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MOLECULAR PHYLOGENETIC SYSTEMATICS IN DENDROBIEAE (ORCHIDACEAE)

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ABSTRACT

Molecular systematic research, using DNA sequences of the internal transcribed spacer (ITS) region of the 18–26S nuclear ribosomal repeat unit, was conducted on a broadly representative sample of the tribe Dendrobieae. The results provide independent support, in addition to evidence from plastid DNA analysis and morphology, for the phylogenetic reassessment of the taxon. At a broad level, Dendrobieae are polyphyletic with *Dendrobium* sect. *Oxystophyllum* being deeply embedded within one of the outgroup taxa, subtribe Eriinae: Podochileae. The remaining taxa form a weakly supported monophyletic group consisting of three major clades, *Epigeneium*, sister to predominantly Asian and Australasian clades. This author has formally recognized these as Epigeneiinae, Dendrobiinae s.s., and Grastidiinae, respectively. Detailed studies using species representative of all major historical taxonomic groups within those subtribes provide strong support for the continued recognition of the genera *Cadetia*, *Diplocaulobium*, and *Flickingeria*, all of which are deeply embedded within Grastidiinae and far removed from *Dendrobium* s.s. in Dendrobiinae. These studies have also identified numerous other strongly supported clades that group species predominantly on the basis of synapomorphic vegetative rather than floral characters. The recognition of these morphologically distinct monophyletic groups as genera is considered to be phylogenetically more informative, predictive, and realistic than any of the previously offered alternatives.

Key words: Dendrobieae, *Dendrobium*, ITS, molecular phylogenetic systematics, Orchidaceae.

INTRODUCTION

Historically, the tribe Dendrobieae was recognized as comprising a large, diverse group of epiphytic, lithophytic, and terrestrial herbs characterized primarily by possession of naked pollinia, lacking caudicles or appendages but with a prominent column foot (Dressler 1993). Lindley considered Dendrobieae nested within the tribe Podochileae, differentiated by the possession of eight pollinia, and the tribe Vandeeae with its monopodial habit and complex stiped pollinia. Within Dendrobieae two subtribes are recognized, Dendrobiinae with 6 genera and 1147 species, and Bulbophyllinae with 15 genera and 1116 species. Species within Dendrobiinae are distributed predominantly throughout tropical regions with extensions to temperate Asia (Veitch 1888; Seidenfaden 1985, 1992; Schlepe and Stewart 1990; Seidenfaden and Woods 1992; O'Byrne 2001), the Philippines (Ames 1908; Valmayor 1981, 1984), the Malay Archipelago (Smith 1905a, b; Comber 1990, 2001; Wood et al. 1993; Wood and Cribb 1994), New Guinea (Schlechter 1912; van Royen 1979), Australia (Rupp and Hunt 1947; Dockrill 1969, 1992; Jones 1988), New Caledonia (Hallé 1977), the southwest Pacific Islands (Lewis and Cribb 1989, 1991; Kores 1991; Cribb and Whistler 1996), and New Zealand (Moore 1970). By comparison, species in Bulbophyllinae have a predominantly pantropical distribution with similar extensions into temperate Asia, Australia, and New Zealand (Rupp and Hunt 1947; Dockrill 1969; Moore 1970; Vermeulen 1987, 1991, 1993; Jones 1988). Both phylogenetic relationships among the tribes and their monophyly, based on molecular analysis of both plastid and nuclear genes have been confirmed in broader studies of the family (Cameron et al. 1999).

Members of Dendrobiinae species vary considerably in their floral and vegetative morphology, especially in the southern part of their range. 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).

HISTORICAL BACKGROUND

The subtribe Dendrobiinae was created in 1829, as a subdivision within tribe Malaxideae Lindl., accompanying the description and illustration of *Dendrobium secundum* published in *The Botanical Magazine* (Lindley 1829). Soon after Lindley (1830–1840) enunciated his concept of a subtribe embracing 20 genera and grouping them together on the possession of two, four, or eight pollinia. *Dendrobium* was grouped together with ten other genera including *Aporum*, *Macrostomium* Blume, *Bulbophyllum* Thouars, and *Polystachya* Hook. on account of the possession of four naked pollinia. Over the next century most authors, including Lindley and Paxton (1851), progressively narrowed the interpretation of Dendrobiinae (Lindley 1859; Reichenbach 1861; Bentham 1873, 1883; Pfitzer 1887, 1889; Schlechter 1905, 1912, 1926), so as to recognize one very large genus *Dendrobium*, with a complex infrageneric classification system, as well as *Cadetia* and *Pseuderia*. Conversely, other authors, such as Kraenzlin (1910), in his complex and confusing thesis on Dendrobiinae, proposed an alternative classification in which he included *Cadetia* within a broader *Dendrobium*, as well as reinstating and recognizing several segregate genera within the subtribe, viz. *Dendrobium*, *Callista*, *Inobulbon*,

Sarcopodium Lindl., *Diplocaulobium*, *Desmotrichum* Blume, and *Adrorhizon* Hook.f. While the proposed changes, *Callista* and *Inobulbon*, have mostly been rejected, others have gradually gained acceptance, i.e., *Sarcopodium* (as *Epigeneium*), *Diplocaulobium*, *Desmotrichum* (as *Flickingeria*), or transferred to another tribe, *Adrorhizon*. Consequently, toward the end of the twentieth century most authors recognized six genera within the subtribe, viz. *Cadetia* (67 spp.), *Dendrobium* (ca. 900 spp.), *Diplocaulobium* (94 spp.), *Epigeneium* (12 spp.), *Flickingeria* (70 spp.), and *Pseuderia* (4 spp.) (Seidenfaden 1985; Dressler 1993).

However, the systematic position and presumed monophyly of Dendrobiinae sensu Schlechter (1926) was challenged when Brieger (1981) published an account of the group as part of a revised classification of the family. He noted that historically the circumscription of the genera had taken a peculiar course. In particular, Lindley had united a great number of taxa into two huge collective genera, *Dendrobium* and *Eria*. A consequence of this approach was that, with the description of many additional species, it became necessary to create a sometimes complex, infrageneric classification to accommodate the various forms. Brieger (1981) took the classification of subtribes Dendrobiinae and Eriinae to new levels of confusion by 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. During this process, he reinstated, recognized, and described many new genera. The systematic position of Dendrobiinae and Eriinae also came under scrutiny. Using patterns of embryological development from reproductive biology studies of the family, a plethora of embryo types were discovered, especially within Dendrobiinae (Clements 2002). Considering the highly conserved nature of embryological developmental types in other tribes observed within the family, the differences that exist in the representative subsample of Dendrobiinae and Eriinae seemed significant. These results suggested that Dendrobiinae, and more particularly *Dendrobium*, was polyphyletic with respect to Eriinae (Podochileae). At about the same time, results from phylogenetic analyses of *rbcL* and *matK* plastid sequences in Dendrobiinae (Yukawa et al. 1993, 1996, 2000; Yukawa and Uehara 1996) also arrived at a similar set of conclusions, where Dendrobiinae were shown to comprise four major clades: (i) *Pseuderia*, which was shown to belong to Podochilinae (Yukawa et al. 1996); (ii) *Epigeneium*; (iii) *Dendrobium* clade 1 containing species predominantly inhabitant of 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 unpublished developmental biology and published molecular results, as well as observed morphological and biological differences, that genera such as *Dockrillia* (Clements and Jones 1996), *Grastidium* (Clements and Jones 1997), *Inobulbon* (Clements and Jones 1998a), *Tetrodon* (Clements and Jones 1998a), *Winika* (Clements et al. 1997), *Cannaeorchis* (Clements and Jones 1998b), *Bouletia*, *Cepobaculum*, *Ceraia*, *Ceratobium*, *Davejonesia*, *Dendrobates*, *Durabaculum*, *Eleutheroglossum*, *Thelychiton* and *Tropilis* (Clements and Jones 2002), from

the Malesian and Australasian regions, were recognized, reinstated, or described.

Since that time, considerable research using both molecular and morphological data has been undertaken on the group, resulting in proposals for considerable change in our interpretation of these taxa (Clements 2003). This paper aims to reiterate, update, and expand on results already published, as well as focus on the status of tribe Dendrobieae and major phylogenetic relationships within these taxa.

METHODS

Plant Material

Material of 143 species, representative of the majority of the principal taxonomic groups within Dendrobieae, especially those within *Dendrobium*, was used in this study (Table 1). Outgroups were chosen on the basis of previous studies by Cameron et al. (1999), including those roughly equivalent to the ones used by Yukawa et al. (1996, 2000) and comprised species of *Cypripedium*, *Paphiopedilum* (Cypripedioideae), *Nervilia* (Nervilieae), *Liparis* (Malaxideae), *Bryobium*, *Eria* (Eriinae: Podochileae), *Adelopetalum*, *Blepharochilum*, *Bulbophyllum*, *Oxysepala*, *Serpenticaulis* (Bulbophyllinae: Dendrobieae), *Drymoanthus* (Aeridinae: Vandeeae) (see Table 1 from Clements 2003). Species used in this study were carefully chosen from among representatives of the ca. 350 species in the study group for which sequences were available. Fresh leaf samples were collected either in the field or from cultivated plants, mostly from the Australian National Botanic Gardens (formerly Canberra Botanic Gardens) collection, and vouchers were deposited at the Australian National Herbarium (CANB).

Morphological Data

For each species, data was collected on plant habitat, plant habit, and inflorescence development, as well as detailed floral morphology. Protocorm and seedling developmental morphology were also recorded for many species.

DNA Extraction, 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 Diurideae (Clements et al. 2002). The complete sequence of the ITS-1–5.8S–ITS-2 region for each sample was determined using Sequencher vers. 3.0 software (Gene Codes Corporation, Ann Arbor, Michigan, USA) to edit and assemble the sequencing chromatograms. Sequences used have been submitted to GenBank and given accession numbers (see Clements 2003).

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 secondarily manually aligned, using BioEdit vers. 4.7.8, and the aligned files converted to a PAUP/NEXUS file. The aligned file was then exported through MacClade

Table 1. Collection details of the species used for these analyses. *Abbreviations for Australian Botanical Districts: Nsc = New South Wales, South Coast; Ncc = New South Wales, Central Coast; Qco = Queensland, Cook; Qkn = Queensland, Kennedy North; Qmo = Queensland, Moreton; Ddg = Northern Territory, Darwin and Gulf. **ORG = Orchid Research Group. ***CBG = Canberra Botanic Gardens (now the Australian National Botanic Gardens). RSBG = Royal Sydney Botanic Gardens. NP = National Park; SF = State Forest. Taxa without GenBank accession numbers are to be submitted at a later date.

Species	Provenance	Collector no.	GenBank accession no.
<i>Aedelopetalum bracteatum</i> Fitzg.	cult. ex Qmo*; Queen Mary Falls NP	Crane 2138 (CANB)	AY239945
<i>Bryobium eriaeoides</i> (F. M. Bailey) M. A. Clem. & D. L. Jones	cult. ex Qkn; Kirrima SF	Mackenzie 25/98 (CANB)	
<i>B. pubescens</i> Lindl.	cult. ex Christmas Is.	Ziesing 307 (CANB)	AY239946
<i>Bulbophyllum baileyi</i> F. Muell.	cult. ex Qco; Moa Is.	Jones 3598 (CANB)	
<i>B. kirkwoodiae</i> T. E. Hunt	cult. ex Qco; Mt. Lewis	ORG** 1041 (CANB)	
<i>B. macphersonii</i> Rupp	Qkn; Kirrima SF	Mackenzie 27/98 (CANB)	
<i>B. nutans</i> Thouars	cult. ex Mauritius	Clements 8108 (CANB)	AY239947
<i>Cadetia chionantha</i> Schltr.	cult. ex Papua New Guinea (PNG); Ambua	Clements 9306 (CANB)	
<i>C. maideniana</i> (Schltr.) Schltr.	cult. ex Qco; Mossman Gorge NP	Jones 4311 (CANB)	AY239948
<i>C. taylori</i> (F. Muell.) Schltr.	cult. ex Qco; Mt. Lewis	CBG ***721695 (CANB)	
<i>C. waryana</i> Schltr.	cult. ex Qco; Iron Range	CBG 721286 (CANB)	
<i>Cannaeorchis cymatoleguua</i> (Schltr.) M. A. Clem. & D. L. Jones	cult. ex New Caledonia (NC); Yaté Rd.	Clements 9382 (CANB)	
<i>C. fractiflexa</i> (A. Finet) M. A. Clem. & D. L. Jones	cult. ex NC; Yaté Rd.	Clements 9348 (CANB)	AY239949
<i>Coelandria smillieae</i> (F. Muell.) Fitzg.	cult. ex Qco; Captain Billy Cr.	Jones 8795 (CANB)	AY239996
<i>Cypripedium pubescens</i> Willd.	cult. ex N. America	Lesemann s.n. [May 1997]	
<i>Dendrobium agathodaemonis</i> J. J. Sm.	cult. ex Indonesia; Irian Jaya	Rose (S 926) (CANB)	AY239950
<i>D. agrostophyllum</i> F. Muell.	cult. ex Qco; Atherton	ORG 3604	
<i>D. alexandrae</i> Schltr.	cult. ex PNG; Waja	ORG 4218 (CANB)	
<i>D. aloifolium</i> (Blume) Rchb. f.	cult. ex Thailand	Clements 9168 (CANB)	AY239951
<i>D. amabile</i> (Lour.) O'Brien	cult. ex Vietnam	Slattery 1 (CANB)	
<i>D. amethystoglossum</i> Rchb. f.	cult. ex Philippines	Cootes (ORG 1482) (CANB)	AY239952
<i>D. anceps</i> Sw.	cult. ex Philippines	Clements 9309 (CANB)	AY239953
<i>D. antennatum</i> Lindl.	cult. ex Indonesia; [Irian Jaya]	ORG 1506 (CANB)	
<i>D. austracaledonicum</i> Schltr.	cult. ex NC; Rivière Bleue	Clements 9400 (CANB)	
<i>D. bicaudatum</i> Reinw. ex Lindl.	cult. ex Philippines; Mindonou	Cootes (ORG 1286) (CANB)	
<i>D. bifalce</i> Lindl.	cult. ex Qco; McIlraith Range	Butler 496 (CANB)	
<i>D. bigibbum</i> Lindl.	cult. ex Qco; Edward R.	Wallace 7/95 (CANB)	
<i>D. bilobum</i> Lindl.	cult. ex PNG; Botopuro	Clements 6612 (CANB)	
<i>D. bracteosum</i> Rchb. f.	cult. ex PNG	CBG 750451 (CANB)	AY239954
<i>D. bulbophylloides</i> Schltr.	cult. ex PNG; Lufa District	CBG 770904 (CANB)	
<i>D. camptoctrum</i> Schltr.	cult. ex Fiji; near Namsori	Clements 5830 (CANB)	AY239955
<i>D. canaliculatum</i> R. Br.	cult. ex Qco; Heathlands	Jones 8942 (CANB)	
<i>D. capitisyork</i> D. L. Jones & M. A. Clem.	cult. ex Qco; Iron Range	Wrigley 268 (CANB)	
<i>D. capituliflorum</i> Rolfe	cult. ex PNG; Wassabamal	Clements 6319 (CANB)	AY239956
<i>D. carrii</i> Rupp & C. T. White	cult. ex Qco; Mt. Haig	Wallace (ORG 4284) (CANB)	
<i>D. cauliculimentum</i> R. S. Rogers	cult. ex PNG	ORG 3598 (CANB)	AY239957
<i>D. ceraula</i> Rchb. f.	cult. ex Philippines	ORG 2921 (CANB)	AY239958
<i>D. cerinum</i> Rchb. f.	cult. ex Philippines	Cootes (ORG 3585) (CANB)	AY239959
<i>D. chalmersii</i> F. Muell.	cult. ex PNG	Clements 5841 (CANB)	
<i>D. chameleon</i> Ames	cult. ex Philippines	ORG 3590 (CANB)	AY239960
<i>D. compactum</i> Rolfe ex W. Hackett	cult. ex China; Yunnan	Wallace 90/747 (CANB)	

Table 1. Continued.

Species	Provenance	Collector no.	GenBank accession no.
<i>D. confusum</i> Schltr.	cult. ex PNG	<i>Banks (ORG 1391)</i> (CANB)	AY239961
<i>D. coxii</i> F. M. Bailey	cult. ex PNG; Botopuro	<i>Clements 6649</i> (CANB)	
<i>D. crassicaule</i> Schltr.	cult. ex NC; Mt. Ouinne	<i>Clements 11267</i> (CANB, NOU)	
<i>D. aff. crocatum</i> Hook. f.	cult. ex Indonesia; Sumatra	<i>Smedley s.n.</i> [28 May 1997] (CANB)	AY239962
<i>D. crumenatum</i> Sw.	cult. ex Thailand	<i>Clements 4890</i> (CANB)	AY239963
<i>D. crumenatum</i>			AF521608
<i>D. cyanocentrum</i> Schltr.	cult. ex PNG; Subatana Sawmill	<i>Spence (Clements 8709)</i> (CANB)	AY239964
<i>D. delacourii</i> Guillaumin	cult. ex Thailand	<i>ORG 1278</i> (CANB)	
<i>D. dicuphum</i> F. Muell.	cult. ex Ddg; Darwin area	<i>Clements 8698</i> (CANB)	
<i>D. dixanthum</i> Rchb. f.	cult. ex Thailand	<i>Clements 9175</i> (CANB)	
<i>D. ellipsophyllum</i> T. Tang & F. T. Wang	cult. ex Thailand	<i>Banks (ORG 3581)</i> (CANB)	AY239965
<i>D. exile</i> Schltr.	cult. ex China	<i>Wallace 16/94</i> (CANB)	
<i>D. fairchildiae</i> Ames & Quisumb.	cult. ex Philippines; Bukidnon	<i>Cootes (Clements 1485)</i> (CANB)	AY239966
<i>D. falconeri</i> Hook.	cult. ex Thailand	<i>ORG 3577</i> (CANB)	
<i>D. finetianum</i> Schltr.	cult. ex NC; Ouinne R.	<i>Clements 7957</i> (CANB)	
<i>D. formosum</i> Roxb. ex Lindl.	cult. ex Thailand	<i>Phillips 457</i> (CANB)	AY239967
<i>D. fulgidum</i> Schltr.	cult. ex PNG	<i>Banks (ORG 3599)</i> (CANB)	AY239968
<i>D. fuscum</i> Fitzg.	cult. ex Qco; Captain Billy Cr.	<i>Jones 8780</i> (CANB)	
<i>D. fytchianum</i> Batem.	cult. ex Burma	<i>Clements 9437</i> (CANB)	
<i>D. gibsonii</i> Lindl.	cult. ex Thailand	<i>ORG 4162</i> (CANB)	
<i>D. golfinchii</i> F. Muell.	cult. ex PNG; Wassabamal	<i>Clements 5860</i> (CANB)	AY239969
<i>D. goldschmidtianum</i> Kraenzl.	cult. ex Taiwan	<i>ORG 3465</i> (CANB)	AY239970
<i>D. govidjoae</i> Schltr.	cult. ex PNG; Garassa	<i>Clements 6810</i> (CANB)	AY239971
<i>D. hainanense</i> Rolfe	cult. ex China	<i>ORG 1574</i> (CANB)	
<i>D. harveyanum</i> Rchb. f.	cult. ex Thailand	<i>CBG 9101155P</i> (CANB)	
<i>D. hellerianum</i> A. D. Hawkes	cult. ex PNG; Karkar Is.	<i>Clements 5927</i> (CANB)	
<i>D. herpethophytum</i> Schltr.	cult. ex PNG; Kandep Divide via Laiagam	<i>ORG 1384</i> (CANB)	
<i>D. indivisum</i> (Blume) Miq.	cult. ex Malaya; Langkawi	<i>Vaughn (Clements 5822a)</i> (CANB)	AY239972
<i>D. inflatum</i> Rolfe	cult. ex Indonesia; Bali	<i>Clements 5820</i> (CANB)	AY239973
<i>D. ionopus</i> Rchb. f.	cult. ex Philippines	<i>Cootes (ORG 3589)</i> (CANB)	AY239974
<i>D. jacobsonii</i> J. J. Sm.	cult. ex Indonesia	<i>ORG 3187</i> (CANB)	
<i>D. jenkinsii</i> Wall. ex Lindl.	cult. ex Thailand	<i>Clements 7353</i> (CANB)	
<i>D. junceum</i> Lindl.	cult. ex Philippines	<i>ORG 3588</i> (CANB)	AY239975
<i>D. kempterianum</i> Schltr.	cult. ex PNG; Wassabamal	<i>Clements 6334</i> (CANB)	
<i>D. lancifolium</i> A. Rich.	cult. ex Indonesia; Sulawesi	<i>Clements 9176</i> (CANB)	AY239976
<i>D. lawesii</i> F. Muell.	cult. ex PNG	<i>Spence D54</i> (CANB)	AY239977
<i>D. leonis</i> (Lindl.) Rchb. f.	cult. ex Thailand	<i>ORG 1983</i> (CANB)	AY239978
<i>D. lichenastrum</i> F. Muell.	Qkn; Kirrima SF	<i>Mackenzie 26/98</i> (CANB)	
<i>D. lindleyi</i> Steud.	cult. ex Thailand	<i>CBG 8915636</i> (CANB)	
<i>D. luecohybos</i> Schltr.	cult. ex PNG; Torricelli Mts.	<i>Clements 9600</i> (CANB)	
<i>D. margaritaceum</i> A. Finet	cult. ex China; Yunnan	<i>ORG 3463</i> (CANB)	
<i>D. microbulbum</i> A. Rich	cult. ex Sri Lanka	<i>ORG 3190</i> (CANB)	
<i>D. mohlianum</i> Rchb. f.	cult. ex Fiji	<i>ORG 3606</i> (CANB)	AY239980
<i>D. moniliforme</i> (L.) Sw.	cult. ex Japan	<i>CBG 9804252</i> (CANB)	AY239981
<i>D. monophyllum</i> F. Muell.	cult. ex Qmo; Kin Kin	<i>Crane 1965</i> (CANB)	

Table 1. Continued.

Species	Provenance	Collector no.	GenBank accession no.
<i>D. monticola</i> P. F. Hunt & Summerh.	cult. ex Thailand	ORG 1276 (CANB)	
<i>D. morrisonii</i> Schltr.	cult. ex Vanuatu	Phillips 1069 (CANB)	AY239982
<i>D. moschatum</i> (Buch-Ham.) Sw.	cult. ex Thailand	Clements 5808 (CANB)	AY239983
<i>D. mutabile</i> (Blume) Lindl.	cult. ex Indonesia; Java	ORG 3608 (CANB)	AY239984
<i>D. ngoyense</i> Schltr.	cult. ex NC; Cr. Pernod	Clements 7865 (CANB)	
<i>D. nindii</i> W. Hill	cult. ex Qco; Daintree R.	Jones 4285 (CANB)	AY239985
<i>D. nothofagicola</i> T. M. Reeve	cult. ex PNG	ORG 3600 (CANB)	AY239986
<i>D. oppositifolium</i> Kraenzl.	cult. ex NC; Yaté Rd.	Clements 9380 (CANB)	
<i>D. paludicola</i> Schltr.	cult. ex Qco; Heathlands	Jones 8922 (CANB)	
<i>D. papilio</i> Loher	cult. ex Philippines	Cootes (Clements 9202) (CANB)	AY239987
<i>D. pectinatum</i> A. Finet	cult. ex NC; Montagne des Sources	Ziesing 224 (CANB)	
<i>D. peguanum</i> Lindl.	cult. ex Thailand	ORG 1987 (CANB)	
<i>D. philippinense</i> Ames	cult. ex Philippines; Malibago	ORG 1499 (CANB)	AY239988
<i>D. pleianthum</i> Schltr.	cult. ex PNG; Kundiawa	CBG 770785 (CANB)	
<i>D. prenticei</i> F. Muell.	cult. ex Qco; Barong	RBGS 862945 (NSW)	
<i>D. punamense</i> Schltr.	cult. ex PNG; New Ireland	Clements 8266 (CANB)	
<i>D. quadrangulare</i> Parish & Rchb. f.	cult. ex Thailand	ORG 1277 (CANB)	AY239989
<i>D. aff. rarum</i> Schltr.	cult. ex Vanuatu; Espirato Santo	Clements 5613 (CANB)	AY239990
<i>D. rhododioides</i> P. Royen	cult. ex PNG	ORG 3601 (CANB)	AY239991
<i>D. sanderæ</i> Rolfe	cult. ex Philippines	Clements 7438 (CANB)	
<i>D. sanderæ</i> var. <i>parviflorum</i> Anschutz ex Quisumb.	cult. ex Philippines	ORG 2922 (CANB)	
<i>D. sanguinolentum</i> Lindl.	cult. ex Malaya; Kedah Pk.	Vaughn s.n. (RBGS 81030) (CANB, NSW)	AY239992
<i>D. secundum</i> (Blume) Lindl.	cult. ex Thailand	Clements 5377 (CANB)	AY239993
<i>D. semifusum</i> (Rchb. f.) Lavarack & P. J. Cribb	cult. ex Qco; Shiptons Flat	ORG 3776 (CANB)	
<i>D. senile</i> Parish ex Rchb. f.	cult. ex Thailand	ORG 3466 (CANB)	
<i>D. serratilabium</i> L. O. Williams	cult. ex Philippines; Luzon, Laguna	Cootes (Clements 9180) (CANB)	AY239994
<i>D. setigerum</i> Ames ex M. A. Clem.	cult. ex Philippines	Spence (Clements 8704) (CANB)	AY239979
<i>D. sinuatum</i> (Lindl.) Lindl. ex Rchb. f.	cult. ex Thailand	ORG 3615 (CANB)	AY239995
<i>D. sophronites</i> Schltr.	cult. ex PNG; Tari Gap	Clements 8583 (CANB)	AY239997
<i>D. speciosum</i> Sm.	cult. ex Nsc; Pidgeon House Mt.	Clements 5058 (CANB)	AY239998
<i>D. spectabile</i> (Blume) Miq.	cult. ex PNG; Garassa	Clements 6455 (CANB)	
<i>D. aff. spurium</i> (Blume) J. J. Sm.	cult. ex Philippines	ORG 3582 (CANB)	
<i>D. stuartii</i> F. M. Bailey	Qco; Mt. Finnigan	Roberts (ORG 3780) (CANB)	AY239999
<i>D. subuliferum</i> Schltr.	cult. ex PNG; Torricelli Mts.	Clements 9523 (CANB)	AY240000
<i>D. terrestre</i> J. J. Sm.	cult. ex PNG; Mt. Albert Edward	OERG 3567 (CANB)	
<i>D. tetragonum</i> A. Cunn.	cult. ex Qmo; Jimma SF	Jones 5889 (CANB)	
<i>D. thysiflorum</i> Rchb. f.	cult. ex Thailand	Clements 5163 (CANB)	AY240001
<i>D. toressæ</i> F. M. Bailey	cult. ex Qco; Palmeston Hwy.	Wallace 30/92 (CANB)	
<i>D. truncatum</i> Lindl.	cult. ex Malaya; Tamannegara	Vaughn (Clements 5806) (CANB)	AY240002
<i>D. usteroides</i> Schltr.	cult. ex Philippines; Bulalacao	ORG 3000 (CANB)	AY240003
<i>D. victoriae-reginae</i> Loher	cult. ex Philippines	Cootes (ORG 1484) (CANB)	AY240004
<i>D. violaceum</i> Kraenzl.	cult. ex PNG	ORG 3597 (CANB)	AY240005
<i>D. virotii</i> Guillaumin	cult. ex NC; Yaté Rd.	Clements 9376 (CANB)	
<i>D. yeageri</i> Ames & Quisumb.	cult. ex Philippines	ORG 3580 (CANB)	AY240006
<i>D. ypsilon</i> Seidenf.	cult. ex Thailand	ORG 4470 (CANB)	

Table 1. Continued.

Species	Provenance	Collector no.	GenBank accession no.
<i>Diplocaulobium angustipetalum</i> W. Harris & M. A. Clem.	cult. ex PNG	<i>Clements 9631</i> (CANB)	
<i>D. glabrum</i> J. J. Sm.	cult. ex Qmo; McIlraith Range	<i>CBG 8805059</i> (CANB)	
<i>D. ischnopetalum</i> Kranzlin	cult. ex PNG; Oomsis near Lae	<i>Clements 7270</i> (CANB)	AY240007
<i>D. regale</i> (Schltr.) A. D. Hawkes	cult. ex PNG; Andita	<i>CBG 78041434</i> (CANB)	
<i>Dockrillia calamiformis</i> (Lodd.) M. A. Clem. & D. L. Jones	cult. ex Qco; Russell R.	<i>ORG 3469</i> (CANB)	AY240008
<i>D. dolichophylla</i> (D. L. Jones & M. A. Clem.) M. A. Clem. & D. L. Jones	cult. ex Qmo; Brisbane Forest Park	<i>Clements 9363</i> (CANB)	
<i>D. linguiformis</i> (Sw.) Brieger	cult. ex Nsc; Crows Nest	<i>Crane 1229</i> (BRI, CANB)	
<i>Drymoanthus flavidus</i> St. George & Molloy	New Zealand; Pounaweia	<i>Molloy 207/00</i> (CHR)	AY240009
<i>Epigeneium amplum</i> (Lindl.) Summerh.	cult. ex India	<i>Banks</i> (ORG 4064) (CANB)	AY240010
<i>E. cymbidioides</i> (Blume) Summerh.	cult. ex Indonesia; Java	<i>ORG 3609</i> (CANB)	AY240011
<i>E. nakaharaei</i> (Schltr.) Summerh.	cult. ex Taiwan	<i>Clements 9167</i> (CANB)	AY240012
<i>E. triflorum</i> (Blume) Summerh.	cult. ex Indonesia; Java	<i>ORG 3591</i> (CANB)	AY240013
<i>Eria coronaria</i> Rchb. f.	cult. ex China	<i>ORG 3594</i> (CANB)	
<i>E. aff. javanica</i> (Sw.) Blume	cult. ex PNG	<i>CBG 740854</i> (CANB)	AY240014
<i>E. kingii</i> F. Muell.	cult. ex Qco; Mossman Gorge	<i>Jones 4305</i> (CANB)	
<i>Flickingeria clemetsii</i> D. L. Jones	cult. ex Qco; Iron Range	<i>Wrigley 354</i> (CANB)	AY240015
<i>F. fimbriata</i> (Blume) A. D. Hawkes	cult. ex Indonesia	<i>OOB001-841</i> (CANB)	
<i>F. interjecta</i> (Ames) A. D. Hawkes	cult. ex Philippines	<i>Banks s.n.</i> [Feb 1998] (CANB)	
<i>F. aff. rhipidoloba</i> (Schltr.) A. D. Hawkes	cult. ex PNG; Garassa	<i>Clements 6666</i> (CANB)	
<i>Grastidium angraecifolium</i> (Schltr.) M. A. Clem. ined.	cult. ex PNG; Wassabamal	<i>CBG 9012913</i> (CANB)	
<i>G. baileyi</i> (F. Muell.) Rasuchert	cult. ex Qco; Milla Milla	<i>Jones 4165</i> (CANB)	AY240016
<i>G. kenjianum</i> (Schltr.) Rauschert	cult. ex PNG; Imbram Gorge	<i>Clements 7249</i> (CANB)	
<i>G. luzonense</i> (Lindl.) M. A. Clem. & D. L. Jones	cult. ex Philippines	<i>Clements 9179</i> (CANB)	
<i>Inobulbum layardii</i> (F. Muell. & Kraenzl.) M. A. Clem. & D. L. Jones	cult. ex NC; Mt. Koghis	<i>Ziesing 270</i> (CANB)	
<i>Liparis fleckeri</i> Nicholls	cult. ex Qco; Mt. Lewis	<i>d'Aubert 67/88</i> (CANB)	
<i>L. habenarina</i> (F. Muell.) Benth.	cult. ex Qco; Stony Cr.	<i>Roberts</i> (ORG 2154) (CANB)	AY240017
<i>Nervilea aragoanna</i> Gaud.	cult. ex Qco; Breakfast Cr.	<i>ORG 2048</i> (CANB)	
<i>N. dallachyana</i> (Benth.) Schltr.	cult. ex Qco; Stony Cr.	<i>ORG 2045</i> (CANB)	
<i>Oxysepala ovalifolia</i> Wight	cult. ex Malaysia; Taiping	<i>RSBG 810771</i> (CANB, NSW)	AY240018
<i>Paphiopedilum rothchildianum</i> (Rchb. f.) Stein	cult. ex Sabah; Mt. Kinabalu	<i>CBG 8414202</i> (CANB)	
<i>Sayeria paradoxa</i> Kraenzl.	cult. ex PNG; Auir	<i>Clements 8568</i> (CANB)	
<i>Thelychiton macropus</i> Endl.	cult. ex Norfolk Is.	<i>Ziesing 345</i> (CANB)	
<i>Tropilis aemula</i> (R. Br.) Raf.	cult. ex Qmo; Brisbane Forest Park	<i>Clements 9358</i> (CANB)	
<i>T. callitrophilis</i> (B. Gray & D. L. Jones) M. A. Clem. & D. L. Jones	cult. ex Qco; Mt. Finnigan	<i>ORG 3777</i>	
<i>Winika cunninghamii</i> (Lindl.) M. A. Clem, D. L. Jones & Molloy	cult. ex New Zealand; Lincoln	<i>Molloy 061/98</i> (CANB, CHR)	AY240019
<i>W. aff. cunninghamii</i>	cult. ex New Zealand	<i>ORG 3605</i>	

(Maddison and Maddison 1992) for analysis using PAUP* vers. 4.0b4a (Swofford 1998). The most-parsimonious trees were determined using a heuristic search algorithm with 100 replicates of random taxon addition, tree bisection reconnection (TBR) branch swapping and the MULTREES option, generating a consensus tree. Successive weighting (Farris 1969) was applied through recalculation of the rescaled consistency indices until a stable topology was attained. Bootstrap analyses were done for both unweighted and successive weighted trees, to determine the relative support for the clades (Felsenstein 1985) and all minimal-length trees were saved.

At the tribal level, an assessment of Dendrobieae, centered on 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: Dendrobieae), *Liparis* (Malaxideae) and *Drymoanthus* (Aceridinae: Vandae). A second and more comprehensive analysis was then undertaken based on 142 species, including representatives of all major historically recognized taxa within Dendrobiinae plus a number of outgroup taxa, viz. *Cypripedium*, *Paphiopedilum* (Cypripedioideae), *Nervilia* (Nervilieae), *Liparis* (Malaxideae), *Bryobium*, *Eria* (Eriinae: Podochileae), and *Adelopetalum*, *Blepharochilum*, *Bulbophyllum*, *Oxysepala*, *Serpenticaulis* (Bulbophyllinae: Dendrobieae).

RESULTS

An assessment of Dendrobieae using 23 representative species produced an alignment that contains 786 nucleotide sites of which 324 were potentially parsimony informative. Analysis of this computer-generated alignment produced three equally, near identical parsimonious trees; tree length (L) = 1440, consistency index (CI) = 0.5743, retention index (RI) = 0.4853, and rescaled consistency index (RC) = 0.2787. One of these trees is shown and compared with that of Yukawa et al. (1993; Fig. 1). These results show, for the ITS tree, a polyphyletic Dendrobiinae with: (i) *D. govidjoae* and *D. sinuatum*, two species representative of *Dendrobium* sect. *Oxystophyllum*, deeply embedded within a strongly supported (100% bootstrap support), monophyletic Eriinae (Podochileae); (ii) a strongly supported (96% bootstrap support), monophyletic *Epigeneium*, sister to the remainder of Dendrobiinae; and (iii) the remaining representatives of Dendrobiinae separated into two major groups, the Australasian and Asian clades. Excluding *Dendrobium* sect. *Oxystophyllum*, these results reveal only weak support (< 50% bootstrap support) for the monophyly of the remainder of the ingroup, including *Epigeneium*. Conversely, there is moderate support for the monophyly of *Epigeneium*, the Australasian (85% bootstrap support) and Asian (91% bootstrap support) clades. These results also show that Dendrobieae are polyphyletic, when Bulbophyllinae are included within that concept, where Eriinae (Podochileae) are embedded between the two main elements of tribe Dendrobieae.

Results from a second more comprehensive study were based on the analyses of 142 species from an alignment of 846 nucleotide sites, of which 529 were potentially parsimony

informative, produced 66 equally parsimonious trees; L = 4797, CI = 0.2760, RI = 0.6318, and RC = 0.1744. One randomly selected tree is shown as a phylogram in Fig. 2. These results show that the outgroup taxa, *Cypripedium* and *Paphiopedilum*, are isolated from the remainder of the study group. Epidendroideae are monophyletic, and within them are contained representatives of strongly supported tribes in Nervilieae, Malaxideae, Podochileae, as well as a weakly supported Dendrobieae comprised of four major clades, Bulbophyllinae, *Epigeneium*, an Asian and an Australasian clade. *Epigeneium* and *Dendrobium* sect. *Oxystophyllum* together with Bulbophyllinae remain isolated from the main body of Dendrobiinae.

Within the Asian clade there are eight definable clades: (1) representatives of sect. *Dendrobium*, including *Dendrobium moniliforme*, the type of the genus; (2) species historically treated under sects. *Dendrobium*, *Fytchiana*, and *Stachyobium*; (3) species representative of sects. *Conostalix*, *Distichophyllum*, and *Formosae*; (4) species representative of sects. *Callista*, *Dendrobium*, and *Formosae*; (5) species representative of sects. *Calcarifera*, *Dendrobium*, *Pedilonum*, and *Platycaulon*; (6) representatives of sects. *Amblyanthe* and *Callista*; (7) representatives of sects. *Aporum*, *Bolbidium*, and *Rhopolanthe*; and (8) species representative of sects. *Calcarifera*, *Calyptrochilus*, *Cuthbertsonia*, *Dendrobium*, *Dolichocentrum*, *Oxyglossum*, and *Pedilonum*.

Within the Australian clade, there is an internal dichotomy separated into two well-supported clades. The smaller contains species representing sects. *Herpethophytum*, *Inobulbon*, *Kinetochilus*, and *Macrocladium*. The larger clade is comprised of eight major clades: (1) two species from sect. *Trachyrhizum*; (2) species representative of sect. *Latourea*; (3) the genus *Cadetia*; (4) species representative of sects. *Grastidium*, *Eriopexis*, *Pleianthe*, and *Monanthus*; (5) species representative of sects. *Euphlebium*, *Eleutheroglossum*; *Phalaenanthe*, and *Spatulata*; (6) a single species representative of sect. *Euphlebium*; (7) species representative of sect. *Latourea* and the genus *Diplocaulobium*; and (8) species representative of sects. *Dendrocoryne*, *Rhizobium*, and *Micromonanthe*, as well as the genus *Flickingeria*.

DISCUSSION

These phylogenetic analyses, based primarily on ITS nrDNA sequence data, in conjunction with morphological data, provide a further insight into the overall relationships of most of Dendrobieae, including elements of the Asian clade, Dendrobiinae, not already accounted for in a recent publication by Clements (2003). Importantly, these results also outline the basic phylogeny of major taxa within the Australian clade, Grastidiinae, further emphasizing the importance to recognize this taxon separate from Dendrobiinae.

At the broader level, using a similar range of species to that used in previous studies of chloroplast *rbcL* and *matK* sequences, results strongly correlate with the phylogeny of Dendrobieae presented by Yukawa et al. (1996, 2000). Both sets of results show remarkable similarity, where representatives of *Epigeneium* grouped together in a strongly supported clade (96–100% bootstrap support) isolated from other ingroup, Bulbophyllinae, Eriinae, Malaxidinae, and outgroup taxa, Cypripedioideae. The strong correlation between

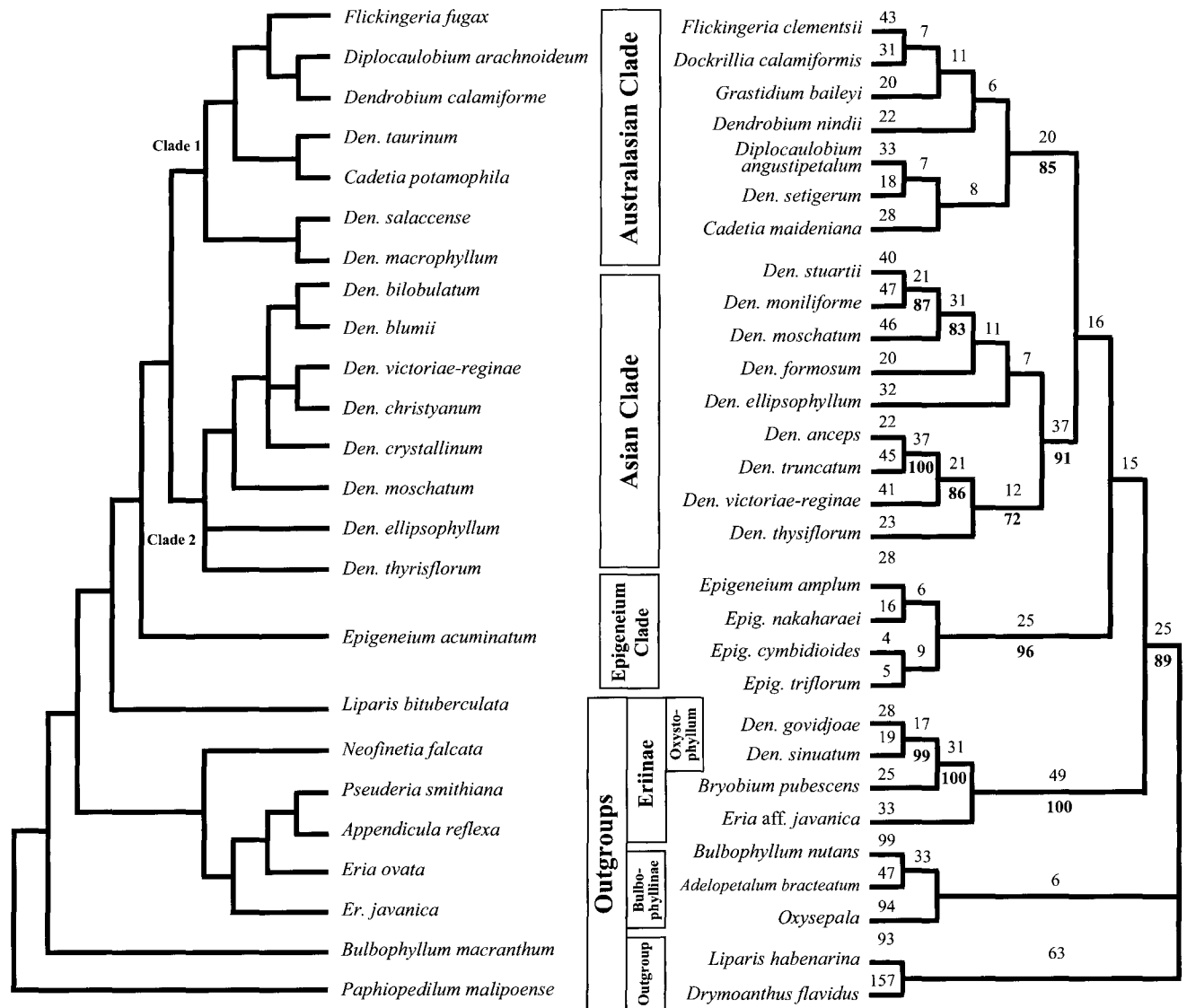


Fig. 1.—A comparison between the cpDNA and ITS generated trees based on a similar range of species, showing the relationships between the main elements of Dendrobieae and outgroups. The left-hand side tree is taken from Yukawa et al. (1993). The right-hand side tree is one of three most-parsimonious trees generated, derived from a data matrix based on nuclear ITS sequences, showing the composition of Dendrobieae with *Oxystophyllum*, *Epigeneium*, and Australasian and Asian clades identified relative to seven outgroup species: L = 1440, CI = 0.5743, RI = 0.4853. Numbers above branches are branch length estimates (ACCTRAN optimization); bootstrap percentages greater than 50% are given below in bold.

these results provides further evidence that the historical treatment of Dendrobieae based primarily on floral morphology is inconsistent with estimates of phylogenetic relationships. One possible outcome from the assessment of these results is the recognition of three clades as subtribes, viz. Epigeneiinae, Dendrobieinae, and Grastidiinae (Clements 2003), with Bulbophyllinae as sister-group to these three subtribes, as proposed by Dressler (1993) and others. Likewise, the presumed close relationship among these four taxa and Podochileae, of which Eriinae are a part, also seems sound. Significantly, these and previous ITS sequence analyses results (Clements 2003) also show *Dendrobium govidjoae* and *D. sinuatum* related to representatives of Eriinae (Podochileae). Both species have historically been treated either as members of *Dendrobium* sect. *Oxystophyllum* (Mi-

quel 1859; Smith 1905a, b; Kraenzlin 1910; Schlechter 1912) or as a section of the genus *Aporum* (Reichenbach 1861; Hooker 1890; Brieger 1981). When treated within *Dendrobium*, sect. *Oxystophyllum* has been interpreted as allied to sects. *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 stem. The position of sect. *Oxystophyllum* outside Dendrobieae renders the tribe paraphyletic unless Podochileae and Bulbophyllinae were included. Amalgamation of these taxa would lead to the creation of a very unwieldy taxon that would be very difficult to define using morphology. The more logical alternative is to reject sect. *Oxystophyllum* as part of Dendrobieae. It belongs to Eriinae, within Podochi-

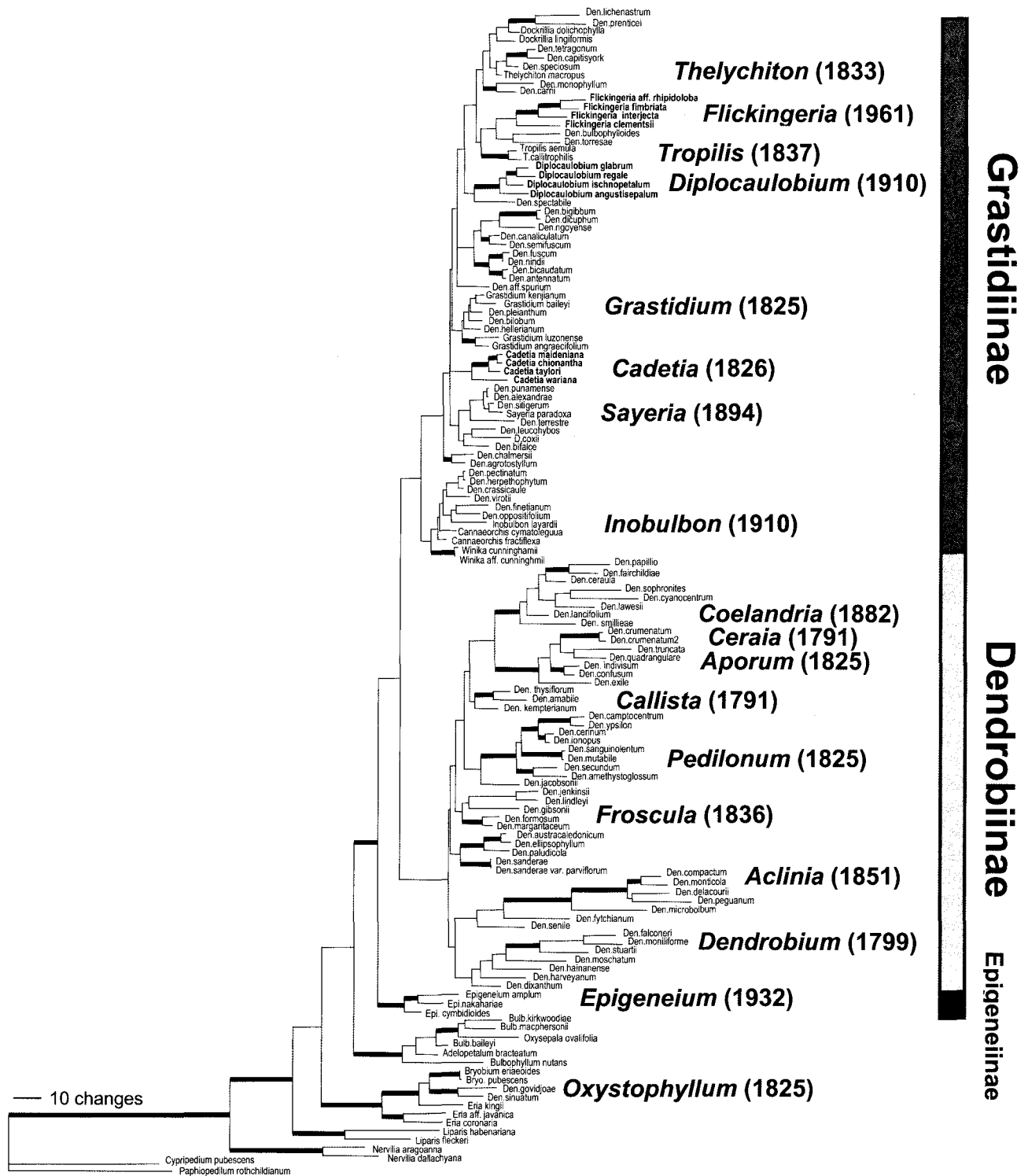


Fig. 2.—A phylogram of one of the 66 most-parsimonious successively weighted trees from the ITS analysis of a study of Dendrobieae and outgroup taxa, based on 143 species showing the relationships between its three subtribes and position of groups therein of previously published generic names and their date of publication. L = 4797, CI = 0.2760, RI = 0.6318. Branches with bootstrap percentages (75% or more) are in bold.

lea. The possession of several morphological characters that are putative synapomorphies and phylogenetic inferences based on ITS (Fig. 1, 2) leads to the proposal that *Oxystophyllum* be recognized at generic rank within the subtribe

Erinae (Podochileae), rather than in Dendrobieae (Clements 2003). The description of Erinae accordingly has been modified to include: pollinia, eight (rarely four) in two sets of four (two), with caudicles.

STATUS OF SCHLECHTER'S CLASSIFICATION OF DENDROBIINAE

With the recognition of *Oxystophyllum*, treated by Schlechter as a section of *Dendrobium* (subgen. *Xerobium*), further consideration of the infrageneric status of the tribe is required. Table 2 shows Schlechter's system of classification of Dendrobiinae, in which genera are spilt into two groups based on possession of either four or eight pollinia. This study concentrates only on those taxa with four pollinia, the three sections in *Cadetia*, and the 41 sections in *Dendrobium*. The remaining genus, *Pseuderia*, for which no material was available for analysis, has recently been shown to belong to Podochilinae (Yukawa et al. 1996) and will not be considered further here. A comparison between results generated by these ITS analyses and Schlechter's classification demonstrates inconsistency with the ITS phylogenetic estimates (Table 2).

A more detailed examination of these results demonstrates the nature of this conflict. For example, Schlechter's concept of *Dendrobium* subgen. *Athecebiium* included 12 sections. Results based on analysis of ITS sequence data support sects. *Desmotrichum* (= *Flickingeria*), *Microphynathe*, and *Diplocaulobium* (with sect. *Goniobulbon* embedded) as a strongly supported clade within Grastidiinae; sect. *Bolbidium* is embedded within subgen. *Rhopalobium* (Dendrobiinae); sect. *Euphlebiium* is paraphyletic within Grastidiinae; sect. *Rhizobium* is part of Grastidiinae; sect. *Sarcopodium* (= *Epigeneium*) is sister to all other Dendrobieae; sects. *Dendrocoryne* and *Latourea* are both paraphyletic within Grastidiinae; sect. *Inobulbium* is monophyletic within a branch of the basal dichotomy within Grastidiinae; and *Callista* represents a well-supported subgroup within Dendrobiinae. On this basis Schlechter's system of classification is demonstrably inconsistent with the phylogeny. A second example, *Sarcopodium* was isolated from *Dendrobium* based on the possession of a single-jointed pseudobulb on a creeping rhizome from which arises a multiflowered inflorescence. Despite having habit and floral characteristics more akin to *Coelogyne* and *Bulbophyllum*, respectively, Schlechter was strongly opposed to the recognition of *Sarcopodium* at generic rank as proposed by Lindley (1850), Rolfe (1910), and Kraenzlin (1910). ITS data demonstrate significant support for *Sarcopodium* (as *Epigeneium* and with 96% bootstrap support), isolated from all other taxa in *Dendrobium* subgen. *Athecebiium*. These results correlate strongly with those based on *rbcL* and *matK* sequences (Yukawa et al. 1993, 1996, 2000), where in one case (Yukawa et al. 1996) there was strong support (96% bootstrap support) for the isolation of these taxa. Because of the unavailability of the name *Sarcopodium* Lindl., a later homonym of *Sarcopodium* Ehrenberg ex A. T. Brongniart (Hyphomycetes), Hawkes (1956) proposed the alternate name *Katherinea* for this orchid genus, overlooking an earlier published legitimate name, *Epigeneium*. The name *Epigeneium* has since been taken up and applied, using a broader circumscription (Summerhayes 1957; Seidenfaden 1980; Garay and Romero-Gonzalez 1999); although, some authors have preferred to maintain both *Epigeneium* and *Katherinea* (Balakrishnan and Chowdhury 1966). To account for its position outside of the two major groups within Dendrobieae, as well as the possession of a combination of morphological synapomorphies, this distinctive taxon has

been recognized as a separate subtribe, Epigeneiinae, within Dendrobieae (Clements 2003).

Focusing on the Australasian clade (Grastidiinae), the presence of the long accepted and established genera, *Cadetia*, *Diplocaulobium*, and *Flickingeria*, deep within the well-supported clade (85% bootstrap support) further supports the traditional circumscription of *Dendrobium* as non-monophyletic (Fig. 2). Again, there is a very strong correlation with the results generated, based on *rbcL* and *matK* (Yukawa et al. 1993; 1996; 2000; Yukawa and Uehara 1996) or the combined results using *matK* and ITS sequence data (Yukawa 2001) based on the same or a similar group of species. *Cadetia* was first described by Gaudichaud (1829), but it was Schlechter (1912) who firmly established it as distinct from *Dendrobium*, within Dendrobiinae. This has been the typical interpretation since. Schlechter characterized *Cadetia* by the possession of the *Pleurothallis*-habit, formation of a spur through cohesion anteriorly in the lower half of the lateral sepals, and papillae in front of the column and labellum. Possession of these characters, coupled with very strong molecular support (100% bootstrap support), add weight to the continued recognition of *Cadetia*. The genus *Diplocaulobium* (Kraenzlin 1910), represented in Schlechter's system of classification by sects. *Goniobulbium* and *Diplocaulobium*, has gradually gained acceptance as being separate from *Dendrobium*. This is based on possession of closely spaced single internode pseudobulbs, mostly solitary inflorescences, pedicels arising from a conspicuous bract at the base of a single terminal leaf, flowers ephemeral (lasting one day, rarely longer), with distinct mentum and articulate labellum (Lavarack et al. 2000). With *D. glabrum*, which was placed in sect. *Goniobulbium* by Schlechter, deeply embedded within a monophyletic *Diplocaulobium*, recognition of sect. *Goniobulbium* is superfluous.

Flickingeria, originally described under the illegitimate name *Desmotrichum* (Blume 1825), has similarly regained acceptance as a genus, having in the interim been treated as a section of *Dendrobium* (Schlechter 1912). The genus *Flickingeria* is characterized by irregularly branched, creeping rhizomes, terminating in an erect pseudobulbous internode with a terminal nonsheathing leaf; single or multiflowered inflorescences, terminal or subterminal to the pseudobulb, adaxial or abaxial to leaf, and covered by persistent sheathing bracts; flowers ephemeral, the labellum midlobe fimbriate plicate, or bilobate (Seidenfaden 1980). Since the type species for *Dendrobium* is within the Asian clade, one option is to accept all species in the Australasian clade as representatives of genera other than *Dendrobium*. Alternatively, *Cadetia*, *Diplocaulobium*, and *Flickingeria* could be reincorporated into a broadly defined *Dendrobium* that includes both the Australian and Asian clades. However, there are several problems with this later option. Since there is only very weak support from ITS sequence analysis for monophyly of the Australasian and Asian clades, the inclusion of these well-established and morphologically well-defined genera into an extremely broad circumscription of *Dendrobium* is not advisable. Such a move would also be retrogressive and cause much nomenclatural confusion. An alternative is to treat the Australasian and Asian clades as two separate genera, but like the expansion of *Dendrobium*, this seems problematic. Such a proposal requires, in the case

Table 2. Comparison of Schlechter's 1912 classification of Dendrobieae with groupings based on ITS sequence data results.

Taxon	Section	Tribe: subtribe (based on ITS)	
Pollinia 4			
<i>Cadetia</i> Gaud.	sect. <i>Eu-Cadetia</i>	Dendrobieae: Grastidiinae	
	sect. <i>Ptero-Cadetia</i>	Dendrobieae: Grastidiinae	
	sect. <i>Sarco-Cadetia</i>	Dendrobieae: Grastidiinae	
<i>Dendrobium</i> Sw.			
subgen. <i>Athecebiium</i>	sect. <i>Bolbidium</i>	Dendrobieae: Dendrobieinae	
	sect. <i>Callista</i>	Dendrobieae: Dendrobieinae	
	sect. <i>Dendrocoryne</i>	Dendrobieae: Grastidiinae	
	sect. <i>Desmotrichum</i> [= <i>Flickingeria</i>]	Dendrobieae: Grastidiinae	
	sect. <i>Diplocaulobium</i>	Dendrobieae: Grastidiinae	
	sect. <i>Euphlebium</i>	Dendrobieae: Grastidiinae	
	sect. <i>Goniobulbon</i>	Dendrobieae: Grastidiinae	
	sect. <i>Inobulbum</i>	Dendrobieae: Grastidiinae	
	sect. <i>Latourea</i>	Dendrobieae: Grastidiinae	
	sect. <i>Microphynathe</i>	Dendrobieae: Grastidiinae	
	sect. <i>Rhizobium</i>	Dendrobieae: Grastidiinae	
	sect. <i>Sarcopodium</i> [= <i>Epigeneium</i>]	Dendrobieae: Epigeneiinae	
	subgen. <i>Eu-Dendrobium</i>	sect. <i>Amblyanthus</i>	Dendrobieae: Dendrobieinae
		sect. <i>Brachyanthe</i>	Dendrobieae: Dendrobieinae
sect. <i>Calyptrorchilus</i>		Dendrobieae: Dendrobieinae	
sect. <i>Ceratobium</i>		Dendrobieae: Grastidiinae	
sect. <i>Cuthbertsonia</i>		Dendrobieae: Dendrobieinae	
sect. <i>Distichophyllum</i>		Dendrobieae: Dendrobieinae	
sect. <i>Eleutheroglossum</i>		Dendrobieae: Grastidiinae	
sect. <i>Eugenanthe</i>		Dendrobieae: Dendrobieinae	
sect. <i>Fytchianthe</i>		Dendrobieae: Dendrobieinae	
sect. <i>Kinetochilus</i>		Dendrobieae: Grastidiinae	
sect. <i>Oxygenianthe</i>		Dendrobieae: Dendrobieinae	
sect. <i>Oxyglossum</i>		Dendrobieae: Dendrobieinae	
sect. <i>Pedilonum</i>		Dendrobieae: Dendrobieinae	
sect. <i>Phalaenanthe</i>		Dendrobieae: Grastidiinae	
sect. <i>Platycaulon</i>		Dendrobieae: Dendrobieinae	
sect. <i>Stachyobium</i>		Dendrobieae: Dendrobieinae	
sect. <i>Trachyrhizum</i>	Dendrobieae: Grastidiinae		
subgen. <i>Rhopalobium</i>	sect. <i>Rhopalanthe</i>	Dendrobieae: Dendrobieinae	
subgen. <i>Xerobium</i>	sect. <i>Aporum</i>	Dendrobieae: Dendrobieinae	
	sect. <i>Conostalix</i>	Dendrobieae: Dendrobieinae	
	sect. <i>Dichopus</i>	Dendrobieae: Grastidiinae	
	sect. <i>Dolichocentrum</i>	Dendrobieae: Dendrobieinae	
	sect. <i>Eriopexis</i>	Dendrobieae: Grastidiinae	
	sect. <i>Grastidium</i>	Dendrobieae: Grastidiinae	
	sect. <i>Herpethophytum</i>	Dendrobieae: Grastidiinae	
	sect. <i>Macrocladium</i>	Dendrobieae: Grastidiinae	
	sect. <i>Monanthos</i>	Dendrobieae: Grastidiinae	
	sect. <i>Oxystophyllum</i>	Podochileae: Eriieae	
sect. <i>Pleianthe</i>	Dendrobieae: Grastidiinae		
<i>Pseuderia</i> (Schltr.) Schult.		Podochileae: (Yukawa et al. 1996)	
Pollinia 8			
<i>Cryptochilus</i> Wall.*		Podochileae: Eriieae	
<i>Eria</i> Lindl.		Podochileae: Eriieae	
<i>Porpax</i> Lindl.*		Podochileae: Eriieae	

* = not included in this study.

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 equally distinct *Grastidium* (Blume 1825), as it represents the oldest generic named available in the clade. As shown previously, *Grastidium* is easily separated from *Den-*

drobium 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 sheath; inflorescences emerging with the protection of two indurated, laterally compressed sheathing bracts; inflorescence much reduced, geminate ra-

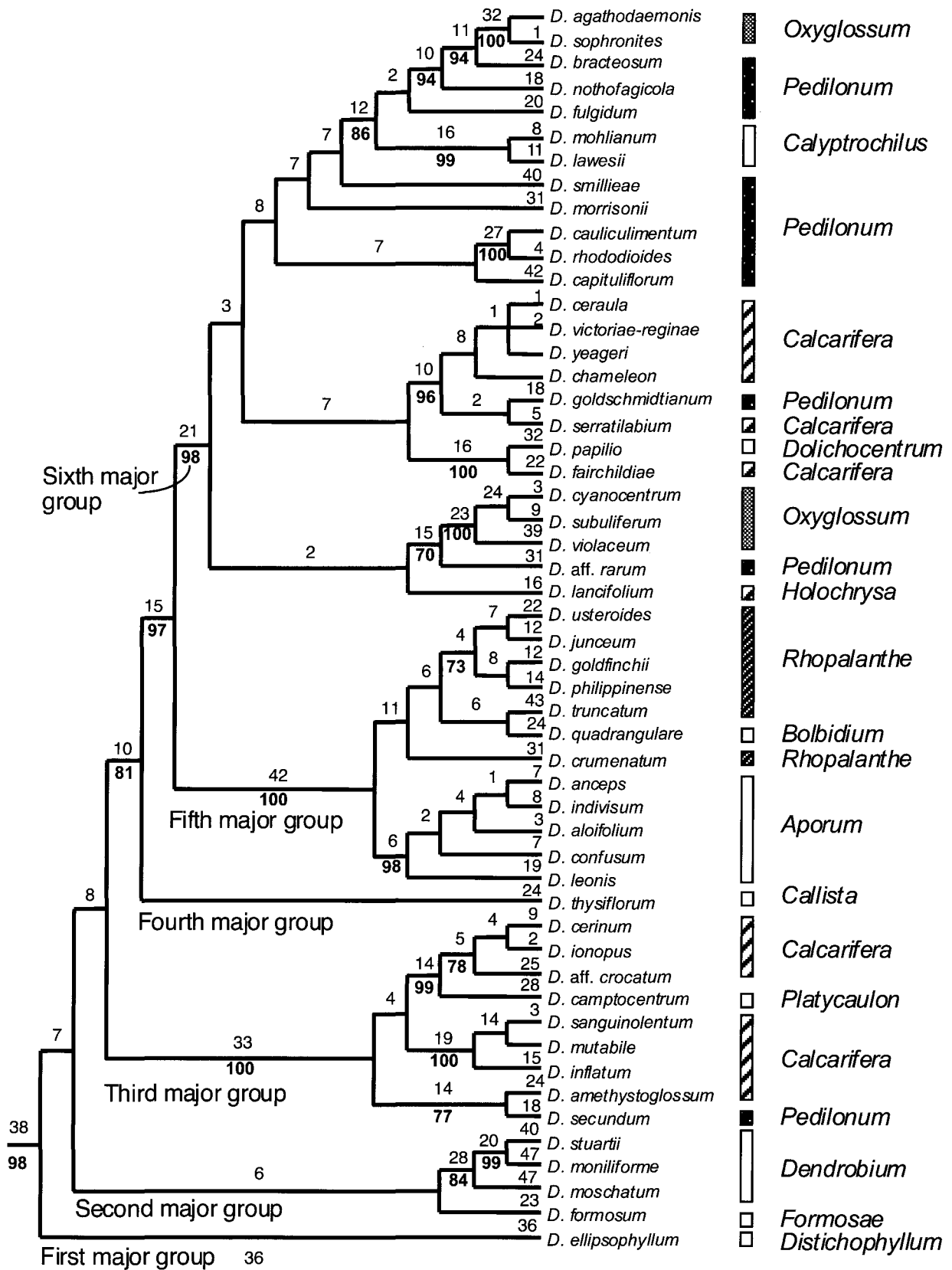


Fig. 3.—Tree showing the details of a portion of Dendrobiinae clade with emphasis on species previously referred to as *Dendrobium* sect. *Pedilonum*, showing one of the three most-parsimonious successively weighted trees from the ITS analysis of Dendrobiinae, and proposed arrangement of the six major 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 optimization); bootstrap percentages greater than 50% are given below in bold (taken from Clements 2003).

come with terminal, inward-facing flowers; and, ephemeral flowers (Clements and Jones 1997). These characters, or combinations thereof, are absent from the remaining species in the Australasian clade so the aggregation of all species into a single genus would create far more confusion than presently exists. Moreover, it would be extremely difficult to find morphological features to characterize such a genus. Yukawa et al. (1996, 2000), Yukawa and Uehara (1996), and Yukawa (2001) 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 recognizing any other genera in the clade. On the basis of molecular phylogenetic inference and morphological considerations, the taxonomic and nomenclatural changes have been proposed for the recognition of three subtribes within Dendrobieae, viz. Dendrobieae, Epigeneiinae, and Grastidiinae (Clements 2003).

If we accept these four—*Cadetia*, *Diplocaulobium*, *Flickingeria*, and include *Grastidium*—as genera, for which the arguments are very compelling, then consideration must also be given to the recognition at similar rank of all other major clades within the tribe supported by the ITS data (Fig. 2). Historically, *Cadetia*, *Diplocaulobium*, *Flickingeria*, and *Grastidium* are not the only generic names available for representatives within Dendrobieae. In fact, the name *Dendrobium* was conserved in favor of two earlier legitimate names, *Callista* and *Ceraia* (Loureiro 1790). Thereafter, the genera *Aporum*, *Pedilonum* (Blume 1825), *Cadetia* (Gaudicaud 1829), *Thelychiton* (Endlicher 1833), *Froscula*, *Tropilis* (Rafinesque 1837–1838), *Aclinia* (Griffith 1851), *Coelandria* (FitzGerald 1882), and *Sayeria* and *Inobulbon* (Kraenzlin 1910) were all described on the basis of perceived morphological differences from *Dendrobium*. These genera are scattered throughout the two major subtribes within Dendrobieae. Treatment of the monophyletic *Cadetia*, *Diplocaulobium*, *Flickingeria*, and *Grastidium* within Grastidiinae at the generic rank, necessitates the recognition of all the other sister groups at a similar rank (Fig. 2). Accordingly, the taxonomic and systematic treatments of most taxa within the Australasian clade are already well advanced (see Appendix 1). A full account of the phylogeny of these taxa based on the results of molecular analyses is in preparation.

The Asian clade (Dendrobieae in the strict sense, Clements 2003), is monophyletic (94% bootstrap support in Fig. 1, but only 52% in Fig. 2), which correlates with the results of Yukawa et al. (1996, 2000, 2001) and Wongsawad et al. (2001). The presence of *Dendrobium moniliforme*, the type species for *Dendrobium* (Holttum et al. 1979) automatically ties that clade to the name Dendrobieae. Apart from the branching order of the clade, these results reveal the strongest supported groups within the tree. Conversely, there is much weaker support along the main spine of the tree, within and between the three main taxa, making up Dendrobieae, excluding Bulbophyllinae and *Oxystophyllum*. In addition, those taxa not adequately covered include species in the numbered clades 1, 2, 3, 4, and 6 (Fig. 3). The situation is mirrored in Grastidiinae where the strongest clades are again internal with little divergence and supported along the spine of the clade.

These results also reveal that many traditionally recog-

nized sections are not monophyletic. This was clearly demonstrated in the recently published paper (Clements 2003), focusing on *Dendrobium* sect. *Pedilonum*. In that study, sects. *Calcarifera*, *Dendrobium*, *Oxyglossum*, *Pedilonum*, and *Rhopalanthe* were all shown to be either para- or polyphyletic (Fig. 3). Results presented here reaffirm those observations as well as highlight others. In addition to those listed above, sect. *Formosae* is paraphyletic and sect. *Dendrobium* is polyphyletic in their present circumscription. A similar situation exists within Grastidiinae. For example, sect. *Latourea* is paraphyletic with *D. coxii* (formerly of sect. *Euphlebiium*) within it, which also renders sect. *Euphlebiium* paraphyletic. The relationship of *D. spectabile*, traditionally treated within sect. *Latourea* (Cribb 1983), is also problematic. In the present studies, *D. spectabile* is placed in the clade containing *Diplocaulobium*. Conversely, these results provide evidence as to why many distinctive groups found particularly in Australia, New Zealand, and New Caledonia have been recognized as separate genera. It is recognized that additional research is still needed to fully resolve the relationships and status between several of these taxa, the monophyly of still other taxa requires further resolution. For example, *Dockrillia*, *Grastidium*, *Kinetochilus*, and *Thelychiton* are all paraphyletic based on ITS sequences. Inclusion of sequence data from one or both plastid genes (*matK* and *rbcL*) as well as those from the ITS region is already underway and should help resolve these areas of ambiguity. Similar studies have already been undertaken by Yukawa (2001) and Wongsawad et al. (2001). Unfortunately, their results cannot be reanalyzed because the sequence data generated for use in those analyses has not been submitted to GenBank. Similar combined analyses using at least one plastid gene as well as the ITS sequence data, using increased species sampling, are underway and should help resolve the identified problem areas and lead to an improved understanding of tribe Dendrobieae. In the meantime, the classification of Dendrobieae, as it currently stands based on the results of this and previously published research is outlined in the Appendix 1.

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- Note added in proof.*—The following re-identifications for collections used in this study have been established since submission of the original manuscript and an earlier submission to GenBank. They are:
- Dendrobium anceps*—redetermined as *D. keithii* Ridl.
D. bilobum—redetermined as *D. piestocaulon* Schltr.
D. confusum—redetermined as *D. litoreum* F. M. Bailey
D. fairchildiae—redetermined as *D. phillipsii* Ames & Quisumb.
D. margaritaceum—redetermined as *D. christyanum* Rchb. f.
D. aff. rarum—redetermined as *D. pseudorarum* Dauncey
Epigeneium amplum—redetermined as *E. coelogyne* (Rchb. f.) Summerh.

Appendix 1. Summary classification of Dendrobieae and Podochileae.

Tribe DENDROBIEAE Lindl. ex Endl., Gen. Pl. p. 190 (1837).—Type: *Dendrobium* Sw.

Subtribe DENDROBIINAE Lindl. ex Endl., Hort. Brit. (Sweet) (Ed. 3) p. 638 (1893).—Type: *Dendrobium* Sw.

ACLINIA Griff., ANISOPETALA (Kraenzl.) M. A. Clem., APORUM Blume, CALLISTA Lour., CERAIA Lour., CHROMATOTRICUM M. A. Clem. & D. L. Jones, COELANDRIA Fitzg., DENDROBIUM Sw., DISTICHORCHIS M. A. Clem. & D. L. Jones, EURYCAULIS M. A. Clem. & D. L. Jones, FROSCULA Raf., MACCRAITHEA M. A. Clem. & D. L. Jones, OXYGLOSELLUM M. A. Clem. & D. L. Jones, PEDILONUM (Blume) Blume

Subtribe EPIGENEINAE M. A. Clem., *Telopea* **10**: 278 (2003).—Type: *Epigeneium* Gagnep.

EPIGENEIUM Gagnep.

Subtribe GRASTIDIINAE M. A. Clem., *Telopea* **10**: 278 (2003).—Type: *Grastidium* Blume.

ABAXIANTHUS M. A. Clem. & D. L. Jones, AUSTRALORCHIS Brieger, BOULETIA M. A. Clem. & D. L. Jones, CADETIA Gaud., CANNAEORCHIS M. A. Clem. & D. L. Jones, CEPOBACULUM M. A. Clem. & D. L. Jones, CERATOBIMUM (Lindl.) M. A. Clem. & D. L. Jones, DAVEJONESIA M. A. Clem., DENDROBATES M. A. Clem. & D. L. Jones, DICHOPUS Blume, DIPLOCAULOBIMUM (Rchb. f.) Kraenzl., DOCKRILLIA Brieger, DURABACULUM M. A. Clem. & D. L. Jones, ELEUTHEROGLOSSUM (Schltr.) M. A. Clem. & D. L. Jones, ERIOPEXIS (Schltr.) Brieger, EUPHLEBIUM (Kraenzl.) Brieger, EXOCHANTHUS M. A. Clem. & D. L. Jones, FLICKINGERIA A. D. Hawkes, GRASTIDIUM Blume, HERPETHOPHYTUM (Schltr.) Brieger, INOBULBON (Schltr.) Schltr. & Kraenzl., KINETOCHILUS (Schltr.) Brieger, LEIOANTHUM M. A. Clem. & D. L. Jones, MICROPHYTANTHE (Schltr.) Brieger, MONANTHOS (Schltr.) Brieger, SARCOCADETIA (Schltr.) M. A. Clem. & D. L. Jones, SAYERIA Kraenzl., STILBOPHYLLUM M. A. Clem. & D. L. Jones, TETRABACULUM M. A. Clem. & D. L. Jones, TETRODON (Kraenzl.) M. A. Clem. & D. L. Jones, THELYCHITON Endl., TRACHYRHIZUM (Schltr.) Brieger, TROPILIS Raf., VAPPODES M. A. Clem. & D. L. Jones, WINIKA M. A. Clem., D. L. Jones & Molloy

Tribe PODOCHILEAE Pfitzer, Entwurf. Anord. Orch. p. 101 (1887) (as “Podochilinae”).—Type: *Podochilus* Blume.

Subtribe ERIINAE Benth., *J. Linn. Soc. Bot.* **18**: 287 (1881).—Type: *Eria* Lindl.

ASCIDIERIA Seidenf., CERATOSTYLUS Blume, EPIBLASTUS Schltr., ERIA Lindl., MEDIOCALCAR J. J. Sm., OXYSTOPHYLLUM Blume, PORPAX Lindl., SARCOSTOMA Blume, STOLZIA Schltr., TRICHOTOSIA Blume

Subtribe PODOCHILINAE Benth. & Hook. f., Gen. Pl. 3: 463 (1883) (as “Podochileae”).—TYPE: *Podochilus* Blume (6 genera).

Subtribe RIDLEYELLINAE Schltr., Orch. 339 (1914).—TYPE: *Ridleyella* Schltr. (1 genus).

Subtribe THELASIINAE Schltr., Orch. 340 (1914).—TYPE: *Thelasis* Blume (6 genera).