non-pseudobulbous, often angular; leaves pedicellate and clasping; inflorescence a highly reduced, lateral periodically developing raceme; flowers solitary (rarely two), each with a papery sheath that persists in the sheathing bracts after anthesis; labellum trilobed, with broadly bilobed mid-lobe, fleshy, minutely papillate and spongy at base on lamina callus, forming a closed, conspicuous, nectiferous spur with basal half to the column-foot; column with centra groove; column-foot concave, papillose on inner surface; and protocorm discoid type. On the basis of these broader results this taxon has been recognised as a distinct genus and given the name *Distichorchis* (Clements & Jones 2002).

Second major group: The type species for the genus *Dendrobium* together with *D. formosum, D. moschatum and D. stuartii,* are contained within the second major group but there is only weak support (<50% bootstrap support) for its acceptance as a monophyletic taxon. Internally however, there is good support for separation of *D. formosum* from the remaining species in the group. *Dendrobium formosum* belongs to a group commonly referred to as section '*Nigrohirsutae*' on account of possession of black hairs on the leaf sheaths of most species (Lindley 1859), but correctly the sectional name *Formosae* should be applied to it (Seidenfaden 1985). Authors such as Lindley (1859) and Reichenbach (1861) treated *D. formosum* and morphologically similar species belonging to section *Dendrobium*, in the subgenus *Nigrohirsuta* (Kraenzlin 1910), or in section *Oxygenianthe* (Schlechter 1912). However, not all species currently placed within *D.* section *Formosae* (e.g. Seidenfaden 1985, 1992, Seidenfaden & Wood 1992, Cootes 2001, Wood et al. 1993, Wood & Cribb 1994, Lavarack et al 2000, Comber 2001) possess the characteristic black hairs on the leaf sheaths, which suggests that further research is required as the taxon may not be monophyletic. The phylogeny and systematics of the group will be the subject of a separate paper. The remaining species in the second major group have historically been included in *D.* section *Eudendrobium* (Lindley 1851, Bentham & Hooker 1883, Kraenzlin 1910), section *Planifolia* (Reichenbach 1861), but more recently been treated as members of *D.* section *Dendrobium* (Seidenfaden 1985) although the nomenclatural history, taxonomy and systematics of the group is very complex and will be the subject of a separate paper. Representatives of this taxon are particularly scarce towards the eastern part of the Malay archipelago and in New Guinea are represented by three species and in Australia by a solitary species, *D. stuartii*.

Third major group: The third major group contains *D. secundum*, the designated type of the genus *Pedilonum*, plus eight other species representative of sections *Calcarifera* and *Platycaulon* of *Dendrobium* (Smith 1908, Schlechter 1912). Other species representative of *Pedilonum* are, however, scattered amongst three separate subclades in the sixth major group of the ingroup. This renders *Pedilonum* polyphyletic in any traditional or modern sense with the bulk of representative species well removed from *D. secundum.* Additionally, the proposed arrangement of species bears little relationship to any proposed infrageneric classification of the Dendrobiinae, which has been based on perceived differences in floral morphology. Sister to *D. secundum*, and with moderately strong bootstrap support, is *D. amethystoglossum.* This proposed

arrangement of these two species seems unusual; firstly, because of the presumed lack of similarity of the two species, and secondly, because historically the possibility has barely been considered. For example, Kraenzlin (1910) included *D. amethystoglossum* with 28 other species, in the subgenus *Pedilonum* section *Glomerata* subsection *Mesocentra*, whereas *D. secundum* was treated in the adjacent section *Secunda* in subgenus *Pedilonum*. Other authors such as Schlechter (1912), Brieger (1981), Rauschert (1983) and Seidenfaden (1985), did not offer an opinion on the phylogenetic position of *D. amethystoglossum.* By comparison, Cootes (2001) in the latest account of the orchids of the Philippines, and Comber (2002), treat the endemic *D. amethystoglossum* as a member of *D.* section *Calcarifera.* On my examination it was found that *D. secundum* and *D. amethystoglossum* shared several morphological features in particular: stems erect or porrect, pseduobulbous, soft, fleshy, long and tapering, covered with leaf sheaths; leaves thin, fleshy, deciduous, the sheath persistent and with slightly thickened red veins; lateral sepals connate in basal half, forming a saccate spur; labellum non-articulate, long, narrow, rigid, with median cross-laminar ridge or spur and concave in basal half forming a nectary with concave column foot and connate lateral sepals; rostellum protruding, acute and rigid; pollinia oblong-orbicular, bright yellow. Other species in this major grouping cluster into two separate clades. One contains *D. inflatum*, *D. mutabile* and *D. sanguinolentum* while the second comprises *D. camptocentrum, D.* aff. *crocatum, D. ionopus* and *D. cerinum.* Apart from *D. platygastrium*, all the other species have been treated as part of the poorly understood and often overlooked *D.* section *Calcarifera* (Smith 1908, Comber 1990, 2001, Lavarack et al. 2000), which is characterised by possession of flowers with a long mentum directed away from the pedicel and ovary; a moderately wide labellum that narrows abruptly towards the base where adnate to the column foot for most of its length and with a small protuberance on the upper surface. In comparison, although superficially florally similar *D. platygastrium* is a member of section *Platygastrium*, so called because of the characteristic flattened, compressed pseudobulbs. There is an historical link within this entire major grouping.

Blume (1825) when describing *Pedilonum* considered it distinct from *Dendrobium* by the absence of an articulate labellum and with flowers with a slipper shaped labellum, dividing the six species in the genus into two sections. The second of these two sections which was distinguished by lateral sepals forming an elongate spur often adnate to the labellum claw, contains *P. secundum* as well as *P. undulatum*, *P. biflorum* and *P. erosum*. Two of these species, *P. undulatum* (as *D. hymenophyllum*) and *P. biflorum* (as *D. gemellum*), have since been transferred to *Dendrobium* and are now treated as members of section *Calcarifera* (Comber 1990, 2001) so Blume's interpretation of presumed relationships between this group of species perhaps has some basis. Blume (1825) also described *Onychium lamellatum*, with its characteristic laterally flattened pseudobulbs. This species has since been transferred to *Dendrobium* (Lindley, 1830) as well as designated as the type of *Dendrobium* section *Platycaulon* (Schlechter 1905), with close affinities to section *Eugenanthe* (Schlechter 1912) Opinions are divided on how to treat this group of species. It has been variously maintained in *D.* section *Platycaulon* (Kraenzlin 1910, Comber 1990, 2001, Lavarack et al. 2000), in *D.* section *Calcarifera* (Wood & Cribb 1994), transferred the genus to *Pedilonum* (Brieger 1981), or incorporated within *D.* section *Pedilonum* (Seidenfaden 1985, 1992, 1997, Seidenfaen & Wood 1992). Comber (2001) recently suggested that the only difference between *D. lamellatum* and species in section *Calcarifera* is the vegetative character of flattened stems. In these ITS sequence analyses *D. platygastrium* groups with species possessing flowers with a long narrow mentum that is adnate to the column foot in the basal half, rather than those species with a similarly inflated mentum and labellum attached only at the base of the column foot. *Dendrobium platygastrium* and its relatives also lack any form of basal protuberance on the labellum. Presence of a representative of this section

in this clade does, however, render section *Calcarifera* paraphyletic. All these data provide a framework for the recognition of the separate sections *Platycaulon-Calcarifera* as distinct from the first group of section *Calcarifera*. Furthermore, whilst there is very strong support for these two individual *Calcarifera* groups (100% and 95% bootstrap support), there is by comparison only poor support for the recognition of these two groups as sister taxa.

The remaining species in this major grouping, *D. mutabile, D. sanguinolentum* and *D. inflatum*, which have also been considered part of *Calcarifera* (Comber 2000), are clearly separated in a well-supported clade (100% bootstrap support). Historically, these species were described by Blume (1825) in the illegitimate genus *Onychium* and then transferred to *Dendrobium* (Lindley 1830). Blume's description of *Onychium* agrees closely with Smith's concept of section *Calcarifera* and two of the species originally described in *Onychium*, namely *O. mutabile and O. nudum* (similar to *D. inflatum*), have since been transferred to this section. Characteristically, this group of species have flowers with an inflated spur; a more membranous labellum that is more or less continuous with the base of the column foot forming a short nectiferous spur; and uniformly obovate-elongate pollinia. Interestingly, the pollinia differ significantly from those found in representatives of the first described group in *Calcarifera*, where they are irregularly shaped, undulate structures. These data together suggest that *Calcarifera* is not a monophyletic group in its current form and that these various elements of the group are deserving of higher taxonomic status separate from that of *Pedilonum*.

Fourth major group: The fourth major group contains a single species, *D. thysiflorum*, representative of a group of species commonly referred to section *Callista* (Reichenbach, 1868, Schlechter 1912, Seidenfaden 1985) or as a separate genus *Callista* (Kraenzlin 1910, Brieger 1981) The genus *Callista* was described by Loureiro (1790) and predates *Dendrobium* by nine years. One consequence of the amalgamation of many genera into *Dendrobium* and recognition by Reichenbach (1868) that *Callista* was synonymous with it, was that by the rules of the International Code of Botanical Nomenclature (ICBN), *Callista* had priority over *Dendrobium*. It was on this basis that Kuntze (1891) automatically transferred most species described in *Dendrobium* to *Callista.* To counteract this, a decision was made at the Second International Botanical Congress to conserve *Dendrobium*. All of this of course is based on the assumption that *Callista* is part of *Dendrobium*, which is easy to understand considering the similarity of floral morphology between species in the two groups. However, on the basis of the results generated in these ITS studies, where *Callista* is separated from *Dendrobium* sens. str. by the third major group containing morphologically disparate species, it would appear that these perceived similarities are yet another example of convergent evolution within the Dendrobieae, or that the floral similarities are symplesiomorphic. Apart from floral morphology, *Callista* is characterised by the possession of erect, angular, fusiforme, pseudobulbous stems, coriaceous, terminal to subterminal leaves, and development of the inflorescence as though being extruded like paste from the original stem bud. Furthermore, in broader based studies the addition of sequences obtained from four morphologically similar species considered part of this group, *D. amabile* (the type species for *Callista*), *D. griffithianum* and *D. palpebrae*, confirmed the group was a strongly supported monophyletic taxon well isolated from *D.* section *Dendrobium*. The combined characteristics of *Callista* enunciated above coupled with its isolated position in these ITS sequence analyses results, provides good evidence that Loureiro's original concept should again be adopted.

Fifth major group: Species in the fifth major group form a strongly supported clade (100% bootstrap support) isolated from the remainder of the ingroup. Within this major grouping are two subgroups, only one of which is strongly supported (98%

bootstrap support) In the strongly supported subgroup, *D. leonis*, *D. aloifolium*, *D. indivisum* and *D. anceps* have been treated by most authors as the genus *Aporum* (Blume 1825, Lindley 1830, 1847, Pfitzer 1889, Brieger 1981) or as section *Aporum* (Lindley 1851, Reichenbach 1861, Bentham & Hooker 1883) or subgenus *Aporum* (Kraenzlin 1910) within *Dendrobium*. *Dendrobium aloifolium* was also originally described by Blume (1825) in the monotypic genus *Macrostomium* while *D. anceps* was treated as the type for another monotypic genus *Ditulima* (Rafinesque 1836). In contrast to these four species, *D. confusum* belongs to an assemblage of species treated under the sectional name *Strongyle* (Smith 1905, Seidenfaden 1985), first devised by Lindley (1851) to account for those species within *Dendrobium* possessing terete leaves. The similarities between species in section *Aporum* and *Strongyle* had been noted by Schlechter (1912) who treated the latter as a part of *Aporum*. Despite some diversity in the origins of the inflorescence and floral morphology, the group is held together on its vegetative characters, in particular: possession of equitant leaves; lack of any form of thickening of the ensheathed wiry stems; production of persistent, compact, lateral and terminal inflorescences with persistent indeterminate meristematic regions from which are generated single (occasionally multiple) flowers. Possession of these common characters and the fact that all these representative species are embedded within a single tight cluster suggests they should be treated as representative of a single taxon, the earliest and most commonly applied generic or sectional name being *Aporum*.

In the second (although poorly supported) subgroup within the fifth major group, all but *D. quadrangulare* have been treated either in the section or subgenus *Crumenata* (Pfitzer 1889, Kraenzlin 1910), or in the (more widely used name) section *Rhopalanthe* in *Dendrobium* (Schlechter 1912, Seidenfaden 1985), or as a component of *Aporum* (Brieger 1981). By comparison, *Dendrobium quadrangulare* is a representative of *D.* section *Bolbidium* (Schlechter 1912, Seidenfaden 1985). In Schlechter's system of classification of the Dendrobiinae, section *Bolbidium* was placed in the first subgenus *Anthecebium* well removed from the third subgenus *Rhopalobium* that contained *D. crumenata*. No species in this group has previously been considered to be closely related to section *Pedilonum*. Careful study of the two subgroups identified by these ITS sequence analyses reveals that although they appear to represent groups of species with different gross vegetative characteristics they nevertheless share many features. For example, the equitant leaf habit common to all species in the first subgroup, section *Aporum*, is also present in species such as *D. goldfinchii* and *D. philippinense* in the second subgroup. A persistent inflorescence covered in the persistent remains of successive floral bracts, and containing an indeterminate meristem that permits the successive production of flowers from the same point on the stems, is however common to all species in the fifth major group. All species in the second, poorly supported subgroup are also united by the common possession of one to several swollen, near-basal, leafless internodes. For those representative species possessing one to several swollen, near basal leafless internodes, the vegetative form varies from the crassulate duplicate two leaved form found in *Bolbidium*, to the conduplicate thin leaves of *D. truncatum*, the thicker multi-leaved stems of *D. crumenatum*, the rigid, terete leaves of *D. junceum* and *D. usteroides*, to the flattened equitant leaves of *D. goldfinchii* and *D. philippinense*. Possession of these features was also noted previously when Loureiro (1790) described *Ceraia simplissisima*, which predates the description of *Dendrobium* by nine years.

Although the type specimen of *Ceraia simplissisima* now lacks any floral material, it is undoubtedly representative of a group of species similar to *D. crumenatum*. Brieger (1981) recognised these differences as significant and raised the taxon to generic rank. Schlechter (1912) also created the solitary section *Rhopalanthe* in his subgenus *Rhopalobium* within *Dendrobium*, for those species with pseudobulbs or stems

thickened on 1–3 internodes only. In so doing he recognised its affinities with *Aporum* and proposed the subsection name *Aporopsis* to accommodate the species with equitant leaves that he was about to describe as distinct from *D. crumenatum* (which has conduplicate leaves and undoubtedly considered by him typical of the subgenus). The affinities of vegetative morphology aside, species in the whole group are characterised by the near-membranous flowers which last only one to several days and synchronous flowering habit; the broad, membranous, concave column foot, very short column, and the thin, spreading labellum with a broadly lobed apex. Also embedded within this general group is *D. quadrangulare*, which is representative of *D.* section *Bolbidium* (Lindley 1850), *D*. subgenus *Bolbidium* (Kraenzlin, 1910 (although he included a large number of *Cadetia* species in the taxon)), *D.* subgenus *Athecebium* section *Bolbidium* (Schlechter 1912) and *Bolbidium* (Brieger 1981). With *Bolbidium* embedded deeply within the whole group, Schlechter's concept of subgenus *Rhopalobium* is rendered paraphyletic. Recognition of *Bolbidium* at the generic rank, such as has been proposed by Brieger (1981), would seem premature on the basis of these ITS sequence analyses results. If additional studies using a greater range of species representatives of the various groups were to establish that *Bolbidium* needed to be treated as a separate genus, it would necessitate the acceptance of at least three other genera including *Ceraia*. If we apply a broader generic concept to this group as a whole, then the first available name is *Ceraia*, despite the uncertainties surrounding the determination of the species described as the type. Either scenario necessitates the re-recognition of the genus *Ceraia*, as distinct from *Dendrobium*, something both the molecular results and morphological data strongly support. There is one further piece of information concerning the group as a whole. All species in this major group, studied to date, including those referred to the subgroup *Aporum*, are also defined by possession of an isobilateral protocorm (Clements 2000), a feature known to be absent from the remainder of the Asian clade. Although further research is clearly needed using a greater range of species, possession of the defining characters and isolation of the group in these ITS results, provides a strong basis for the re-instatement of the group as a whole and recognition of at least two genera therein.

Sixth major group: The sixth major group is strongly supported (99% bootstrap support) and represents a complex of taxa with many different vegetative and floral forms. Historically most species in the complex have been placed in at least ten different infrageneric taxa within *Dendrobium*, including section *Pedilonum* or those sections considered closely related to it, e.g. *Calyptrochilus*, *Cuthbertsonia* and *Oxyglossum* (Schlechter 1912, Brieger 1981, Reeve & Wood 1989). Since the type of *Pedilonum* (*D. secundum*) is isolated in the third major group in these analyses, it is apparent that *Pedilonum* as taditionally defined, is entirely artificial. Isolated at the base of the sixth major group is a clade containing *D. lancifolium.* This species is characterised by possession of a cluster of thin stems with lanceolate, grape-like leaves and has short lateral or terminal inflorescences of one to a few pink flowers. It has variously been included in section *Chrysantha* (Reichenbach 1861), subgenus *Pedilonum* section *Glomerata* and subgenus *Grastidium* section *Revoluta* (Kraenzlin 1910), or section *Calcarifera* (Schlechter 1925, van Bodegom 1973, O'Byrne 2001, Cootes 2001) of *Dendrobium*. Reichenbach's section *Chrysantha* is a renamed and expanded version of the ill-defined and often overlooked *Dendrobium* section *Holochrysa* of Lindley (1859). D*endrobium section Holochrysa* was first described to accommodate a small group of Indian species with 'stems on all sides leafy and flowers entirely yellow' but Reichenbach expanded its limits to cover many more species including *D. lancifolium* which has pink and white, rather than yellow, flowers. Most subsequent authors have never seriously considered using Reichenbach's system of classification for *Dendrobium* because it is confusing (Seidenfaden 1985). Kraenzlin (1910), in his much critised monograph of the Dendrobiinae, was clearly confused about the

relationship of *D. lancifolium* as he simultaneously included it as 'Species dubia' under *D.* subgenus *Pedilonum* section *Glomerata* and then again in *D.* subgenus *Grastidium* section *Revoluta*. Both taxa are highly artificial, containing species that, in more modern accounts of *Dendrobium*, are treated in many different taxa including some that are now recognised as representative of distinct genera such as *Grastidium sens. str*. (Clements & Jones 1998) and *Cannaeorchis* (Clements & Jones 1999). The non-monophyletic nature of section *Calcarifera* has been dealt with above and the isolation of the *D. lancifolium* group from those in the third major group in the present ITS results provides further evidence of the artificiality of that taxon. The isolation of *D. lancifolium* from any other subgroups of species in this major group suggests it should be recognised as a separate genus or infraheneric taxon,but further study is required. Clustered with *D. lancifolium* is *D.* aff. *rarum* from Vanuatu, a representative of section *Pedilonum*, and three species representative of *D.* section *Oxyglossum* (Schlechter 1912). Reeve and Woods (1989), in their revision of the group considered species belonging to sections *Oxyglossum* and *Cuthbertsonia*, on account of the overall similarity of floral features, should be amalgamated into a single taxon under the name *D.* section *Oxyglossum*. Results from the present ITS studies reveal the exact opposite, where *D. sophronites* and *D. agathodaemonis* are present in another arm of the sixth major group, rendering Reeve and Woods' concept of section *Oxyglossum* polyphyletic. There is, however, strong ITS and morphological support for the monophyly of the *Oxyglossum* group for which *D. cyanocentrum* is the type. These species are readily recognised by possession of short tapering pseudobulbs with a few terminal to subterminal leaves, and one- to multi-flowered inflorescences, multi-ribbed ovaries, and flowers with acute to acuminate segments including the labellum. In comparison, species in the *Cuthbertsonia* group possess, amongst other things, flowers with an obtuse labellum apex. *Dendrobium* aff. *rarum* possesses some floral features common to those found in section *Oxyglossum*, but differs in plant habit where the elongate, thinly pseudobulbous stems are semi-pendulous. The weak–moderate level of support for the inclusion of *D.* aff. *rarum* into section *Oxyglossum* suggests this presumed relationship needs further investigation.

All remaining species in the sixth major grouping fall into two weakly supported clades (bootstrap values below 50%), but with several strongly supported subgroups in each. The first of these weakly supported clades comprises *D. fairchildiae, D. papilio, D. serratilabium, D. goldschmidtianum, D. chameleon, D. ceruela, D. yeageri* and *D. victoriae-reginae,* in two strongly supported groups (96% and 100% bootstraps values). Ames and Quisumbing (1932) in describing *D. fairchildiae*, placed it in section *Calcarifera*w while *D. papilio* has been considered to have affinities to section *Virgatae* (Ames 1908), subgenus *Crumenata* (Kraenzlin 1910), section *Calcarifera* (Lavarack et al. 2000), and section *Dolichocentrum* (Cootes 2001). Only the last of these proposals are supported on the basis of these ITS sequence analyses. As indicated above, section *Calcarifera* was created by Smith (1908), when describing *D. pedicellatum*, and this species equates to the clade containing *D. mutabile, D. sanguinolentum* and *D. inflatum* in the third major grouping of these results. The treatment of *D. fairchildiae* as a member of section *Calcarifera* renders that section polyphyletic in the present analysis, and the relationship is clearly artificial. Section *Virgatae* (Hooker 1885) and the subgenus *Crumenata* are both roughly equivalent to section *Rhopalanthe* of Schlechter (1912) and contain species grouped together in the fifth major group of these ITS analyses, rendering that taxon paraphyletic. Cootes (2001), in assigning *D. papilio* to section *Dolichocentrum,* relied heavily on the similarities in both vegetative and floral morphology to those of *D. furcatum*, the type of the taxon, in particular the thin wiry stems with grass-like leaves, elongate spur formed through fusion of the base of the lateral sepals. The furthur addition of the vegetative and florally similar species, *D. auriculatum* and *D. miyasakii* seems logical. On the basis of these ITS results, the

treatment of section *Dolichocentrum* by Brieger (1981) as a separate genus seems premature and further research is needed to clarify its relationship with *D. fairchildiae* and similar species. A second strongly supported clade (96% bootstrap support) accounts for all remaining species in this sub grouping, *viz*. *D. serratilabium, D. goldschmidtianum, D. chameleon, D. ceraula, D. yargeri* and *D. victoriae-reginae*. Internally the clade is divided into two subgroups. Historically these species have variously been treated as: belonging to section *Dendrobium* (Reichenbach 1877), subgenus *Pedilonum* section *Revoluta* (Kraenzlin 1910); section *Pedilonum* (Williams 1937); section *Calcarifera* (Lavarack 2000, Cootes 2001); or remained unassigned to any particular taxon within *Dendrobium* (Schlechter 1919, Ames & Quisumbing 1931, Liu & Su 1978); or were treated as part of the genus *Pedilonum* (Rauschert 1984). In describing *D. ceraula* Reichenbach (1877) considered it belonged to *Dendrobium* presumably on account of possession of the clustered, lateral inflorescences. Species representative of *Dendrobium* are by necessity related to *D. moniliforme* the designated type of the genus. As shown in these ITS sequence analyses, *D. moniliforme* sits well away from the sixth major group so its presumed alliance with species in this grouping is entirely artificial. As stated earlier, *Pedilonum* is polyphyletic with the type within the third major group, well-isolated from *D. ceraula* and other presumed members of the taxon. Furthermore, the inclusion of *D. goldschidtianum* renders this group paraphyletic. Cootes (2001) treated *D. serratilabium, D. chameleon, D. ceraula, D. yargeri* and *D. victoriae-reginae* in section *Calcarifera,* on account of the plants branching along the pseudobulb and their pendulous habit. Typical members of section *Calcarifera* are only present in one clade within the third major group identified in these ITS analyses. Treatment of this group of species in section *Calcarifera* again renders that taxon polyphyletic. Apart from similarities in plant habit, species in the group have an elongate, narrow labellum spur.

The remaining weakly supported group contains a mixture of strongly as well as weakly supported subgroups and isolated species, with some similarities in floral and vegetative morphology. Part of this group is a poorly supported clade (<50% bootstrap support) containing an isolated *D. capituliflorum* (with thickened canes, capitulate inflorescence, and rigid, concave cymbidiform labellum with an acute apex), and a strongly supported clade (100% bootstrap support) containing *D. cauliculimentum* and *D. rhododioides* (with a pendulous, much-branched habit, and flowers with thin texture). On the basis of these results, species in these two clades are representative of two distinct taxa, well isolated from the type of *Pedilonum*. Sister to the clade containing the proceeding three species is a chained lineage arm of the group with *D. morrisonii* and *D. smillieae* at the base. *Dendrobium smillieae*, with its distinctive large thickened elongate canes, bottlebrush-like inflorescences, and thick, rigid, concave cymbidiform labellum, was described as a separate genus, *Coelandria* (FitzGerald 1882) but typically is included within sections of *Dendrobium*, viz. section *Dendrocoryne* (Bentham 1873), or section *Pedilonum* (Schlechter 1912, Dockrill 1969, 1992, Lavarack et al. 2001). Results of these ITS sequence analyses do not support its continued placement within section *Pedilonum*, rather they support recognition as a separate genus *Coelandria*, which is the oldest available generic name for any taxon within the sixth major group. *Dendrobium morrisonii* has also been treated as a typical member of section *Pedilonum* (Lewis & Cribb 1989) but again these results do not support this proposal.

Dendrobium mohlianum and *D. lawesii* are typically treated as members of section *Calyptrochilus* on account of possession of highly visible colourful flowers with an elongate column foot pressed to the ovary, lateral sepals forming an elongated spur, and labellum adnate to the base of the column foot, and labellum apex in turned with lacerate margins. These species are representative of one of the most characteristic taxonomic groups within the Dendrobiinae, comprising over 70 species. Possession of these features coupled with the very strong molecular support for the clade adds

weight to the concept of their treatment as a separate taxon. This leaves a strongly supported clade containing *D. sophronites* and *D. agathodaemonis*; and three species – *D. fuligidum, D. nothofagicola* and *D. bracteosum*, that have been treated as members of section *Pedilonum*. Although clearly part of the broader (but weakly supported), major grouping, the true phylogenetic relationship of these three species awaits the study of additional species. What is clear however, is that this is yet another example of the polyphyly of section *Pedilonum*.

Aside from providing support for the overall taxonomic conclusions about the study taxa, there is also a suggestion of some biogeographical groupings within the study taxa. For example the clade containing *D. fairchildiae, D. papilio, D. serratilabium, D. mayakei, D. chameleon, D. ceruela, D. yargeri* and *D. victoriae-reginae* are all representative of species that are endemic to the Philippines and Taiwan. Likewise the remaining major elements of that same clade are all predominantly species found in the New Guinea region of Malesia. These groupings are suggestive of radiation from these regional centres, a feature not uncommon in other orchid genera, e.g. most genera in the tribe Diurideae (Jones & Clements 2001).

Conclusion

The overall results obtained in these ITS sequence analyses coupled with data on the morphology of study species, provides a basis for a clearer understanding of the phylogeny of a major part of the Dendrobiinae. At the broadest level, the present ITS results correlate strongly with those produced from analyses of *rbc*L and *mat*K chloroplast DNA sequences and chloroplast DNA restriction sites (Yukawa et al. 1993, 1996, 2000). This support confirms that a fundamental division exists within the Dendrobiinae into three separate major lineages, viz (i) *Epigeneium*, (ii) a predominantly Australasian group, and (iii) a predominantly Asian group. The isolation of *Dendrobium* section *Oxystophyllum* in the Eriinae is new, providing yet further strong evidence of the polyphyletic nature of the Dendrobiinae. Considering the constant recurrence of these three strongly supported clades in results in all molecular studies, it now seems appropriate and necessary to formally recognise these three distinct lineages of the Dendrobieae. Additionally these results provide evidence for the following: (i) that Brieger's interpretation of *Pedilonum* is polyphyletic; (ii) that the subsequent automatic transfer by Rauschert (1983) of most species to *Pedilonum*, and other genera within the Dendrobiinae, is not supported; (iii) that Blume's original concept of *Pedilonum* had merit; (iv) that Schlechter's concepts of sections *Oxyglossum*, *Calyptochilus* and *Cuthbertsonia* appear monophyletic, whereas his concept of section *Pedilonum* does not; (v) that Schelchter's interpretation of a close relationship between these four taxa, excluding the type of *Pedilonum*, was fundamentally sound; (vi) and that section *Calcarifera* defined by Smith (1908) and later authors is polyphyletic. Consequently these data provide evidence for the recognition and reinstatement of the long established genera *Ceraia* and *Pedilonum,* as well as the recognition of several other monophyletic groups at generic rank. Whilst in some authors' opinions the formal recognition of these monophyletic taxa at generic rank might seem premature, the strong body of molecular and morphological evidence from independent data sets and different sources of plant material provides ample support for the proposed reclassification of many of these taxa. In many cases this simply involves the elevation of infrageneric taxa ,but in other cases it involves the redefinition or description of these taxa. Recognition, at generic rank, of major monophyletic taxa within the Dendrobiinae, also provides a far more realistic framework for understanding phylogenies than exists at present. The alternative, of maintaining all these taxa within a greater *Dendrobium*, is not practical in terms of the complexities of classification now

required to account for all variation known to exist within this very large and diverse assemblage of species. Additionally, recognition of a broadly circumscribed *Dendrobium* would sink several well-established useful genera.

Appropriate formal taxonomic changes follow in Appendix 2. The present results have also identified complex areas requiring further research before their phylogeny and systematics can be fully enunciated.

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Appendix 1. Collection details of the species used for these analyses.

Species	Provenance	Collection No.	GenBank Accession No.
Adelopetalum bracteatum Fitzg.	cult. ex Qmo*; Queen Mary Falls NP	Crane 2138	AY239945
Bryobium pubescens Lindl.	cult. ex Christmas Island	Ziesing 307	AY239946
Bulbophyllum nutans Thouars	cult. ex Mauritius	Clements 8108	AY239947
Cadetia maideniana (Schltr.) Schltr.	cult. ex Qco*;	Jones 4311	AY239948
Cannaeorchis fractiflexa (A.Finet) M.A.Clem. Et D.L.Jones	cult. ex New Caledonia; Yaté Road	Clements 9348	AY239949
Dendrobium agathodaemonis J.J.Sm.	cult. ex Indonesia; Irian Jaya	Rose (S 926)	AY239950
Dendrobium aloifolium (Blume) Rchb.f.	cult. ex Thailand	Clements 9168	AY239951
Dendrobium amethystoglossum Rchb.f.	cult. ex Philippines	Cootes(ORG 1482)	AY239952
Dendrobium anceps Sw.	cult. ex Philippines	Clements 9309	AY239953
Dendrobium bracteosum Rchb.f.	cult. ex Papua New Guinea (PNG)	CBG 750451	AY239954
Dendrobium camptocentrum Schltr.	cult. ex New Caledonia	Clements 5830	AY239955
Dendrobium capituliflorum Rolfe	cult. ex PNG; Wassabamal	Clements 6319	AY239956
Dendrobium cauliculimentum R.S.Rogers	cult. ex PNG	ORG 3598	AY239957
Dendrobium ceraula Rchb.f.	cult. ex Philippines	ORG 2921	AY239958
Dendrobium cerinum Rchb.f.	cult. ex Philippines	Cootes (ORG 3585)	AY239959
Dendrobium chameleon Ames	cult. ex Philippines	ORG 3590	AY239960
Dendrobium confusum Schltr.	cult. ex PNG	Banks (ORG 1391)	AY239961
Dendrobium aff. *crocatum* Hook.f.	cult. ex Indonesia; Sumatra	Smedley s.n.	AY239962
Dendrobium crumenatum Sw.	cult. ex Thailand	Clements 4890	AY239963
Dendrobium cyanocentrum Schltr.	cult. ex PNG	Spence (Clements 8709)	AY239964
Dendrobium ellipstophyllum T.Tang et F.T. Wang	cult. ex Thailand	Banks (ORG 3581)	AY239965
Dendrobium fairchildiae Ames et Quisumb	cult. ex Philippines; Bukidnon	Cootes (Clements 1485)	AY239966
Dendrobium formosum Roxb. ex Lindl.	cult. ex Thailand	Phillips 457	AY239967
Dendrobium fulgidum Schltr.	cult. ex PNG	Banks (ORG 3599)	AY239968

* Abbreviations for Australian Botanical Districts: Nsc = New South Wales, South Coast; Qco = Queensland, Cook; Qmo = Queensland, Moreton.

ORG = Orchid Research Group.

CBG = Canberra Botanic Gardens (now the Australian National Botanic Gardens).

RBGS = Royal Botanic Gardens Sydney

Species	**Provenance**	**Collection No.**	**GenBank Accession No.**
Dendrobium goldfinchii F.Muell.	cult. ex PNG; Wassabamal	Clements 5860	AY239969
Dendrobium goldschmidtianum Kraenzl.	cult. ex Taiwan	ORG 3465	AY239970
Dendrobium govidjoae Schltr.	cult. ex PNG; Garassa	Clements 6810	AY239971
Dendrobium indivisum (Blume) Miq.	cult. ex Malaya; Langkawi	Vaughn (Clements 5822a)	AY239972
Dendrobium inflatum Rolfe	cult. ex Indonesia; Bali	Clements 5820	AY239973
Dendrobium ionopus Rchb.f.	cult. ex Philippines	Cootes (ORG 3589)	AY239974
Dendrobium junceum Lindl.	cult. ex Philippines	ORG 3588	AY239975
Dendrobium lancifolium A.Rich.	cult. ex Indonesia; Sulawesi	Clements 9176	AY239976
Dendrobium lawesii F.Muell.	cult. ex PNG	Spence D54	AY239977
Dendrobium leonis (Lindl.) Rchb.f.	cult. ex Thailand	ORG 1983	AY239978
Dendrobium macrophyllum A.Rich.	cult. ex Philippines?	Spence (Clements 8704)	AY239979
Dendrobium mohlianum Rchb.f.	cult. ex Fiji	ORG 3603	AY239980
Dendrobium moniliforme (L.) Sw.	cult. ex Japan	no collector 3544	AY239981
Dendrobium morrisonii Schltr.	cult. ex Vanuatu	Phillips 1069	AY239982
Dendrobium moschatum (Buch.-Ham.) Sw.	cult. ex Thailand	Clements 5808	AY239983
Dendrobium mutabile (Blume)	cult. ex Indonesia; Java	ORG 3608	AY239984
Dednrobium nindii W.Hill	cult. ex Qco*; Daintree River	Jones 4285	AY239985
Dendrobium nothofagicola T.M.Reeve	cult. ex PNG	ORG 3600	AY239986
Dendrobium papilio Loher	cult. ex Philippines	Cootes (Clements 9202)	AY239987
Dendrobium philippinense Ames	cult. ex Philippines	ORG 1499	AY239988
Dendrobium quadrangulare Parish & Rchb.f.	cult. ex Thailand	ORG 1277 (s#3500)	AY239989
Dendrobium aff. *rarum* Schltr.	cult. ex Vanuatu; Espirato Santo	Clements 5613	AY239990
Dendrobium rhododioides P.Royen	cult. ex PNG	ORG 3601	AY239991
Dendrobium sanguinolentum Lindl.	cult. ex Malaya;	Vaughn s.n.	AY239992
Dendrobium secundum (Blume) Lindl.	cult. ex Thailand	Clements 5377	AY239993
Dendrobium serratilabium	cult. ex Phillipines; Luzon, Laguna	Cootes & L.O.Williams (Clements 9180)	AY239994
Dendrobium sinuatum (Lindl.) Lindl. ex Rchb.f.	cult. ex Thailand;	ORG 3615	AY239995
Dendrobium smillieae F.Muell.	cult. ex Qco*; Captain Billy Ck	Jones 8795	AY239996
Dendrobium sophronites Schltr.	cult. ex PNG;	Spence s.n.	AY239997
Dendrobium speciosum Sm.	cult. ex Nsc*; Pidgeon House Mountain	Clements 5058	AY239998
Dendrobium stuartii F.M.Bailey	Qco*; Mt Finnigan	Roberts s.n.	AY239999

Species	**Provenance**	**Collection No.**	**GenBank Accession No.**
Dendrobium subuliferum Schltr.	cult. ex PNG; Torricelli Mts	Clements 9523	AY240000
Dendrobium thysiflorum Rchb.f.	cult. ex Thailand	Clements 5163	AY240001
Dendrobium truncatum Lindl.	cult. ex Malaya; Tamannegara	Vaughn (Clements 5806)	AY240002
Dendrobium usteroides Schltr.	cult. ex Philippines; Bulalacao	ORG 3000	AY240003
Dendrobium victoriae-reginae Loher	cult. ex Philippines	Cootes (ORG 1484)	AY240004
Dendrobium violaceum Kraenzl.	cult. ex PNG	ORG 3597	AY240005
Dendrobium yeageri . Ames et Quisumb	cult. ex Philippines	ORG 3580	AY240006
Diplocaulobium ischnopetalum (Schltr.) Kraenzl.	cult. ex PNG; near Lae	Clements 7270	AY240007
Dockrillia calamiformis (Lodd.) M.A.Clem. et D.L.Jones	cult. ex Qco*	ORG 3469	AY240008
Drymoanthus flavidus St.George et Molloy	New Zealand; Pounawea	Molloy 207/00	AY240009
Epigeneium amplum (Lindl.) Summerh.	cult. ex India	Banks s.n.	AY240010
Epigeneium cymbidioides (Blume) Summerh	cult. ex Indonesia; Java	Banks s.n. (ORG 3609)	AY240011
Epigeneium nakaharaei (Schltr.) Summerh	cult. ex Taiwan	Clements 9167	AY240012
Epigeneium triflorum (Blume) Summerh.	cult. ex Indonesia; Java	ORG 3591	AY240013
Eria aff. javanica (Sw.) Blume	cult. ex PNG	CBG 740854	AY240014
Flickingeria comata (Blume) A.Hawkes	cult. ex Qco*; Iron Range	Wrigley 354	AY240015
Grastidium baileyi (F.Muell.) Rasuchert	cult. ex Qco*	Jones 4165	AY240016
Liparis habenarina (F.Muell.) Benth.	cult. ex Qco*; Stony Creek	Roberts (ORG 2154)	AY240017
Oxysepala ovalifolia Wight	cult. ex Thailand	RBGS 810771	AY240018
Winika cunninghamii (Lindl.) M.A.Clem., D.L.Jones & Molloy	cult. ex New Zealand; Lincoln	Molloy 061/98	AY240019

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Appendix 2: Taxonomy

Some essential taxonomic and nomenclatural changes arising as a result of these analyses are provided as the next step towards the re-classification of this scientific, horticultural and commercially important group within the Orchidaceae.

Tribe: Podochileae Pfitz., *Entw. Nat. Anord. Orch.* 101 (1887) (as 'Podochilinae').

Type: *Podochilus* Blume

Subtribe: Eriinae Benth., *J. Linn. Soc., Bot.* 18: 287 (1881).

Type: *Eria* Lindl.

Oxystophyllum Blume, *Bijdr.* 335–336 (20 Sep–7 Dec 1825).

Type species: *Oxystophyllum rigidum* Blume, *vide* Brieger (1981).

Dendrobium Sw. sect. *Oxystophyllum* (Blume) Miq., *Fl. Ind. Neerl. Bat.* 3: 644 (1855).

Dendrobium Sw. subg. *Aporum* (Blume) Kraenzl. sect. *Holophylla* Karenzl. in Engl., *Pflanzenr. Orch.-Mon.-Dendr.* 1: 201, 203–204 (1910), *pro parte min*.
Type species: not designated.

Aporum Blume sect. *Oxystophyllum* (Blume) Brieger, *Schltr. Die Orchideen* 3, Aufl. 1: 670, 676 (1981).

Epiphytic, erect, reptant to pendulous herbs. Roots thin, wiry, hirsute, rusty brown, the growing apex purplish, arising from the base or from internodes along the stem. Stem thin, flexible, covered with equitant leaf sheath. Leaves equitant, rigid, falcate to lanceolate, with abscission layer towards base, apex sharply acute. Inflorescence simple or compound, compressed raceme, lateral or terminal, equitant, indeterminate, the solitary flowers arising intermittently from the developing raceme; floral bracts persistent and often forming dense tufts. Flowers with sombre colours and thick, fleshy and rigid, with short, acute dorsal sepal and petals, the larger lateral sepals adnate to column-foot forming a saccate base with the labellum. Labellum ligulate, on a short hinge, thick fleshy, and secreting sticky fluids on upper surface. Column very short and with a long, broad curved column-foot. Pollinia 4 in two separate sets of 2, small, irregularly shaped, pinkish cream, and with prominent caudicles.

Distribution: South-East Asia and Malesia as far east as the Solomon islands.

Oxystophyllum acianthum (Schltr.) M.A.Clem., ***comb. nov***.
Basionym: *Dendrobium acianthum* Schltr., *Repert. Spec. Nov. Regni Veg.,* Beih. 1: 572–572 (1912).

Oxystophyllum ambotiense (J.J.Sm.) M.A.Clem., ***comb. nov***.
Basionym: *Dendrobium ambotiense* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 9: 466–467 (1928).

Oxystophyllum araneum (J.J.Sm.) M.A.Clem., ***comb. nov***.
Basionym: *Dendrobium araneum* J.J.Sm., *Repert. Spec. Nov. Regni Veg.* 12: 397 (1913).

Oxystophyllum atropurpureum Blume, *Rumphia* 4: 41. t. 193. f. 4; 198 f. C (1858); *Dendrobium atropurpureum* (Blume) Miq., *Fl. Ind. Bat.* 3: 644 (1855).

Oxystophyllum atrorubens (Ridl.) M.A.Clem., ***comb. nov***.
Basionym: *Dendrobium atrorubens* Ridl., *J. Linn. Soc., Bot.* 32: 247 (1896).

Oxystophyllum bipulvinatum (J.J.Sm.) M.A.Clem., ***comb. nov***.
Basionym: *Dendrobium bipulvinatum* J.J.Sm., *Repert. Spec. Nov. Regni Veg.* 12: 397 (1913).

Oxystophyllum buruense (J.J.Sm.) M.A.Clem., ***comb. et stat. nov***.
Basionym: *Dendrobium excavatum* (Blume) Miq. var. *buruense* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 9: 466 (1928).

Oxystophyllum capitellatum M.A.Clem., ***nom. nov***.
Basionym: *Dendrobium capitellatum* Kraenzl. in Engl., *Pflanzenr. Orch.-Mon.-Dendr.* 1: 215 (1910), non J.J.Sm. (1906).

Oxystophyllum carnosum Blume, *Bijdr.* 335 (1825); *Dendrobium carnosum* (Blume) Rchb.f. in Walp., *Ann. Bot.* 6: 280 (1861), non Presl. (1827), nec Teijsm. et Binn. (1853).

Oxystophyllum changiiangense (S.J.Cheng et C.Z.Tang) M.A.Clem., ***comb. nov***.
Basionym: *Dendrobium changiiangense* S.J.Cheng et C.Z.Tang, *Acta Phytotax. Sin.* 18(1): 98–99, f. (1980).

Oxystophyllum cultratum (Schltr.) M.A.Clem., ***comb. nov***.
Basionym: *Dendrobium cultratum* Schltr., *Repert. Spec. Nov. Regni Veg.* 10: 71–72 (1911).

Oxystophyllum cuneatipetalum (J.J.Sm.) M.A.Clem., ***comb. nov***.
Basionym: *Dendrobium cuneatipetalum* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 9: 157–159 (1927).

Oxystophyllum deliense (Schltr.) M.A.Clem., ***comb. nov***.
Basionym: *Dendrobium deliense* Schltr., *Repert. Spec. Nov. Regni Veg.* 11: 143 (1912).

Oxystophyllum elmeri (Ames) M.A.Clem., ***comb. nov***.
Basionym: *Dendrobium elmeri* Ames in Elmer, *Leafl. Philipp. Bot.* 5: 1573 (1912).

Oxystophyllum excavatum Blume, *Bijdr.* 335 (1825); *Dendrobium excavatum* (Blume) Miq., *Fl. Ind. Bat.* 3: 644 (1855).

Oxystophyllum floridanum (Guillaumin) M.A.Clem., ***comb. nov***.
Basionym: *Dendrobium floridanum* Guillaumin, *Bull. Mus. Hist. Nat. Paris* (ser. 2), 37: 199 (1965).

Oxystophyllum govidjoae (Schltr.) M.A.Clem., ***comb. nov***.
Basionym: *Dendrobium govidjoae* Schltr., *Repert. Spec. Nov. Regni Veg.,* Beih. 1: 572 (1912).

Oxystophyllum hagerupii (J.J.Sm.) M.A.Clem., ***comb. nov***.
Basionym: *Dendrobium hagerupii* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 5: 78–79 (1922).

Oxystophyllum helvolum (J.J.Sm.) M.A.Clem., ***comb. nov***.
Basionym: *Dendrobium helvolum* J.J.Sm., *Bot. Jahrb. Syst.* 48: 99 (1912).

Oxystophyllum hypodon (Schltr.) M.A.Clem., ***comb. nov***.
Basionym: *Dendrobium hypodon* Schltr., *Repert. Spec. Nov. Regni Veg.* 8: 502 (1910); *Aporum hypodon* (Schltr.) Rauschert, *Feddes Repert.* 94(7–8): 440 (1983).

Oxystophyllum kaudernii (J.J.Sm.) M.A.Clem., ***comb. nov***.
Basionym: *Dendrobium kaudernii* J.J.Sm, *Svensk Bot. Tidskr.* 20: 475–477 (1927).

Oxystophyllum lepoense (Schltr.) M.A.Clem., ***comb. nov***.
Basionym: *Dendrobium lepoense* Schltr., *Repert. Spec. Nov. Regni Veg.* 9: 285–286 (1911).

Oxystophyllum lockhartioides (Schltr.) M.A.Clem., ***comb. nov***.
Basionym: *Dendrobium lockhartioides* Schltr., *Repert. Spec. Nov. Regni Veg.* 8: 507 (1910).

Oxystophyllum longipecten (J.J.Sm.) M.A.Clem., ***comb. nov***.
Basionym: *Dendrobium longipecten* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 10: 61–62 (1928).

Oxystophyllum minutigibbum (J.J.Sm.) M.A.Clem., ***comb. nov***.
Basionym: *Dendrobium minutigibbum* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 2), 13: 3 (1914).

Oxystophyllum moluccense (J.J.Sm.) M.A.Clem., ***comb. nov***.
Basionym: *Dendrobium moluccense* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 2), 13: 11 (1914).

Oxystophyllum nitidiflorum (J.J.Sm.) M.A.Clem., ***comb. nov***.
Basionym: *Dendrobium nitidiflorum* J.J.Sm., *Repert. Spec. Nov. Regni Veg.* 12: 396 (1913).

Oxystophyllum oblongum (Ames et C.Schweinf.) M.A.Clem., ***comb. nov***.
Basionym: *Dendrobium oblongum* Ames et C.Schweinf., *Orchidaceae* 6: 108 (1920).

Oxystophyllum oligadenium (Schltr.) M.A.Clem., ***comb. nov***.
Basionym: *Dendrobium oligadenium* Schltr., *Repert. Spec. Nov. Regni Veg.* 8: 502–503 (1910).

Oxystophyllum paniferum (J.J.Sm.) M.A.Clem., ***comb. nov***.
Basionym: *Dendrobium paniferum* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 2), 14: 34 (1914).

Oxystophyllum rigidum Blume, Bijdr. 336 (1825); *Dendrobium rigidum* (Blume) Miq., *Fl. Ind. Neerl. Bat.* 3: 644 (1859), *nom illeg*., non R.Br. (1810), *nec* Lindl. (1830); *Aporum rigidum* (Blume) Brieger, *Schltr., Die Orchideen* 3, Aufl. 1: 676 (1981).

Oxystophyllum sinuatum (Lindl.) M.A.Clem., ***comb. nov***.
Basionym: *Aporum sinuatum* Lindl., *Edwards' Bot. Reg. 27;* Misc. 3 (1841).

Oxystophyllum speculigerum (Schltr.) M.A.Clem., ***comb. nov***.
Basionym: *Dendrobium speculigerum* Schltr., *Repert. Spec. Nov. Regni Veg.* 8: 507–508 (1910).

Oxystophyllum subsessile (Schltr.) M.A.Clem., ***comb. nov***.
Basionym: *Dendrobium subsessile* Schltr., *Repert. Spec. Nov. Regni Veg.* Beih. 1: 571–572 (1912).

Oxystophyllum torricellianum (Kraenzl.) M.A.Clem., ***comb. nov***.
Basionym: *Dendrobium torricellianum* Kraenzl. in Engl., *Pflanzenr. Orch.-Mon.-Dendr.* 1: 215–216 (1910), *nom.*; *Aporum torricellianum* (Kraenzl.) Rauschert, *Feddes Repert.* 94(7–8): 442 (1983). *Dendrobium atrorubens* Schltr. in K.Schum. et Lauterb., *Nachtr. Fl. Deutsch. Südsee* 175 (1905), *nom. illeg*. non Ridl. (1896); *Dendrobium simile* Schltr., *Repert. Nov. Spec. Regni Veg.* 3: 80 (1906), *nom. illeg.*, non Schltr. (1905).

Oxystophyllum tropidoneuron (Schltr.) M.A.Clem., ***comb. nov***.
Basionym: *Dendrobium tropidoneuron* Schltr., *Bot. Jahrb. Syst.* 45, Beibl. 104, 32 (1911).

Oxystophyllum tumoriferum (J.J.Sm.) M.A.Clem., ***comb. nov***.
Basionym: *Dendrobium tumoriferum* J.J.Sm., *Bull. Dep. Agric. Indes Néerl.* 39: 11 (1910).

Oxystophyllum validipecten (J.J.Sm.) M.A.Clem., ***comb. nov***.
Basionym: *Dendrobium validipecten* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 10: 59–60 (1928).

Tribe: Dendrobieae Endl., *Gen. Pl.* 190 (1837).
Type: *Dendrobium* Sw.

Subtribe: Epigeneiinae M.A.Clem., ***subtribus nov***.

Dendrobiinis affinis, sed *Bulbophylli* et *Coelogyne* habitu; pseudobulbis turgidis uninodis, aggregatis vel repenti rhizomati separato; pseudobulbis terminalibus foliis 1–3; inflorescentia terminali, uni- vel multi-flora; petalis latera columnae adnatis; mento prominenti, differt.

Type: *Epigeneium* Gagnep. **(here designated)**

Plants epiphytic or lithophytic; stems rhizomatous terminating in a single internode pseudobulb; leaves conduplicate, coriaceous,1–3, terminal; inflorescence subterminal, determinate, single or mutli-flowered, erect or pedant, arising from a prominent erect, imbricate bract; flowers long-lasting, with spreading segments, non-articulate labellum, a prominent long column-foot, petals obliquely attached for greater part or not, glabrous elongate column, with prominent apical often ornate anther attachment.

Distribution: The subtribe comprises one genus distributed throughout South-East Asia and much of the Malaya archipelago.

Note: A full account of the subtribe is in preparation. For further details of the genera *Epigeneium* and *Katherinea* A.D.Hawkes, see Balakrishnan and Chowdhury (1966) and Garay and Romero-Gonzalez (1999).

Subtribe: Grastidiinae M.A.Clem., ***subtribus nov***.

Dendrobiinis affinis sed caulibus vel praecipue durobaculoidibus vel pseudobulbis elongatis et duris; inflorescentia racemosa laterali vel subterminali, abbreviata vel prolongata, uni- vel multi-flora; labello articulato, raro pedi columnae adnato; protocormis discoidis vel globosis, raro late isobilateralibus, differt.

Type: *Grastidium* Blume. **(here designated)**

Terrestrial, lithophytic or epiphytic herbs. Stems comprising one to many internodes, hard, wiry, slender or forming pseudobulbs, indeterminate or determinate. Leaves distichous, duplicate, ligulate, terete or sagittate, articulate, with or without sheaths at base. Inflorescence, lateral or pseudoterminal, usually upper axillary, racemose, rarely paniculate. Flowers solitary, in pairs or numerous, ephemeral, or lasting a few days to several weeks, resupinate or non-resupinate, conspicuous. Sepals, laterals dissimilar to dorsal. Petals similar. Labellum showy, trilobed, sometimes obscurely so, articulate, or fused at base to column-foot, with central callus ridges. Column elongate or short, glabrous, entire. Anther fleshy, glabrous. Pollinia hard, waxy, glabrous, four, in two pairs appressed together. Protocorms discoid or globose rarely isobilateral-globose.

Distribution: Genera in the subtribe are distributed mainly in Australasia and Malesia with a small number of representative species reaching the Asian mainland.

Note: The Grastidiinae comprises the following genera and for most the taxonomy and nomenclature has been dealt with preliminarily elsewhere. A full account of all taxa within these genera based primarily on the results of molecular analyses of ITS sequence data is in preparation.

Abaxianthus M.A.Clem. et D.L.Jones, *Orchadian* 13(11): 485 (2002).
Type species: *Desmotrichum convexa* Blume.

Australorchis Brieger in Schltr., *Die Orchideen* 1(11–12): 741 (1981).
Type species: *Australorchis monophylla* (F.Muell.) Brieger (= *Dendrobium monophyllum* F.Muell).

Bouletia M.A.Clem. et D.L.Jones, *Orchadian* 13(11): 485 (2002).
Type species: *Dendrobium finetianum* Schltr.

Cadetia Gaud. in Freycinet, *Voy. Uranie* 422, t. 33 (1826 [Sept. 1829]).
Type species: *Cadetia umbellatum* Gaud.

Cannaeorchis M.A.Clem. et D.L.Jones, *Lasianthera* 1(3): 132 (1998).
Type species: *Dendrobium fractiflexum* Finet.

Cepobaculum M.A.Clem. et D.L. Jones, *Orchadian* 13(11): 486 (2002).
Type species: *Dendrobium canaliculatum* R.Br.

Ceratobium (Lindl.) M.A.Clem. et D.L.Jones, *Orchadian* 13(11): 486 (2002).
Type species: *Dendrobium antennatum* Lindl.

Davejonesia M.A.Clem*, Orchadian* 13(11): 487 (2002).
Type species: *Dockrillia lichenastra* (F.Muell.) Brieger.

Dendrobates M.A.Clem. et D.L. Jones, *Orchadian* 13(11): 487 (2002).
Type species: *Dendrobium virotii* Guillaumin.

Dichopus Blume, *Mus. Bat.* 2: 176 (1856).
Type species: *Dichopus insignis* Blume.

Diplocaulobium (Rchb.f.) Kraenzl., *Pflanzenreich Orch.-Mon.-Dendr.* 45: 331 (1910).
Type species: *Diplocaulobium nitidissimum* (Rchb.f.) Kraenzl. (= *Dendrobium nitidissimum* Rchb.f.).

Dockrillia Brieger, *Schltr., Die Orchideen* 3(1): 745 (1981).
Type species: *Dendrobium linguiforme* Sw.

Durabaculum M.A.Clem. et D.L. Jones, *Orchadian* 13(11): 487 (2002).
Type species: *Dendrobium undulatum* R.Br.

Eleutheroglossum (Schltr.) M.A.Clem. et D.L. Jones, *Orchadian* 13(11): 489 (2002).
Type species: *Dendrobium eleutheroglossum* Schltr.

Eriopexis (Schltr.) Brieger, *Schltr., Die Orchideen* 3 (1): 656 (1981).
Type species: *Dendrobium eriopexis* Schltr. (= *Eriopexis schlechteri* Brieger).

Euphlebium (Kraenzl.) Brieger, *Schltr., Die Orchideen* 3(1): 722 (1981).
Type species: *Dendrocolla spurium* Blume.

Exochanthus M.A.Clem. et D.L. Jones, *Orchadian* 13(11): 496 (2002).
Type species: *Dendrobium pleianthum* Schltr.

Flickingeria A.Hawkes, *Orchid Weekly* 2(46): 451 (6 Jan. 1961).
Type species*: Desmotrichum angulatum* Blume (= *Flickingeria angulata* (Blume) A.D.Hawkes), a substitute name for *Desmotrichum* Blume 1825 (*nom. rej*.), non Kuetzing 1845 (*nom. cons*.).

Grastidium Blume, *Bijdr.* 7: 333 (1825).
Type species: *Grastidium salaccense* Blume.

Herpethophytum (Schltr.) Brieger, *Schltr., Die Orchideen* 1(11–12): 660 (July 1981).
Type species: *Herpethophytum schlechteri* S. Rauschert, (= *Dendrobium herpethophytum* Schltr.).

Inobulbum (Schltr.) Schltr. et Kraenzl. in Engl. *Pflanzenreich, Orch.-Mon.-Dendr.* 1: 316 (1910).
Type species: *Inobulbum muricatum* (Finet) Kraenzl. (= *Dendrobium muricatum* Finet).

Kinetochilus (Schltr.) Brieger, *Schltr., Die Orchideen* 1(11–12): 686 (July 1981).
Type species: *Kinetochilus pectinatus* (Finet) Brieger (= *Dendrobium pectinatum* Finet).

Leioanthum M.A.Clem. et D.L. Jones, *Orchadian* 13(11): 490 (2002).
Type species: *Dendrobium biflace* Lindl.

Microphytanthe (Schltr.) Brieger, *Schltr., Die Orchideen* 3(1): 742 (1981).
Type species: *Dendrobium bulbophylloides* Schltr.

Monanthos (Schltr.) Brieger, *Schltr., Die Orchideen* 3(1): 660 (1981) (as '*Monanthus*').
Type species: *Monanthos biloba* (Lindl.) Brieger (= *Dendrobium bilobum* Lindl.).

Sarcocadetia (Schltr.) M.A.Clem. et D.L. Jones, *Orchadian* 13(11): 490 (2002).
Type species: *Cadetia funiformis* (Blume) Schltr.

Sayeria Kraenzl., *Ost. Bot. Zeitsch*. 44: 257–59 (1894).
Type: *Sayeria paradoxa* Kraenzl.

Stelbophyllum M.A.Clem. et D.L. Jones, *Orchadian* 13(11): 490 (2002).
Type species: *Dendrobium toressae* F.M.Bailey.

Tetrabaculum M.A.Clem. et D.L. Jones, *Orchadian* 13(11): 490 (2002).
Type species: *Dendrobium tetragonum* A.Cunn.

Tetrodon (Kraenzl.) M.A.Clem. et D.L.Jones, *Orchadian* 12(7): 310 (1998).
Type species: *Eria oppositifolia* Kraenzl. (= *Dendrobium oppositifolium* (Kreanzl.) N. Hallé***.***

Thelychiton Endl., *Prod. Fl. Norf.* 32 (1833).
Type species: *Thelychiton macropus* Endl.

Trachyrhizum (Schltr.) Breiger, *Die Orchideen* 3(1): 687 (1981).
Type species: *Dendrobium chalmersii* F. Muell.

Tropilis Rafin., *Fl. Tell.* 2: 95 (1837).
Type species: *Dendrobium aemulum* R.Br. (= *Tropilis emulum* (R.Br.) Rafin.).

Vappodes M.A.Clem. et D.L. Jones, *Orchadian* 13(11): 492 (2002).
Type species: *Dendrobium bigibbum* Lindl.

Winika M.A.Clem., D.L.Jones et Molloy, *Orchadian* 12(5): 214 (1997).
Type species: *Dendrobium cunninghamii* Lindl.

Subtribe: Dendrobiinae Lindl., *Gen. Sp. Orch. Pl.* 45 (1830) (as Section II. Dendrobieae).
Type: *Dendrobium* Sw., *fide* Butzin (1971: 323).

First major group

Distichorchis M.A.Clem. et D.L.Jones, *Orchadian* 13(11): 487 (2002).

Basionym: *Dendrobium* Sw. sect. *Distichophyllum* Hook.f., *Fl. Brit. India* 5: 711 (1890).
Type species: *Dendrobium uniflorum* Griffith, *fide* Brieger (1981).

Dendrobium Sw. subgen. *Grastidium* (Blume) Kraenzl. sect. *Revoluta* (pars 2) Kraenzl. in Engl., *Pflanzenr. Orch.-Mon.-Dendr.* 1: 181 (1910), *pro parte max*.
Type species: *Dendrobium revolutum* Lindl.

Epiphytic or lithophytic herb. Stems psuedobulbous or non-pseudobulbous to c. 80 cm long. Inflorescence a highly reduced, lateral, periodically developing raceme, protected in a terminal sheathing bract. Flowers solitary, one, occasionally two per inflorescence, each with a papery sheath that persists in the sheathing bracts after anthesis. Labellum fleshy, minutely papillate, towards base on lamina callus, forming a closed, conspicuous, nectiferous spur at the base through fusion of basal half to the column-foot. Column short, concave, papillose on inner surface. Column-foot longer than column. Pollinia four, obliquely-obovate, elongate, glabrous, bright yellow. Capsules near globular, glabrous or hirsute, splitting open longitudinally when mature. Discoid protocorm-seedling type.

Distribution: South-East Asia, Malesia and South-west Pacific Islands.

Notes: The following species are transferred to this genus following detailed research of types and the literature.

Distichorchis angusta (Quisumb.) M.A.Clem., ***comb. et stat. nov.***
Basionym: *Dendrobium uniflorum* Griff. var. *angustum* Quisumb., *Philipp. Orch. Rev.* 3(3): 9, t. 1 (1950).

Distichorchis angustipetala (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium angustipetalum* J.J.Sm., *Orch. Ambon* 59 (1905).

Distichorchis barisana (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium barisanum* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 2), 25: 45–46 (1917).

Distichorchis bifaria (Lindl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium bifarium* Lindl., *Wall., Cat.* N. 2002 (1828); *Gen. Sp. Orch. Pl.* 81 (1830).

Distichorchis bihamulata (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium bihamulatum* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 2), 25: 43–45 (1917).

Distichorchis cerina M.A.Clem. et D.L.Jones, *Orchadian* 13(11): 487 (2002).
Basionym: *Dendrobium cerinum* Schltr., *Bot. Jahrb. Syst.* 39: 72 (1906), non Rchb.f. (1879); *Dendrobium austrocaledonicum* Schltr., *Repert. Spec. Nov. Regni Veg.* 3: 80 (1906), *nom*.

Distichorchis connata (Blume) M.A.Clem., ***comb. nov.***
Baisonym: *Onychium connatum* Blume, *Bijdr.* 328 (1825).

Distichorchis dissitifolia (Ridl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium dissitifolium* Ridl., *Trans. Linn. Soc., Bot.* 9: 168 (1916).

Distichorchis distachya (Lindl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium distachyon* Lindl., *J. Linn. Soc., Bot.* 3: 13 (1859).

Distichorchis elephantina (Finet) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium elephantinum* Finet, *Bull. Soc. Bot., France* 50: 373, t. 11, f. 20–31 (1903).

Distichorchis ellipsophylla (T.Tang et F.T. Wang) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium ellipsophyllum* T.Tang et F.T. Wang, *Acta Phytotax. Sin.* 1, 1: 81 (1951).

Distichorchis hepatica (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium hepaticum* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 2), 25: 48 (1917).

Distichorchis igneonivea (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium igneoniveum* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 9: 161 (1927).

Distichorchis kenepaiensis (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium kenepaiense* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 2), 25: 46–47 (1918).

Distichorchis lambii (J.J.Wood) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium lambii* J.J.Wood, *Kew Bull.* 38(1): 79, f. 1 (1983).

Distichorchis lamriana (C.L.Chan) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium lamrianum* C.L.Chan, *Sandakania* 5: 67–77, f. 1–2 (1994).

Distichorchis maraiparensis (J.J.Wood et C.L.Chan) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium maraiparense* J.J.Wood et C.L.Chan in C.L.Chan, A.Lamb, P.S.Shim and J.J.Wood, *Orch. Borneo* 1: 119, f. 25, t. 5E (1994).

Distichorchis melanotricha (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium melanotrichum* Schltr., *Repert. Spec. Nov. Regni Veg.*, Beih. 1: 558–559 (1912).

Distichorchis mellicolor (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium mellicolor*.J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 9: 160 (1927).

Distichorchis metachilina (Rchb.f.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium metachilinum* Rchb.f., *Bonplandia* 3: 222 (1855).

Distichorchis moquetteana (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium moquetteanum* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 2) 25: 50–51 (1917).

Distichorchis multicostata (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium multicostatum* J.J.Sm., *Bull. Dép. Agric. Indes Néerl.* 5: 11 (1907).

Distichorchis nabawanensis (J.J.Wood et A.Lamb) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium nabawanense* J.J.Wood et A.Lamb in J.J.Wood et P.J.Cribb, *Checklist Orch. Borneo* 258, f 32 (1994).

Distichorchis olivacea (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium olivaceum* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 2), 8: 41 (1912).

Distichorchis osmophytopsis (Kraenzl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium osmophytopsis* Kraenzl. in Engl., *Pflanzenr. Orch.-Mon.-Dendr.* 1: 172 (1910).

Distichorchis ovatifolia (Ridl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium ovatifolium* Ridl., *J. Linn. Soc., Bot.* 31: 271 (1896).

Distichorchis pachyantha (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium pachyanthum* Schltr., *Repert Spec. Nov. Regni Veg.* 9: 290 (1911).

Distichorchis pahangensis (Carr) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium pahangense* Carr, *Gard. Bull. Straits Settlements* 5: 126 (1930).

Distichorchis pandaneti (Ridl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium pandaneti* Ridl., *J. Linn. Soc., Bot.* 32: 257 (1896).

Distichorchis piranha (C.L.Chan et P.J.Cribb) M.A.Clem. et D.L.Jones, ***comb. nov.***
Basionym: *Dendrobium piranha* C.L.Chan et P.J.Cribb in C.L.Chan, A.Lamb, P.S.Shim et J.J.Wood, *Orch. Borneo* 1: 127, f. 28, t. 6B (1994).

Distichorchis pluricostata (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium pluricostatum* Schltr., *Repert. Spec. Nov. Regni Veg.,* Beih. 1: 557–558 (1912).

Distichorchis quadrisulcata (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium quadrisulcatum* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 2), 25: 49–50 (1917).

Distichorchis refracta (Teijsm. et Binn.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium refractum* Teijsm. et Binn., *Tijdschr. Nederl. Ind.* 24: 315–316 (1862).

Distichorchis revoluta (Lindl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium revolutum* Lindl., *Edwards' Bot. Reg.* 27; Misc. 51 (1840).

Distichorchis rupicola (Ridl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium rupicolum* Ridl., *J. Fed. Mal. States Mus.* 1: 174 (1915).

Distichorchis sandsii (J.J.Wood et C.L.Chan) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium sandsii* J.J.Wood et C.L.Chan in C.L.Chan, A.Lamb, P.S.Shim et J.J.Wood, *Orch. Borneo* 1: 129, f. 29, t. 6C (1994).

Distichorchis siberutensis (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium siberutense* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 5: 82–83 (1922).

Distichorchis spathipetala (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium spathipetalum* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 2) 13: 20 (1914).

Distichorchis striatiflora (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium striatiflorum* J.J.Sm., *Repert. Spec. Nov. Regni Veg.* 12: 114 (1913).

Distichorchis torquisepala (Kraenzl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium torquisepalum* Kraenzl. in Engl., *Pflanzenr. Orch.-Mon.-Dendr.* 1: 187 (1910).

Distichorchis uniflora (Griff.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium uniflorum* Griff., *Notul.* 3: 305–306 (1851); *Icon. Pl. Asia.* t. 303 (1851).

Distichorchis xanthophaea (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium xanthophaeum* Schltr., *Repert. Spec. Nov. Regni Veg.,* Beih. 1: 558 (1912).

Second major group

Dendrobium *Sw., Nov. Act. Soc. Sci. Upsal.* 6: 82 (1799) (nom. cons.).
Type species: *Dendrobium moniliforme* Sw. (type cons. *vide* Holttum et al. 1979).

Ormostema Raf., *Fl. Tellur.* 4: 38 (1836).
Type species: *Ormostema purpurea* Raf. (*Epidendrum moniliforme* L. = *Dendrobium moniliforme sensu* Lindl. ≡ *D. linawianum* Rchb.f.); *O. albiflora* Raf. (*Epidendrum monile* Thunb. = *Dendrobium monile* (Thunb.) Kuntze ≡ *Dendrobium moniliforme* (L.) Sw.)

Peirardia Raf., *Fl. Tellur.* 4: 41 (1836).
Type species: *Peirardia bicolor* Raf. (= *Dendrobium pierardii* Roxb.).

Dendrobium Sw. sect. *Dendrobium* Lindl., *Edwards' Bot. Reg.* 30: misc. 62 (1844); Lindl. et Paxton in Paxton's *Fl. Gard.* 1: 135 (1850–51), (as 'sect. Eudendrobium').

Dendrobium Sw. subgen. *Dendrobium* (Lindl.) Kraenzl. in Engl., *Pflanzenr. Orch.-Mon.-Dend.* 1: 26–27 (1910), (as 'subg. Eudendrobium').

Dendrobium Sw. subgen. *Dendrobium* (Lindl.) Kraenzl. sect. *Eugenanthe* Schltr., *Repert. Spec. Nov. Regni Veg.,* Beih. 1: 445 (1912).

Epiphytic or lithophytic herbs. Roots thick and fleshy, white, arising at base of new growths. Stems pseudobulbous, thickest near the middle, often with aerial growths. Leaves duplicate, deciduous; sheaths not overlapping. Inflorescence lateral, determinate racemose, with one to five flowers lasting several to many days. Flowers usually showy, erect with spreading segments. Petals and sepals glabrous, spreading, often similar in size and shape, but petals may also be broader. Labellum fleshy, showy, distinctly different to petals, continuous with the column-foot, non-articulate, forming a cavity at their base, obscurely trilobed, covered in papillae, sometimes granular in appearance. Column short, concave, broad nearest the base, glabrous. Anther cap large and ornate. Pollinia elongate, lunate, four (2 x 2) appressed together, yellow glabrous. Capsule elongate, fusiform. Elongate protocorm-seedling type.

Distribution: Found throughout South-East Asia, Malesia and Australia (represented by a single species).

Note: Furthur systematics of this group will be published separately (Clements et al. in prep.).

Third major group

Anisopetala (Kraenzl.) M.A.Clem., ***gen. et stat. nov***.

Basionym: *Dendrobium* Sw. subgen. *Dendrobium* sect. *Anisopetala* Kraenzl. in Engl., *Pflanzenr. Orch.-Mon.-Dendr.* 1: 27, 68 (1910).
Type species: *Dendrobium mutabile* (Blume) Lindl., *vide* Brieger (1981: 698).

Pedilonum Blume sect. *Sanguinolenta* Brieger, *Schltr., Die Orchideen* 3(1): 681 (1981).
Type species: *Pedilonum sanguinolentum* (Lindl.) Brieger (= *Dendrobium sanguinolentum* Lindl.).

Plants epiphytic herbs. Stems elongate, narrow, relatively fleshy. Leaves along almost their entire length when young, deciduous prior to flowering. Inflorescence lateral, the peduncles short and usually pendulous, bearing 1–14 flowers. Flowers showy, with a distinct mentum fusion of the basal part of the lateral sepals, and always held away from the ovary and pedicel; free parts of sepals and petals spreading; labellum with distinct claw, with or without a small projection on the upper surface near the base, the apical part spreading, usually without distinct sidelobes, and with a bilobed apex.

Distribution: South-East Asia, western Malesia and the Philippines.

Notes: The following species are transferred to this genus following detailed research of types and the literature.

Anisopetala acutimenta (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium acutimentum* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 2), 25: 53–54 (1917).

Anisopetala annae (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium annae* J.J.Sm, *Orch. Java* 354–355 (1905).

Anisopetala biflora (Blume) M.A.Clem., ***comb. nov.***
Basionym: *Pedilonum biflorum* Blume, *Bijdr.* 1: 322 (1825).

Anisopetala calicopis (Ridl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium calicopis* Ridl., *J. As. Soc. Straits* 39: 72 (1903).

Anisopetala filicaulis (Gapnep.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium filicaule* Gagnep., *Bull. Mus. Hist. Nat. Paris* (ser. 2), 21: 741 (1949).

Anisopetala fulminicaulis (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium fulminicaule* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 2), 25: 51–53 (1917).

Anisopetala hughii (Rchb.f.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium hughii* Rchb.f., *Gard. Chron.* (new ser.) 17: 764 (1882).

Anisopetala inflata (Rolfe) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium inflatum* Rolfe, *Kew Bull.* 61 (1895).

Anisopetala lucens (Rchb.f.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium lucens* Rchb.f., *Bot. Zeit. (Berlin)* 21: 128 (1863).

Anisopetala montana (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium montanum* J.J.Sm., *Orchid. Java* 363–364 (1905).

Anisopetala mutabilis (Blume) M.A.Clem., ***comb. nov.***
Basionym: *Onychium mutabile* Blume, *Bijdr.* 324 (1825).

Anisopetala nuda (Blume) M.A.Clem., ***comb. nov.***
Basionym: *Onychium nudum* Blume, *Bijdr.* 324 (1825).

Anisopetala rigida (Blume) M.A.Clem., ***comb. nov.***
Basionym: *Onychium rigidum* Blume, *Bijdr.* 324 (1825).

Anisopetala sanguinolenta (Lindl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium sanguinolentum* Lindl., *Edwards' Bot. Reg.* 28: 62, misc. 73 (1842).

Anisopetala spathilinguis (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium spathilingue* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 2), 9: 64 (1913).

Anisopetala transtillifera (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium transtilliferum* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 5: 85–86 (1922).

Eurycaulis M.A.Clem. et D.L.Jones, *Orchadian* 13(11): 490 (2002).

Basionym: *Dendrobium* Sw. sect. *Platycaulon* Schltr. in K.Schum. et Laut., *Fl. Schutzg. Südsee, Nachtr.* 150 (1905) (as '*Platybulbon*', orth. error).
Type species: *Dendrobium lamellatum* (Blume) Lindl. (as 'lamellatus').

Dendrobium Sw. sect. *Dendrocoryne* Lindl.. *Edwards' Bot. Reg.* 28: Misc. 76 (1842).
Type species: *Dendrobium compressum* Lindl.

Pedilonum Blume sect. *Platycaulon* (Schltr.) Brieger, *Schltr., Die Orchideen* 3(1): 685 (1981).
Type species: *Onychium lamellatum* Blume ≡ *Dendrobium lamellatum* (Blume) Lindl. ≡ *Pedilonum lamellatum* (Blume) Brieger

Dendrobium Sw. subgen. *Dendrocoryne* (Lindl.) Kraenzl. sect. *Platycaula* Kraenzl. in Engl., *Pflanzenr. Orch.-Mon.-Dendr.* 1: 242, 266–267 (1910).
Type species: *Dendrobium platycaulon* Rolfe.

Notes: The following species are transferred to this genus following detailed research of types and the literature. The genus comprises two subgenera based on the results of these studies.

Eurycaulis subgen. Eurycaulis

Plants epiphytic; stems elongate, fusiform, narrowest in basal half, laterally flattened, fleshy; leaves thin, conduplicate, alternate, present in upper half, deciduous prior to flowering; inflorescence short lateral, peduncles short and usually pendulous, bearing 1–14 flowers; flowers showy, or if not opening widely these usually being cleistogamous, forming a distinct mentum fusion of the basal part of the lateral sepals and always held away from the ovary and pedicel; free parts of sepals and petals spreading; labellum with distinct claw, with or without a small projection on the upper surface near the base, the apical part spreading, without distinct sidelobes, and with bilobed apex.

Distribution: Malesia as far east as the Solomon Islands.

Eurycaulis camptocentrus (Schltr.) M.A.Clem. et D.L.Jones, *Orchadian* 13(11): 490 (2002).

Eurycaulis compressus (Lindl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium compressum* Lindl., *Edwards' Bot. Reg.* 28, Misc. 76 (1842).

Eurycaulis discocaulon (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium discocaulon* Schltr., *Repert. Spec. Nov. Regni Veg.,* Beih. 1: 501 (1912).

Eurycaulis lamellatus (Blume) M.A.Clem. et D.L.Jones, *Orchadian* 13(11): 490 (2002).
Basionym: *Onychium lamellatum* Blume, *Bijdr.* 526 (1825).

Eurycaulis lamprocaulon (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium lamprocaulon* Schltr. in K. Schum. et Laut., *Nachtr. Fl. Deutsch. Südsee* 166 (1905).

Eurycaulis milaniae (H.Fessel et E.Lückel) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium milaniae* H.Fessel et E.Lückel, *Orchidee* 47(3): A131 (1996).

Eurycaulis platycaulon (Rolfe) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium platycaulon* Rolfe, *Kew Bull.* 139 (1892).

Eurycaulis platygastrius (Rchb.f.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium platygastrium* Rchb.f., *Otia Bot. Hamb.* 55 (1878).

Eurycaulis praetermissus (Seidenf.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium praetermissum* Seidenf., *Contr. Orch. Fl. Thailand* XIII: 34, f. 7 (1997).

Eurycaulis remiformus (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium remiforme* J.J.Sm., *Repert. Spec. Nov. Regni Veg.* 12: 111 (1913).

Eurycaulis septemcostulatus (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium septemcostulatum* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 2: 8384 (1920).

Eurycaulis treubii (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium treubii* J.J. Sm., *Orch. Ambon* 65 (1905); *Ic. Bogor.* 3: 29–30, t. 212 (1906).

Eurycaulis ypsilon (Seidenf.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium ypsilon* Seidenf., *Opera Bot.* 83: 158 (1985).

Eurycaulis subgen. Calcariferus (J.J.Sm.) M.A.Clem., ***subgen. et stat. nov*.**

Basionym*: Dendrobium Sw.* sect*. Calcarifera* J.J.Sm., *Bull. Dép. Agric. Indes Néerl.* 15: 14 (1908).
Type species: *Dendrobium pedicellatum* J.J.Sm.

Plants epiphytic; stems elongate, narrow, relatively fleshy; leaves along almost their entire length, deciduous prior to flowering; inflorescences lateral, the peduncles short and usually pendulous, bearing 1–14 flowers; flowers showy, forming a distinct mentum fusion of the basal part of the lateral sepals and always held away from the ovary and pedicel; free parts of sepals and petals spreading; labellum with distinct claw, with or without a small projection on the upper surface near the base, the apical part spreading, without distinct sidelobes, and with bilobed apex.

Distribution: South-East Asia and Malay archipelago.

Eurycaulis acutifolius (Ridl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium acutifolium* Ridl., *J. Fed. Mal. States Mus.* 8: 91–92 (1917).

Eurycaulis annamensis (Rolfe) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium annamense* Rolfe., *Kew Bull.* 113–114 (1906).

Eurycaulis anthrene (Ridl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium anthrene* Ridl., *J. Linn. Soc., Bot.* 31: 272 (1896).

Eurycaulis appendiculoides M.A.Clem., ***nom. nov***.
Basionym: *Dendrobium appendiculoides* Ames, *Orchidaceae* 7: 93–94 (1922), *nom. illeg.,* non J.J.Sm. (1913).

Eurycaulis arcuatus (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium arcuatum* J.J.Sm., *Orch. Java* 357 (1905).

Eurycaulis atjehensis (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium atjehense* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 12: 137 (1932).

Eurycaulis bicallosus (Ridl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium bicallosum* Ridl., *J. Fed. Mal. States Mus.* 8(4): 92–93 (1917).

Eurycaulis boumaniae (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium boumaniae* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 8: 55–56 (1926).

Eurycaulis calcariferus (Carr) M.A.Clem., ***nom. nov***.
Basionym: *Dendrobium calcariferum* Carr, *Gard. Bull. Straits Settlement* 8: 107–108 (1935).

Eurycaulis cerinus (Rchb.f.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium cerinum* Rchb.f., *Gard. Chron.* (ser. 2), 12: 554 (1879).

Eurycaulis cinereus (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium cinereum* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 2: 78–79 (1920).

Eurycaulis compressimentus (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium compressimentum* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 10: 63–64 (1928).

Eurycaulis corallorhizus (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium corallorhizon* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 10: 140–141 (1931).

Eurycaulis courtauldii (Summerh. ex J.J.Wood) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium courtauldii* Summerh. ex J.J.Wood, *Orchid Rev.* 89(1056): 322 (1981).

Eurycaulis crabro (Ridl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium crabro* Ridl., *J. As. Soc. Straits* 50: 133 (1908).

Eurycaulis crassimarginatus (L.O.Williams) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium crassimarginatum* L.O.Williams, *Bot. Mus. Leafl. Harvard Univ.* 5: 42–44 (1937).

Eurycaulis crocatus (Hook.f.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium crocatum* Hook.f., *Fl. Brit. Ind.* 6: 185 (1890).

Eurycaulis croceocentrus (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium croceocentrum* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 2: 75–76 (1920).

Eurycaulis cumulatus (Lindl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium cumulatum* Lindl., *Gard. Chron.* 756 (1855).

Eurycaulis curvus (Ridl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium curvum* Ridl., *J. Fed. Mal. States Mus.* 8: 91 (1917).

Eurycaulis cymbiformis (Rolfe) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium cymbiforme* Rolfe, *Kew Bull.* 192 (1898).

Eurycaulis cymboglossus (J.J.Wood et A.Lamb) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium cymboglossum* J.J.Wood et A.Lamb in J.J.Wood et P.J.Cribb, *Checklist Orch.Borneo* 247–248, f. 29, t. 8C (1994).

Eurycaulis derryi (Ridl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium derryi* Ridl., *Mat. Fl. Mal. Penins.* 1: 52 (1907).

Eurycaulis diffusus (L.0.Williams) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium diffusum* L.0.Williams, *Bot. Mus. Leaf. Harvard Univ.* 5: 44–45 (1937).

Eurycaulis endertii (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium endertii* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3),11: 138 (1931).

Eurycaulis exilicaulis (Ridl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium exilicaule* Ridl., *Fl. Mal. Penins.* 4: 50 (1924).

Eurycaulis fimbrilabius (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium fimbrilabium* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 2: 81–82 (1920).

Eurycaulis foetens (Kraenzl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium foetens* Kraenzl. in Engl., *Pflanzenr. Orch.-Mon.-Dendr.* 1: 77–78 (1910).

Eurycaulis foxii (Ridl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium foxii* Ridl., *J. Bot.* 38: 70 (1900).

Eurycaulis grastidioides (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium grastidioides* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 2: 80–81 (1920).

Eurycaulis groeneveldtii (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium groeneveldtii* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 2: 79–80 (1920).

Eurycaulis guerreroi (Ames et Quisumb.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium guerreroi* Ames et Quisumb., *Philipp. J.. Sci.* 49: 489 (1932).

Eurycaulis hamatus (Rolfe) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium hamatum* Rolfe, *Kew Bull.* 183 (1894).

Eurycaulis hamaticalcar (J.J.Wood et Dauncey) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium hamaticalcar* J.J.Wood et Dauncey in J.J.Wood, Baeman et Beaman, *Pl. Mt Kinabalu* 2, Orch. 168, f. 20 (1993).

Eurycaulis huttonii (Rchb.f.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium huttonii* Rchb.f., *Gard. Chron.* 686 (1869).

Eurycaulis hymenanthus M.A.Clem., ***nom. nov***.
Basionym: *Dendrobium hymenanthum* Hook.f., *Fl. Brit. Ind.* 5: 732 (1890); Icon. Pl. t. 2032 (1890); 6: 185 (1890), *nom. illeg.,* non Rchb.f. (1855).

Eurycaulis intricatus (Gagnep.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium intricatum* Gagnep., *Bull. Mus. Hist. Nat. Paris* (ser. 2), 2: 236 (1930).

Eurycaulis ionopus (Rchb.f.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium ionopus* Rchb.f., *Gard. Chron.* 2: 808 (1882).

Eurycaulis kentrochilus (Hook.f.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium kentrochilum* Hook.f., *Fl. Brit. Ind.* 5: 731(1890); Icon. Pl. t. 2030 (1890).

Eurycaulis kruiensis (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium kruiense* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 8: 56–57 (1926).

Eurycaulis lampongensis (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium lampongense* J.J.Sm., *Bull. Dépt. Agric. Néerl.* 15: 14–15 (1908).

Eurycaulis lankaviensis (Ridl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium lankaviense* Ridl., *J. As. Soc. Straits* 54: 49 (1910).

Eurycaulis leucochlorus (Rchb.f.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium leucochlorum* Rchb.f., *Gard. Chron.* 1: 202 (1879).

Eurycaulis lilacinus M.A.Clem., ***nom. nov***.
Basionym: *Dendrobium lilacinum* Rchb.f., *Gard. Chron.* 674 (1865), non Teijsm. et Binn.(1864).

Eurycaulis lucens (Rchb.f.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium lucens* Rchb.f., *Bot. Zeit. (Berlin)* 21: 128 (1863).

Eurycaulis maierae (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium maierae* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 2: 76–78 (1920).

Eurycaulis megaceras (Hook.f.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium megaceras* Hook.f., *Fl. Brit. Ind.* 5: 713 (1888); Icon. Pl. t. 2031 (1890).

Eurycaulis modestus M.A.Clem., ***nom. nov***.
Basionym: *Dendrobium modestum* Ridl., *J. Bot.* 211(1898), non Rchb.f.(1855)

Eurycaulis multiflorus M.A.Clem., ***nom. nov***.
Basionym: *Dendrobium multiflorum* Ridl., *Journ. As. Soc. Straits* l: 134 (1908), non Par. et Rchb.f. (1874).

Eurycaulis nieuwenhuisii (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium nieuwenhuisii* J.J.Sm., *Ic. Bogor*. 3: 25–27: t. 211 (1906).

Eurycaulis obrienianus (Kraenzl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium o'brienianum* Kraenzl., *Gard. Chron.* (ser. 3), 11: 266 (1892).

Eurycaulis paathii (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium paathii* J.J.Sm., *De Orchidee (Bandoeng)* 4: 183 (1935); Orch. Rev. 43: 290, in obs (1935); *Gard. Bull. Straits Settlements* 9: 90 (1935).

Eurycaulis panduriferus (Hook.f.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium panduriferum* Hook.f., *Fl. Brit. India* 6: 186 (1890).

Eurycaulis pedicellatus (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium pedicellatum* J.J.Sm., *Bull. Dép. Agric. Indes Néerl.* 15: 13 (1908).

Eurycaulis peralu (Rchb.f.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium peralu* Rchb.f., *Hamb. Gartenz.* 21: 298 (1865).

Eurycaulis pictus (Lindl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium pictum* Lindl., *Gard. Chron.* 548 (1862).

Eurycaulis profusus (Rchb.f.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium profusum* Rchb.f., *Gard. Chron.* 1: 510 (1884).

Eurycaulis rantii (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium rantii* J.J.Sm., *Repert. Spec. Nov. Regni Veg.* 36: 114–115 (1934).

Eurycaulis rappardii (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium rappardii* J.J.Sm., *Blumea* 5: 308 (1943).

Eurycaulis rhodocentrum (Rchb.f.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium rhodocentrum* Rchb.f., *Gard. Chron.* 426 (1872).

Eurycaulis roseatus (Ridl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium roseatum* Ridl., *J. Linn. Soc.* 32: 261 (1896).

Eurycaulis singalanensis (Kraenzl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium singalanense* Kraenzl. in Engl., *Pflanzenr. Orch.-Mon.-Dendr.* 1: 167 (1910).

Eurycaulis subflavidus (Ridl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium subflavidum* Ridl., *J. Linn. Soc., Bot.* 38: 324 (1908).

Eurycaulis tropaeoliflorus (Hook.f.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium tropaeoliflorum* Hook.f., *Fl. Brit. Ind.* 6: 186 (1890).

Eurycaulis undulatus (Lindl.) M.A.Clem., ***comb. nov.***
Basionym: *Pedilonum undulatum* Blume, *Bijdr.* 322, t. 36 (1825).

Eurycaulis ventrilabius (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium ventrilabium* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 5: 84–85 (1922).

Eurycaulis viriditepalus (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium viriditepalum* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 2), 25: 54–56 (1917).

Eurycaulis viridulus (Ridl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium viridulum* Ridl., *J. Linn. Soc.* 32: 259 (1896).

Eurycaulis zamboangensis (Ames) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium zamboangense* Ames, *Orchidaceae* 5: 145 (1915

Pedilonum (Blume) Blume, *Bijdr. Fl. Ned. Ind.*: 320 (1825)

Dendrobium Sw. sect. *Pedilonum* Blume, *Bijdr. Fl. Ned. Ind*.: tab. 4 (1825).
Type species: *Dendrobium secundum* (Blume) Lindl. ex Wall., *vide* Rafinesque (1836: 44).

Dendrobium Sw. sect. *Dendrobium* subsect. *Pedilonum* (Blume) Pfitzer in Engl. and Prantl, *Nat. Pflanzenfam.* 2(6): 174 (1888).

Dendrobium Sw. subgen. *Pedilonum* (Blume) Kraenzl. in Engl., *Pflanzenr. Orch.-Mon.-Dendr.* 1: 96 (1910).

Erect to pendulous epiphytic herb. Stems stout, clustered, cylindric to more or less cylindric-fusiform. Leaves coriaceous, somewhat twisted at base, linear-oblong to elliptic-ovate. Inflorescence densely multi-flowered, arising from upper nodes of leafless stems. Flowers secund, waxy, purple, pink, rarely white, the labellum lamina usually orange or yellow; pedicellate ovary cylindric-clavate. Dorsal sepal slightly concave, ovate-triangular to elliptic-oblong, acute. Lateral sepals obliquely falcate to tringular, elliptic-oblong, acute to acuminate; mentum equalling or slightly longer than free part, fused to labellum, saccate. Petals small, obliquely linear-obovate to narrowly elliptic, acute. Labellum linear-spathulate, lamina narrowly linear-elliptic to obovate-cuneate, acute to acuminate, saccate for basal two-thirds, shallowly concave above, fused to column-foot, transverse callus V-shaped to semilunate. Column short, laterally dilated toward apex, with sunken stigma, and protruding hard, plate-like rostellum. Column-foot curved, slightly thickened below stigma, with basal nectary. Capsule oblique ellipsoidal-ovoid.

Distribution: South-East Asia and the Malesian Archipelago.

Pedilonum amethystoglossum (Rchb.f.). M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium amethystoglossum* Rchb.f., *Gard. Chron.* 109 (1872).

Pedilonum secundum Blume, *Bijdr. Fl. Ned. Ind*.: 322 (1825).

Fourth major group

Callista Lour., *Fl. Cochinch.* 2: 519 (1790).
Type species: *Callista amabilis* Lour.

Endeisa Rafin., *Fl. Tellur.* 2: 52 (1836)[1837].
Type species: *Endeisa flava* Raf. (= *Dendrobium densiflorum* Lindl.).

Dendrobium Sw. sect. *Densiflora* Finet, *Bull. Mus. Nat. Hist. (Paris)* 9: 295–303 (1903).
Type species: *Dendrobium densiflorum* Lindl.

Dendrobium Sw. sect. *Callista* (Lour.) Schltr., *Repert. Spec. Nov. Regni Veg.,* Beih. 1: 444–445 (1912).
Type species: *Callista amabilis* Lour.

Epiphytic herbs. Roots thick, fleshy, white. Stems erect, fusiforme to clavate, often angular, pseudobulbous, comprising several to many internodes; Leaves one to five, coriaceous, terminal to subterminal, near sheathless. Inflorescence pendant, multi-flowered, arising from near terminal nodes, development as though being extruded like paste from the stem buds. Flowers yellow, white or pink, with or without contrasting orange or yellow labellum. Lateral sepals similar and thin textured, spreading. Petals broader and often with serrate erose margins. Labellum broadly orbicular with constricted base, lacking side lobes, the base continuous with column-foot, flexible but non-articulate; the upper surface papillose-pubescent, basal transverse callus, and concave base. Column short with prominent sunken stigma. Column-foot relatively short, with prominent shortly falcate staminodia and with distal, glabrous, shiny, basal nectiferous cavity. Anther cap elongate, glabrous. Pollinia four in two groups of two, obovate-elongate, thin, glabrous, light yellow.

Distribution: South-East Asia.

Notes: The following species were recognized as belonging to this genus following detailed research of types and the literature.

Callista amabilis Lour., *Fl. Cochinch.* 2: 519 (1790).

Callista densiflora (Lindl.) Kuntze, *Rev. Gen. Pl.* 2: 654 (1891).

Callista farmeri (Paxt.) Kuntze, *Rev. Gen. Pl.* 2: 654 (1891).

Callista griffithiana (Lindl.) Kuntze, *Rev. Gen. Pl.* 2: 654 (1891).

Callista guibertii (Carriere) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium guibertii* Carriere, *Rev. Hortic.* 48: 430 (1876).

Callista palpebrae (Lindl.) Kuntze, *Rev. Gen. Pl.* 2: 655 (1891).

Callista thyrsiflora (Rchb.f.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium thyrsiflorum* Rchb.f. in Andre, *Illustr. Hortic.* 22: 88, t. 207 (1875).

Fifth major group

Ceraia Lour., *Fl. Cochinch.* 2: 518 (1790) (as '*Ceraja*').
Type species: *Ceraia simplicissima* Lour.

Dendrobium Sw. sect. *Crumenata* Pfitz. in Engl. et Prantl, *Pflanzenr*. II (6): 174 (1889).
Type species: *Dendrobium crumenatum* Sw.

Dendrobium Sw. subgen. *Crumenata* Kraenzl. in Engl., *Pflanzenr. Orch.-Mon.-Dend.* 1: 224 (1910).

Aporum Blume sect. *Crumenata* (Pfitz.) Brieger, *Schltr., Die Orchideen* 1(11–12): 671 (1981).

Dendrobium Sw. sect. *Ampullaria* Pfitz. in Engl. et Prantl, *Pflanzenr.* II (6): 174 (1889).
Type species: *Dendrobium planibulbe* Lindl.

Dendrobium Sw. subgen. *Rhopalobium* Schltr. sect. *Ceraia* Schltr., *Repert. Spec. Nova. Regni Veg.*, Beih. 1: 442, 449 (1914).
Type species: *Dendrobium crumenatum* Sw.

Aporum Blume sect. *Linearifolia* Brieger in Schltr., Die. *Die Orchideen* 674 (1981).
Type species: *Onychium gracile* Blume (= *Dendrobium linearifolium* Teijsm. et Binn.).

Dendrobium Sw. sect. *Rhopolanthe* Schltr. subsect. *Aporopsis* Schltr., *Repert Spec. Nov. Regni Veg.*, Beih. 1: 565 (1912), *nom. nud*.

Aporum Blume sect. *Aporopsis* (Schltr.) Brieger, *Schltr., Die Orchideen* 674 (1981), *nom. inval*.
Type species: *Onychium tetraedre* Blume

Aporopsis (Schltr.) M.A.Clem. et D.L. Jones, *Orchadian* 13(11): 485 (2002), *nom. inval*.
Type species: *Dendrobium macfarlanei* F.Muell.

Dendrobium Sw. sect. *Virgatae* Hook.f., *Fl. Brit. Ind.* 5: 711, 726 (1890), *pro parte min*.

Epiphytic or lithophytic herb; pseudobulbous stems to c. 1m long, the swollen part comprising three or four nodes and internodes at least four nodes from the base of a shoot; aerial growths arising above the swollen pseudobulb, capable of forming a swollen pseudobulb; roots arising from the nodes at the base of each shoot; sheaths overlapping; inflorescence enclosed in a covering sheath, a highly reduced indeterminate, raceme; flowers one to three per inflorescence, spontaneous at any time following a drop in air temperature, and synchronous for all plants in the same area; flowers lasting only a few hours in a single day, of superficial substance; very fragrant perfume; labellum non-articulate, attached directly to base of column-foot where it forms a short spur containing nectar; column-foot longer than column. Stelidia reduced not divided. Pollinia four, obliquely elliptical, loosely held together in two groups of two. Capsule fusiforme. Protocorm-seedling type, narrowly isobilateral.

Distribution: Frequent throughout South-East Asia, and the Malay archipelago including Christmas Island which is an Australian Territory, and as far east as Papua New Guinea.

Notes: The following species are transferred or recognised as belonging to this genus following detailed research of Types and the literature.

Ceraia acaciifolia (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium acaciifolium* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 2), 25: 34–36 (1917).

Ceraia acicularis (Lindl.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium aciculare* Lindl., *Edwards' Bot. Reg.* 26: 81, misc. 188 (1840).

Ceraia alabensis (J.J.Wood) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium alabense* J.J.Wood, *Lindleyana*, 5(2): 90 (1990).

Ceraia aurantiflammea (J.J.Wood) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium aurantiflammeum* J.J.Wood, *Orchid Rev.* 106: 337–342, f. (1998).

Ceraia batanensis (Ames et Quisumb.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium batanense* Ames et Quisumb., *Philipp. J. Sc.* 47: 200, f. (1932).

Ceraia boothii (Teijsm. et Binn.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium boothii* Teijsm. et Binn., *Natuurk. Tijdschr. Ned.-Indie* 24: 318 (1862).

Ceraia bukidnonensis (Ames et Quisumb.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium bukidnonense* Ames et Quisumb., *Philipp. J. Sc.* 59: 5 (1936).

Ceraia calceola (Roxb.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium calceolum* Roxb., *Hort. Beng.* 63 (1814), *nom. nud.*; *Fl. Ind.* 3: 488 (1832).

Ceraia carinata (L.) M.A.Clem., ***comb. nov.***
Basionym: *Epidendrum carinatum* L., *Sp. Pl.* 1350 (1753); *Dendrobium carinatum* (L.) Willd., *Sp. Pl.* 4: 133–134 (1805).

Ceraia chrysotainia (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium chrysotainium* Schltr., *Repert. Spec. Nov. Regni Veg.* 8: 508 (1910).

Ceraia cinnabarina (Rchb.f.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium cinnabarinum* Rchb.f., *Gard. Chron*. 14: 166 (1880).

Ceraia clavator (Ridl.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium clavator* Ridl., *J. Linn. Soc.* 32: 255 (1896).

Ceraia compressicaulis (J.J.Sm.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium compressicaule* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 10: 57–58 (1928).

Ceraia confunda (Kraenzl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium confundens* Kraenzl. in Engl., *Pflanzenr. Orch.-Mon.-Dendr.* 1: 205 (1910).

Ceraia cultrifolia (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium cultrifolium* Schltr., *Repert. Spec. Nov. Regni Veg.* 16: 111 (1919).

Ceraia cuneata (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium cuneatum* Schltr., *Bull. Herb. Boiss.* (ser. 2) 6: 454–455 (1906).

Ceraia cuneilabra (J.J.Sm.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium cuneilabrum* J.J.Sm., *Icon. Bogor.* 3: 11–12, t. 205 (1906).

Ceraia cymbulipes (J.J.Sm.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium cymbulipes* J.J.Sm., *Mitt. Inst. Bot. Hamburg* 7: 51, t. 8, f. 41 (1927).

Ceraia dentata (Seidenf.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium dentatum* Seidenf., *Nordic J. Bot.*, 1(2): 206 (1981).

Ceraia eboracensis (Kraenzl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium eboracense* Kraenzl., *Oest. Bot. Zeitschr.* 44: 419 (1894).

Ceraia ephemera (J.J.Sm.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium ephemerum* J.J.Sm. in Merrill, *Interpr. Rumph. Herb. Amboin.* 174 (1917).

Ceraia equitans (Kraenzl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium equitans* Kraenzl. in Engl., *Pflanzenr. Orch.-Mon.-Dendr.* 1: 228 (1910).

Ceraia exilis (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium exile* Schltr., *Repert. Spec. Nov. Regni Veg.* 2: 85 (1906).

Ceraia facifera (J.J.Sm.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium faciferum* J.J.Sm., *Bull. Dép. Agric. Indes Néerl.* 15: 10 (1908).

Ceraia fimbriata (Blume) M.A.Clem. ***comb. nov.***
Basionym: *Onychium fimbriatum* Blume, *Bijdr.* 325 (1825); *Dendrobium blumei* Lindl., *Gen. Sp. Orch. Pl.* 88 (1830), *nom*.

Ceraia fugax M.A.Clem., ***nom. nov***.
Basionym: *Dendrobium fugax* Schltr., *Bull. Herb. Boiss.* (ser. 2), 6: 455 (1906), *nom. illeg.,* non Rchb.f. (1871).

Ceraia gedeana (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium gedeanum* J.J.Sm., *Bull. Dép. Agric. Indes Néerl.* 8: 29 (1907).

Ceraia gerlandiana (Kraenzl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium gerlandianum* Kraenzl., *Repert. Spec. Nov. Regni Veg.* 6: 317 (1909).

Ceraia goldfinchii (F.Muell.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium goldfinchii* F.Muell., *Wings South Sc. Record* 3: 4 (Jan. 1883).

Ceraia gracilis (Blume) M.A.Clem. ***comb. nov.***
Basionym: *Onychium gracile* Blume, *Bijdr.* 327 (1825).

Ceraia grootingsii (J.J.Sm.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium grootingsii* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 2), 25: 33–34 (1917).

Ceraia gynoglottis (Carr) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium gynoglottis* Carr, *Gard. Bull. Straits Settlements* 8: 105 (1935).

Ceraia humboldtensis (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium humboldtense* J.J.Sm., *Repert. Spec. Nov. Regni Veg.* 11: 131 (1912).

Ceraia hymenocentra (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium hymenocentrum* Schltr., *Repert. Spec. Nov. Regni Veg.,* Beih. 1: 567 (1912).

Ceraia hymenopetala (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium hymenopetalum* Schltr., *Bot. Jahrb. Syst.* 45, Beibl. 104: 33 (1911).

Ceraia hypopoga (Kraenzl.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium hypopogon* Kraenzl. in Engl., *Pflanzenr. Orch.-Mon.-Dendr.* 1: 232–234 (1910).

Ceraia inconcinna (Ridl.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium inconcinnum* Ridl., *J. Linn. Soc.* 32: 255 (1896).

Ceraia inconspicua (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium inconspicuum* J.J.Sm. in L. S. Gibbs, *Phytogeogr. & Fl. Arfak Mts.* 205 (1917).

Ceraia incurvociliata (J.J.Sm.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium incurvociliatum* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 11: 137–138 (1931).

Ceraia juncea (Lindl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium junceum* Lindl., *Edwards' Bot. Reg.* 28, Misc. 11 (1842).

Ceraia juncifolia (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium juncifolium* Schltr., *Repert. Spec. Nov. Regni Veg.* 10: 76 (1911).

Ceraia koeteiana (Schltr.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium koeteianum* Schltr., *Bull. Herb. Boissier* (ser. 2), 6: 456 (1906).

Ceraia kohlmeyeriana (Teijsm. et Binn. ex Miq.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium kohlmeyerianum* Teijsm. et Binn. ex Miq., *Choix, Pl. Jard. Buitenzorg* t. 24. f.1 (1867).

Ceraia kurashigei (T.Yakawa) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium kurashigei* T.Yakawa, *Lindleyana* 13(1): 28–30, f.2 (1998).

Ceraia lagara (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium lagarum* Seidenf., *Opera Bot.* 83: 187 (1985).

Ceraia lamatochila (Seidenf.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium lamatochilum* Seidenf., *Nordic J. Bot.* 1(2):206 (1981).

Ceraia lamellifera (Carr) M.A.Clem. ***comb. et stat. nov***.
Basionym: *Dendrobium cinnabarinum* Rchb.f. var. *lamelliferum* Carr, *Gard. Bull. Straits Settlem.* 8: 103 (1935).

Ceraia lamellulifera (J.J.Sm.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium lamelluliferum* J.J.Sm., *Mitt. Inst. Bat. Hamburg* 7: 52, t. 8, f. 42 (1927).

Ceraia lanciloba (J.J.Wood) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium lancilobum* J.J.Wood, *Lindleyana* 5(2): 90 (1990).

Ceraia lawiensis (J.J.Sm.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium lawiense* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 2), 3: 60 (1912).

Ceraia limii (J.J. Wood) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium limii* J.J. Wood in J.J.Wood et P.J.Cribb, *Checklist Orch. Borneo* 254–255, f. 31 (1994).

Ceraia linearifolia (Teijsm. et Binn.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium linearifolium* Teijsm. et Binn., *Tijdschr. Nederl. Ind.* 24: 318 (1862).

Ceraia litoralis (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium litorale* Schltr., *Repert. Spec. Nov. Regni Veg.*, Beih. 1: 567 (1912).

Ceraia macfarlanei (F.Muell.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium macfarlanei* F.Muell., *Papuan Pl.* 1: 29 (1875).

Ceraia macrapora (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium macraporum* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 2), 8: 38 (1912).

Ceraia maleolens (Kraenzl.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium maleolens* Kraenzl. in Engl., *Pflanzenr. Orch.-Mon.-Dendr.* 1: 54 (1910).

Ceraia minima (Ames et C.Schweinf.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium minimum* Ames et C.Schweinf., *Orchidaceae* 6: 107, t. 91 (1920).

Ceraia modesta (Rchb.f.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium modestum* Rchb.f., *Bonplandia* 3: 222 (1855).

Ceraia multiramosa (Ames) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium multiramosum* Ames, *Orchidaceae* 5: 129 (1915).

Ceraia odorata (Schltr.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium odoratum* Schltr., *Repert. Spec. Nov. Regni Veg.* 8: 503–504 (1910).

Ceraia ovatipetala (J.J.Sm.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium ovatipetalum* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 12: 134–135 (1932).

Ceraia papilionifera (J.J.Sm.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium papilioniferum* J.J.Sm., *Orch. Ambon* 49 (1905).

Ceraia parviflora (Ames et C.Schweinf.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium crumenatum* Sw. var. *parviflorum* Ames et C.Schweinf., *Orchidaceae* 6: 100–101 (1920).

Ceraia patentiloba (Ames et C.Schweinf.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium patentilobum* Ames et C.Schweinf., *Orchidaceae* 6: 110–112 (1920).

Ceraia peculiaris (J.J.Sm.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium peculiare* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 10: 58–59 (1928).

Ceraia philippinensis (Ames) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium philippinense* Ames, *Philipp. J. Sc.* Bot. 8: 424 (1914).

Ceraia planibulbis (Lindl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium planibulbe* Lindl., *Edwards' Bot. Reg.* 29: 70, misc. 54. (1843).

Ceraia platybasis (Ridl.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium platybasis* Ridl., *Trans. Linn. Soc., Bot.* 9: 165 (1916).

Ceraia plebeja (J.J.Sm.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium plebejum* J.J.Sm., *Bull. Dép. Agric. Indes Néerl.* 5: 6–7 (1907).

Ceraia polytricha (Ames) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium polytrichum* Ames, *Orchidaceae* 2: 183–184 (1908).

Ceraia pseudocalceola (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium pseudocalceolum* J.J.Sm., *Bull. Dép. Agric. Indes Néerl.* 5: 34 (1907).

Ceraia pseudoequitans (H.Fessel et E.Luckel) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium pseudoequitans* H.Fessel et E.Luckel, *Die Orchidee* 51(1): 83–85, t. (2000).

Ceraia pseudotenella (Guillaumin) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium pseudotenellum* Guillaumin, *Bull. Mus. Hist. Nat. Paris* (ser. 2), 36: 697 (1965).

Ceraia puberilinguis (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium puberilingue* J.J.Sm., *Mitt. Inst. Allg. Bot. Hamburg* 7: 53, t. 8., f. 43 (1927).

Ceraia ridleyana M.A.Clem., ***nom. nov***.
Basionym: *Dendrobium ridleyanum* Kerr, *Kew Bull.* 218 (1927) nom. illeg, non Schltr. (1905).

Ceraia robinsonii (Ames) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium robinsonii* Ames, *Philipp. J. Sc., Bot.* 8: 425 (1914).

Ceraia saaronica (J.König) M.A.Clem. et D.L.Jones, *Orchadian* 13(11): 486 (2002).
Basionym: *Epidendrum saaronicum* J.König, *Retz. Obs.* 6: 58 (1791). *Angraecum crumenatum* Rumph., *Herb. Amb.* 6: t. 472 (1750), nom. illeg. (pre 1753). *Dendrobium crumenatum* Sw., *Schrad. J. Bot.* 2: 237 (1799).

Ceraia sanguinea M.A.Clem. ***nom. nov***.
Basionym: *Dendrobium sanguineum* Rolfe, *Gard. Chron.* (ser. 3) 18: 292 (1895), non Sw. (1799).

Ceraia scirpoides (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium scirpoides* Schltr., *Repert. Spec. Nov. Regni Veg.* 9: 103 (1911).

Ceraia setifera M.A.Clem., ***nom. nov***.
Basionym: *Dendrobium tenellum* (Blume) Lindl. var. *setifolium* Guillaumin, *Bull. Mus. Paris* (ser. 2), 28: 484 (1956).

Ceraia setifolia (Ridl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium setifolium* Ridl., *J. Linn. Soc.* 31: 270 (1896).

Ceraia simplicissima Lour., Fl. Indoch. 578 (1790). *Dendrobium podagraria* Hook.f., *Fl. Brit. Ind.* 5: 728 (1890); *Icon. Pl.* t. 2026 (1890).

Ceraia stelidiifera (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium stelidiiferum* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 3), 2: 66–67 (1920).

Ceraia strigosa (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium strigosum* Schltr., *Bot. Jahrb. Syst.* 45, Beibl. 104, 34 (1911).

Ceraia tenella (Blume) M.A.Clem., ***comb. nov.***
Basionym: *Onychium tenellum* Blume, *Bijdr.* 327 (1825).

Ceraia tenuis (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium tenue* J.J.Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 2), 25: 31–33 (1917).

Ceraia tenuicaulis (Hook.f.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium tenuicaule* Hook.f., *Fl. Brit. Ind.* 6: 184 (1890).

Ceraia tetraedris (Blume) M.A.Clem., ***comb. nov.***
Basionym: *Onychium tetraedre* Blume, *Bijdr.* 327 (1825).

Ceraia torajaensis (O'Byrne) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium torajaense* O'Byrne, *Malayan Orchid Rev.* 33: 45–46, 95, f., t. (1999).

Ceraia tricuspis (Blume) M.A.Clem., ***comb. nov.***
Basionym: *Onychium tricuspe* Blume, *Bijdr.* 326 (1825).

Ceraia tridentata (Ames et C.Schweinf.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium tridentatum* Ames et C.Schweinf., *Orchidaceae* 6: 115–117 (1920).

Ceraia truncata (Lindl.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium truncatum* Lindl., *J. Linn. Soc.* 3: 15 (1859).

Ceraia usterii (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium usterii* Schltr., *Bull. Herb. Boiss.* (ser. 2), 6: 458–459 (1906).

Ceraia usterioides (Ames) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium usterioides* Ames, *Orchidaceae* 5: 142 (1915).

Ceraia ventricosa (Kraenzl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium ventricosum* Kraenzl. in Engl., *Pflanzenr. Orch.-Mon.-Dendr.* 1: 209 (1910).

Ceraia ventripes (Carr) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium ventripes* Carr, *Gard. Bull. Straits Settlem.* 8: 103 (1935).

Aporum Blume, *Bijdr.* 6: f. 39; 7: 334 (1825).
Type species: *Aporum lobatum* Blume (*vide* Brieger 1981), non *Aporum indivisum* Blume (*vide* Seidenfaden 1985).

Macrostomium Blume, *Bijdr.* 335 (1825); *Aporum* Blume sect. *Macrostomium* (Blume) Bieger, *Schltr., Die Orchideen* 3 (ed. 1): 676 (1981).
Type species: *Macrostomium aloifolium* Blume

Schismoceras Presl, *Rel. Haenk.* 1: 96–97, t. 13, f. 2a–e (1827).
Type species: *Schismoceras disticha* Presl.

Ditulima Rafin., *Fl. Tellur.* 4: 41 (1836)[1838].
Type species: *Ditulima anceps* Raf. (= *Dendrobium anceps* Sw.)

Dendrobium Sw. sect. *Aporum* (Blume) Lindl. in Paxt., *Fl. Gard.* 1: 134 (1851).

Aporum Blume sect. *Aporum* Brieger, *Schltr., Die Orchideen*, 3 Aufl. 1: 677 (1981).

Erect, porrect or pendulous, small to large, epiphytic or lithophytic, herbs. Roots thin wiry, divided. Stems thin, wiry, covered with lead sheaths for most of their length but exposed in most species towards the apex, often branching. Leaves equitant, hard, fleshy, broadest near the basal half of each stem, then tapering towards the apex, with a distinct abscission layer, apices acute, persistent for several years, those nearest the apex becoming increasingly smaller and bract like. Inflorescence lateral on exposed apical part of stem, the bract from successive flowering forming a tuft at each node, comprising one or a few flowers. Flowers solitary arising from a lateral meristematic persistent inflorescence, lasting only a few days, synchronous with other plants of the same species in the immediate vicinity; fleshy. Lateral sepals connate at base and spreading towards the apices, together with the labellum and column-foot forming a small spur or saccate base. Dorsal sepal free often much smaller than the lateral sepals. Petals free and often smaller than the dorsal sepal. Labellum fleshy, sessile, rigid with distinct thickened callus of small glands on the laminar surface. Column short with truncate apex, and prominent staminodes. Pollinia small, hard waxy, yellow in two globose hemipollinia. Protocorm-seedling type narrowly isobilateral.

Distribution: throughout South-East Asia and Malesia.

Aporum acinaciforme (Roxb.) Griff., *Cal. J. Nat. Hist.* 5: 370 (1845).

Aporum albayense (Ames) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium albayense* Ames, *Philipp. J. Sc., Bot.* 7: 14 (1912).

Aporum aloifolium (Blume) Brieger, *Schltr., Die Orchideen*, 3 Aufl. 1: 676 (1981).

Aporum anceps (Sw.) Lindl., *Gen. Sp. Orch. Pl.* 71 (1830).

Aporum auyongii (T.Yukawa) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium auyongii* T.Yukawa, *Lindleyana* 13(1): 28, f.1 (1998).

Aporum babiense (J.J.Sm.) Rauschert, *Feddes Repert.* 94(7–8): 438 (1983).

Aporum banaense (Gagnep.) Rauschert, *Feddes Repert.* 94(7–8): 438 (1983).

Aporum basilanense (Ames) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium basilanense* Ames, *Philipp. J. Sc., Bot.* 7: 14–15 (1912).

Aporum bicornutum (Schltr.) Rauschert, *Feddes Repert.* 94(7–8): 438 (1983).

Aporum bilobulatum (Seidenf.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium bilobulatum* Seidenf., *Opera Bot.* 83: 218, f. 147 (1985).

Aporum brevimentum (Seidenf.) M.A.Clem. ***comb. nov.***
Basionym: *Dendrobium brevimentum* Seidenf., *Opera Bot.* 83: 225–226, f. 154 (1985).

Aporum calceolariae (J.König) M.A.Clem., ***comb. nov.***
Basionym: *Epidendrum calceolariae* J.König, *Retz. Obs.* 6: 45 (1791). *Dendrobium acerosum* Lindl., *Edwards' Bot. Reg.* 30: misc. 86 (1841).

Aporum capitellatoides (J.J.Sm.) Rauschert, *Feddes Repert.* 94(7–8): 438 (1983).

Aporum capitellatum (J.J.Sm.) Rauschert, *Feddes Repert.* 94(7–8): 438 (1983).

Aporum cochinchinense (Ridl.) Rauschert, *Feddes Repert.* 94(7–8): 438 (1983).

Aporum compressistylum (J.J.Sm.) Rauschert, *Feddes Repert.* 94(7–8): 438 (1983).

Aporum concavum (J.J.Sm.) Rauschert, *Feddes Repert.* 94(7–8): 438 (1983).

Aporum confusum (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium confusum* Schltr., *Repert. Spec. Nov. Regni Veg.* 10: 72 (1911).

Aporum crucilabre (J.J.Sm.) Rauschert, *Feddes Repert.* 94(7–8): 438 (1983).

Aporum curviflorum (Rolfe) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium curviflorum* Rolfe, *Kew Bull.* 281(1805).

Aporum dalatense (Gagnep.) Rauschert, *Feddes Repert.* 94(7–8): 439 (1983).

Aporum diaphanum (Schltr.) Rauschert, *Feddes Repert.* 94(7–8): 439 (1983).

Aporum distichum (Presl.) Rauschert, *Feddes Repert.* 94(7–8): 438 (1983).

Aporum escritorii (Ames) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium escritorii* Ames, *Orchidaceae* 5: 123 (1915).

Aporum ferdinandi (Kraenzl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium ferdinandi* Kraenzl. in Engl., *Pflanzenr. Orch.-Mon.-Dendr.* 1: 209 (1910).

Aporum flexile (Ridl.) Rauschert, *Feddes Repert.* 94(7–8): 439 (1983).

Aporum fuscum (O'Byrne) M.A.Clem., ***comb. et stat. nov***.
Basionym: *Dendrobium indivisum* (Blume) Miq. var. *fuscum* O'Byrne, *Malayan Orch. Rev.* 31: 21–22, 77, t. f. (1997).

Aporum grande (Hook.f.) Rauschert, *Feddes Repert.* 94(7–8): 439 (1983).

Aporum indivisum Blume, *Bijdr.* 6: 334. t. 39 (1825).

Aporum jenkinsii Griff., *Calc. J. Nat. Hist.* 5: 367, t. 25 (1854). *Dendrobium parciflroum* Rchb.f. ex Lindl., *J.Linn. Soc.* 3: 4 (1859).

Aporum jennae (O'Byrne) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium jennae* O'Byrne, *Malayan Orch. Rev.* 30: 24 (1996).

Aporum keithii (Ridl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium keithii* Ridl., *J. Linn. Soc.* 32: 247–248 (1896).

Aporum kentrophyllum (Hook.f.) Brieger, *Schltr., Die Orchideen* 3 (ed. 1): 676 (1981).

Aporum kiauense (Ames et C.Schweinf.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium kiauense* Ames et C.Schweinf., *Orchidaceae* 6: 103–105 (1920).

Aporum kjellbergii (J.J.Sm.) Rauschert, *Feddes Repert.* 94(7–8): 440 (1983).

Aporum korthalsii (J.J.Sm.) Rauschert, *Feddes Repert.* 94(7–8): 440 (1983).

Aporum kuyperi (J.J.Sm.) Rauschert, *Feddes Repert.* 94(7–8): 440 (1983).

Aporum leonis Lindl. in Edwards', *Bot. Reg.* 26: misc. 59–60 (1840).

Aporum litoreum (F.M.Bailey) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium litoreum* F.M.Bailey, *Queensl. Agric. J.* 16: 411 (1906).

Aporum lobatum Blume, *Bijdr.* 6: 334 (1825).

Aporum lobbii M.A.Clem., ***nom. nov***.
Basionym: *Dendrobium lobbii* Lindl., *J. Linn. Soc.* 3: 3 (1859), non Teijsm. et Binn. (1853).

Aporum lobulatum (Rolfe ex J.J.Sm.) Brieger, *Schltr., Die Orchideen* 3 Aufl. 1: 677 (1981).

Aporum lunatum (Lindl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium lunatum* Lindl., *J. Linn. Soc.* 3: 4 (1859).

Aporum macgregorii M.A.Clem., ***nom. nov***.
Basionym: *Dendrobium macgregorii* Ames, *Philipp. J. Sc., Bot.* 7: 17–18 (1912), non F.Muell. et Kraenzl. (1894); *Dendrobium quisumbingii* A.D.Hawkes et A.H.Heller, *Lloydia* 20: 123 (1957), *nom*.

Aporum mannii (Ridl.) Rauschert, *Feddes Repert.* 94(7–8): 440 (1983).

Aporum marivelense (Ames) Rauschert, *Feddes Repert.* 94(7–8): 440 (1983).

Aporum merrillii (Ames) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium merrillii* Ames, *Orchidaceae* 2: 181–182, f. (1908).

Aporum mindanaense (Ames) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium mindanaense* Ames, *Philipp. J. Sc., Bot.* 8: 423 (1914).

Aporum mirandum (Schltr.) Rauschert, *Feddes Repert.* 94(7–8): 440 (1983).

Aporum modestissimum (Kraenzl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium modestissimum* Kraenzl. in Engl., *Pflanzenr. Orch.-Mon.-Dendr.* 1: 206–207 (1910).

Aporum nathanielis (Rchb.f.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium nathanielis* Rchb.f. in Schill., *Cat. Orch.* (ed. 3). 26 (1857).

Aporum nycteridoglossum (Rchb.f.) Rauschert, *Feddes Repert.* 94(7–8): 441 (1983).

Aporum pendulicaule (Hayata) Rauschert, *Feddes Repert.* 94(7–8): 441 (1983).

Aporum porphyrophyllum (Guillaumin) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium porphyrophyllum* Guillaumin, *Bull. Mus. Hist. Nat. Paris* (ser. 2), 27: 395 (1955).

Aporum prostratum (Ridl.) Rauschert, *Feddes Repert.* 94(7–8): 441 (1983).

Aporum pseudoaloifolium (J.J.Wood) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium pseudoaloifolium* J.J.Wood, *Kew Bull.*, 39(1): 82–84, f. 7 (1984).

Aporum pseudoequitans (H.Fessel et E.Lückel) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium pseudoequitans* H.Fessel et E.Lückel, *Orchidee* 51(1): 83 (2000).

Aporum quadrilobatum (Carr) Rauschert, *Feddes Repert.* 94(7–8): 441 (1983).

Aporum ramificans (J.J.Sm.) Rauschert, *Feddes Repert.* 94(7–8): 441 (1983).

Aporum reflexibarbatulum (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium reflexibarbatulum* J.J.Sm., *Mitt. Inst. Bot. Hamburg* 7: 54, t. 8., f. 44 (1927).

Aporum reflexitepalum (J.J.Sm.) Rauschert, *Feddes Repert.* 94(7–8): 441 (1983).

Aporum rhodostele (Ridl.) Rauschert, *Feddes Repert.* 94(7–8): 441 (1983).

Aporum rhombopetalum (Kraenzl.) Rauschert, *Feddes Repert.* 94(7–8): 441 (1983).

Aporum rosellum (Ridl.) Rauschert, *Feddes Repert.* 94(7–8): 441 (1983).

Aporum roseonervatum (Schltr.) Rauschert, *Feddes Repert.* 94(7–8): 442 (1983).

Aporum roseostriatum (Ridl.) Rauschert, *Feddes Repert.* 94(7–8): 442 (1983).

Aporum sagittatum (J.J.Sm.) Rauschert, *Feddes Repert.* 94(7–8): 442 (1983).

Aporum salicornioides (Teijsm. et Binn.) Brieger in Schlechter *Die Orchideen*, 1(11–12): 676 (1981).

Aporum sambasanum (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium sambasanum* J.J.Sm., *Bull. Dép. Agric. Indes Néerl.* 22: 25 (1909).

Aporum shompenii (B.K.Sinha et P.S.N.Rao) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium shompenii* B.K.Sinha et P.S.N.Rao, *Nordic J. Bot.*, 18(1): 27–30, f. (1998).

Aporum sinuosum (Ames) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium sinuosum* Ames, *Orchidaceae* 7: 96 (1922).

Aporum smithianum (Schltr.) Rauschert, *Feddes Repert.* 94(7–8): 442 (1983).

Aporum spatella (Rchb.f.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium spatella* Rchb.f., *Hamb. Gartenz.* 21: 298 (1865).

Aporum sphenochilum (F.Muell. et Kraenzl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium sphenochilum* F.Muell. et Kraenzl., *Oest. Bot. Zeitschr.* 44(7): 254–255 (1894).

Aporum subpandifolium (J.J.Sm.) Rauschert, *Feddes Repert.* 94(7–8): 442 (1983).

Aporum subulatoides (Schltr.) Rauschert, *Feddes Repert.* 94(7–8): 442 (1983).

Aporum subulatum (Blume) Rauschert, *Feddes Repert.* 94(7–8): 442 (1983).

Aporum teloense (J.J.Sm.) Rauschert, *Feddes Repert.* 94(7–8): 442 (1983).

Aporum teres Rauschert, *Feddes Repert.* 94(7–8): 442 (1983).

Aporum terminale (Par. et Rchb.f.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium terminale* Par. et Rchb.f., *Trans. Linn. Soc.* 30: 149 (1874).

Aporum tetralobum (Schltr.) Rauschert, *Feddes Repert.* 94(7–8): 442 (1983).

Aporum thysanophorum (Schltr.) Rauschert, *Feddes Repert.* 94(7–8): 442 (1983).

Aporum uncatum (Lindl.) Brieger in Schltr., *Die Orchideen* 3 (ed. 1): 676 (1981).

Aporum vanhulstijnii (J.J.Sm.) Rauschert, *Feddes Repert.* 94(7–8): 443 (1983).

Aporum wenzelii (Ames) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium wenzelii* Ames, *Orchidaceae* 5: 144 (1915).

Aporum xanthoacron (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium xanthoacron* Schltr., *Bull. Herb. Boiss.* (ser. 2), 6: 459–460 (1906).

Aporum xiphophyllum (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium xiphophyllum* Schltr., *Repert. Spec. Nov. Regni Veg.* 9: 291–292 (1911).

Sixth major group

Species in this clade are in need of much additional study. Present evidence suggests that the group as a whole could be treated as a single genus with a number of infrageneric taxa, the first available name being *Coelandria*. However, further study is required on the remaining species in this major group before a decision can be made on their phylogenetic relationships and status. In the interim, it is here proposed that only those species that clearly fall into a small group directly containing *Coelandria smillieae*, be transferred to that genus.

Coelandria Fitzg., *Austral. Orch.* 1(7): [t. 2] (1882).

Type species: *Coelandria smillieae* (F. Muell.) Fitzg.

Erect, spreading to pendulous epiphytic, occasionally lithophytic herb. Stems robust, clustered, cylindric to cylindric-fusiform, not branching. Leaves membranous to leathery, seasonally deciduous, slightly recurved, linear-ovate to elliptic; sheaths slightly shorter to longer than internodes, papery, persistent. Inflorescences densely multi-flowered, bottle-brush like, lateral, usually on leafless stems; peduncle short, thick, cylindrical. Flowers, rigid, shiny, glabrous, white, pink, purple, orange, green, the labellum often contrasting in colour. Dorsal sepal small, ovate to obovate-oblong. Lateral sepals obliquely narrowly obovate to somewhat spatulate, fused at apex, truncate. Petals small, similar to dorsal sepal. Labellum cymbidiform, thick, fleshy, parallel to column-foot, embracing column, constricted nearest the base, fused to column-foot along basal margin, transverse callus. Column short, thick fleshy and very short stelidia, the stigma sunken, a prominent tooth-like, hard, rostellum, with large viscidia. Column-foot with central longitudinal groove, and nectary at base. Pollinia four, fused together, obovate, concave, light brown to blackish-blue, smooth waxy.

Distribution: Malesia and Australia.

Coelandria andreemillariae (T.M.Reeve) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium andreemillarae* T.M.Reeve, *Orchadian* 7: 130, f. 1 (1982).

Coelandria chrysoglossa (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium chrysoglossum* Schltr., *Repert. Spec. Nov. Regni Veg.*, Beih. 1: 509–510 (1912).

Coelandria coccinea (Kraenzl.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium coccineum* Kraenzl. in Engl., *Plfanz. Orch.-Mon.-Dendr.* 1:129–130 (1910).

Coelandria concavissima (J.J.Sm.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium concavissimum* J. J. Sm., *Bull. Jard. Bot. Buitenzorg* (ser. 2) 2: 11 (1911).

Coelandria fornicata (Schltr.) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium fornicatum* Schltr., *Repert. Spec. Nov. Regni Veg.*, Beih. 1: 509 (1912).

Coelandria fracta (T.M.Reeve) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium fractum* T. M. Reeve, *Orchadian* 7: 133–134, f. 3 (1982).

Coelandria glomerata (Rolfe) M.A.Clem., ***comb. nov.***
Basionym: *Dendrobium glomeratum* Rolfe, *Kew Bull.* 1894: 155 (1894); *Gard. Chron*. 1: 653, f. 80 (1894).

Coelandria obtusa (Schltr.) M.A.Clem., ***comb. nov***.
Basionym: *Dendrobium obtusum* Schltr. in K. Schum. et Lauterb., *Nachtr. Fl. Schutzgeb. Südsee* 177 (1905), non Rchb. f. (1861).

Coelandria smillieae (F. Muell.) Fitzg., *Austral. Orch.* 1(7): t. 2 (1882).
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