

Molecular phylogenetic analyses of Drakaeinae: Diurideae (Orchidaceae) based on DNA sequences of the internal transcribed spacer region

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Abstract. Results of the analysis of rDNA sequences based on 55 collections representative of 32 Drakaeinae orchid species and outgroups supported the monophyly of the subtribe, with weak support for the inclusion of *Spiculaea*, and revealed six strongly supported monophyletic, well defined morphological groups. *Caleana* is monophyletic. *Chiloglottis s.lat.* is monophyletic when *Simpliglottis* and *Myrmechila* are included. Our results also suggested that the segregate genus *Phoringopsis* is better treated as part of *Arthrochilus*. There is sufficient molecular and morphological support for recognition of the leafless, mycoheterotrophic *Thynninorchis* to be maintained as a separate genus. A taxonomic summary is provided, including reassignment of taxa at generic ranks and new combinations for *Caleana alcockii* (Hopper & A.P.Br.) M.A.Clem., *Caleana brockmanii* (Hopper & A.P.Br.) M.A.Clem., *Caleana disjuncta* (D.L.Jones) M.A.Clem., *Caleana dixonii* (Hopper & A.P.Br.) M.A.Clem., *Caleana gracilicordata* (Hopper & A.P.Br.) M.A.Clem., *Caleana granitica* (Hopper & A.P.Br.) M.A.Clem., *Caleana hortiorum* (Hopper & A.P.Br.) M.A.Clem., *Caleana lyonsii* (Hopper & A.P.Br.) M.A.Clem., *Caleana parvula* (Hopper & A.P.Br.) M.A.Clem., *Caleana terminalis* (Hopper & A.P.Br.) M.A.Clem. and *Caleana triens* (Hopper & A.P.Br.) M.A.Clem.

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Introduction

One of the most intriguing groups of Australian terrestrial orchids, with colloquial names to match, are the ant, bird, wasp, hammer, flying duck, elbow and truffle orchids (Jones 2006). Traditionally, this group of orchids has been classified as subtribe Drakaeinae Schltr. and had been interpreted as comprising *Arthrochilus* F.Muell., *Caleana* R.Br., *Chiloglottis* R.Br., *Drakaea* Lindl., *Paracaleana* Blaxell and *Spiculaea* Lindl., which is how they were treated in the most recent taxonomic treatment of the group (Jones and Clements 2001) or in separate revision of genera *Paracaleana* (Hopper and Brown 2006) and *Drakaea* (Hopper and Brown 2007). Drakaeinae are unusual because, although small in number (~66 species), they occur across mesic Australia, with outliers in New Zealand and New Guinea.

The 14 species of elbow and truffle orchids, *Arthrochilus*, inhabit woodlands, forests, heathlands and savanna woodlands of eastern and northern Australia, including the Torres Strait Islands, with outliers in the Kimberley in north-western Western Australia and Arnhem Land in the Northern Territory, as well as occurring in the savanna woodlands of southern New Guinea. The monospecific *Caleana*, flying duck orchid, is locally common and widespread throughout south-eastern Australia, where it favours sandy habitats. The 27 species of *Chiloglottis*,

the ant, bird and wasp orchids, are also locally common and widespread throughout the forests and woodlands of south-eastern Australia, with two species also occurring in New Zealand, one as far south as the subantarctic Campbell Island. *Drakaea*, the hammer orchids, with 10 described species, are confined to south-western Western Australia, where they grow in sandy open-area habitats in woodlands. The 13 species of *Paracaleana*, also known as duck orchids, are distributed across southern and eastern Australia, with an outlier in the north island of New Zealand, where they favour sandy open forest habitats. *Spiculaea*, also an elbow orchid, is a monospecific genus endemic to south-western Western Australia, mainly inhabiting shallow moss-covered soils on granite tors.

Like so many other Australian taxa, the group has been in taxonomic turmoil, with no resolution because of conflicting alternative generic concepts coupled with the discovery of an earlier valid generic name for *Paracaleana*. The primary cause of these conflicts is differing interpretations of the level of significance placed on various morphological traits found in this unusual group of orchids. Although the initial taxonomic changes were by Blaxell (1972), when he described the segregate genus *Paracaleana*, the catalyst for a renewed wave of taxonomic activity was the splitting of *Chiloglottis* and recognition of

the segregate genus, *Simpliglottis* (Szlachetko 2001), which was soon followed by the further division of that genus and *Arthrochilus* (Jones and Clements 2005; Jones *et al.* 2006). The resulting nomenclatural instability has inhibited conservation efforts of some of the rare taxa.

Taxonomic history and phylogeny of the tribes (Table 1)

Lindley (1840a) first treated *Caleana*, *Chiloglottis*, *Drakaea* and *Spiculaea*, along with other predominantly Australian genera, such as *Thelymitra*, *Pterostylis*, *Lyperanthus*, *Microtis* and *Acianthus*, in tribe Arethuseae Div. 2 Euarethuseae. Bentham and Hooker (1883) transferred these to tribe Diurideae. The German morphologist, Pfitzer (1887, 1889), proposed an alternative classification based on possession of the hinged labellum, which united *Caleana* and *Spiculaea* (including *Arthrochilus*) into the subtribe Pterostylidinae, a position followed by Dressler and Dodson (1960).

Subtribe Drakaeinae was created by Schlechter (1911) to encompass *Arthrochilus*, *Caleana*, *Chiloglottis*, *Drakaea* and *Spiculaea*, which all possess winged columns, as distinct from Pterostylidinae (now considered part of the Cranichideae). Rogers (1921) did not accept the Drakaeinae and linked the group to Caladeniinae. Dressler's interpretation of the group changed in his various treatments of the family (Dressler 1974, 1979, 1981, 1983, 1986; Dressler and Dodson 1960), until he reinstated Schlechter's concept, albeit with the proviso that it may prove merely a subclade of the Caladeniinae (Dressler 1993). Developmental embryological studies of the tribe Diurideae confirmed the alliance of Drakaeinae as part of tribe Diurideae, where they all shared a 'diurid' embryo developmental pattern (Clements 1995, 1996, 1999), although this character state is not restricted to this tribe (Kores *et al.* 2001). Molecular data from *rbcL* (Kores *et al.* 1997; Cameron *et al.* 1999), *matK* and *trnL-F* plastid genes (Kores *et al.* 2000, 2001), *psaB* (Cameron 2004) and internal transcribed spacer (ITS) nuclear rDNA (Clements *et al.* 2002; Górnjak *et al.* 2010) confirmed this relationship of subtribe Drakaeinae within the tribe Diurideae, although there are still conflicting data on its position and monophyly. Other authors, such as Szlachetko (1991), have proposed alternative interpretations of these taxa, on the basis of morphological studies of the column, and created the separate subtribes Chiloglottidinae and Caleaninae. Chase *et al.* (2003) recognised fewer subtribes, amalgamating subtribe Drakaeinae with Thelymitrinae, within tribe Diurideae, on the basis of a combined analysis of plastid *atpB*, *rbcL*, *matK*, *psaB*, *trnL-F*, nuclear 26S rDNA and *nad1* intron and mitochondrial (non-coding) DNA.

Generic relationships

The systematics of the group have also been the subject of change and controversy at the generic level. Initially, confusion existed about the limits of *Drakaea*, *Spiculaea* and *Arthrochilus*. Blaxell (1972) eventually clarified the situation, recognising each genus in its own right, and also splitting *Caleana* by creating *Paracaleana* for the two species with tuberculate labella. The concept of *Paracaleana* was initially accepted by many authors of popular and scientific literature (Erickson *et al.* 1973; Clements 1982; Hoffman and Brown 1984; Woolcock and Woolcock 1984; Green 1985; Weber and Bates 1986; Rye 1987; Jones 1988;

Table 1. Alternative taxonomies of the Drakaeinae

This paper	Jones <i>et al.</i> (2002) and Jones and Clements (2005)	Szlachetko (2001); Szlachetko and Rutkowski (2002)	Jones and Clements (2001)	Dressler (1993)	Blaxell (1972)	Schlechter (1926)	Reichenbach (1871), Bentham (1873), Pfitzer (1889), von Mueller (1889)	Lindley (1840a)
<i>Chiloglottis</i>	<i>Chiloglottis</i>	<i>Chiloglottis</i>	<i>Chiloglottis</i>	<i>Chiloglottis</i>		<i>Chiloglottis</i>	<i>Chiloglottis</i>	<i>Chiloglottis</i>
<i>Chiloglottis</i>	<i>Myrmecichila</i>		<i>Chiloglottis</i>			<i>Chiloglottis</i>		
<i>Chiloglottis</i>	<i>Simpliglottis</i>	<i>Simpliglottis</i>	<i>Chiloglottis</i>	<i>Chiloglottis</i>		<i>Chiloglottis</i>	<i>Chiloglottis</i>	<i>Chiloglottis</i>
<i>Drakaea</i>	<i>Drakaea</i>	<i>Drakaea</i>	<i>Drakaea</i>	<i>Drakaea</i>	<i>Drakaea</i>	<i>Drakaea</i>	<i>Chiloglottis</i>	<i>Chiloglottis</i>
<i>Caleana</i>	<i>Paracaleana</i> /Sullivania	<i>Paracaleana</i>	<i>Caleana</i>	<i>Caleana</i>	<i>Paracaleana</i>	<i>Caleana</i>	<i>Drakaea</i>	<i>Drakaea</i>
<i>Caleana</i>	<i>Caleana</i>	<i>Caleana</i>	<i>Caleana</i>	<i>Caleana</i>	<i>Caleana</i>	<i>Caleana</i>	<i>Caleana</i>	<i>Caleana</i>
<i>Arthrochilus</i>	<i>Arthrochilus</i>	<i>Arthrochilus</i>	<i>Arthrochilus</i>	<i>Arthrochilus</i>	<i>Arthrochilus</i>	<i>Spiculaea</i> sect. <i>Arthrochilus</i>	<i>Drakaea</i> (syn. <i>Arthrochilus</i>)	<i>Drakaea</i>
<i>Arthrochilus</i>	<i>Phoringopsis</i>	<i>Arthrochilus</i> subgen. <i>Phoringopsis</i>	<i>Arthrochilus</i>	<i>Arthrochilus</i>	<i>Arthrochilus</i>			
<i>Thymnorchis</i>	<i>Thymnorchis</i>		<i>Arthrochilus</i>	<i>Arthrochilus</i>	<i>Arthrochilus</i>	<i>Spiculaea</i> sect. <i>Arthrochilus</i>	<i>Drakaea</i>	
<i>Spiculaea</i>	<i>Spiculaea</i>	<i>Spiculaea</i>	<i>Spiculaea</i>	<i>Spiculaea</i>	<i>Spiculaea</i>	<i>Spiculaea</i> sect. <i>Eu-Spiculaea</i>	<i>Drakeae</i>	<i>Spiculaea</i>

Dixon *et al.* 1989). *Paracaleana* was rejected by Clements (1989) on the basis that none of the characters used was sufficiently different to maintain it as separate genus from *Caleana*. Despite this assessment, *Paracaleana* was accepted by most subsequent authors (Hoffman and Brown 1992, 2011; Backhouse and Jeanes 1995; Kores *et al.* 2001; Jones *et al.* 2002; Jeanes and Backhouse 2001; Hopper and Brown 2006; Brown *et al.* 2008). A preliminary analysis of the ITS nrDNA (Clements *et al.* 2002) failed to resolve this issue because of low taxon sampling. Additional controversy also surrounds this genus, with the recent discovery of an earlier published generic name, *Sullivania*, that was inadvertently, although legitimately, published for the rare apomitic form with fixed, vestigial labellum *Caleana sullivanii* (Jones and Clements 2005; Hopper and Brown 2006; St George 2010).

Additional names were added when Szlachetko (2001) created the genus *Simpliglottis* for a group of species related to *Chiloglottis gunnii*. Following detailed study of freshly collected material representative of all genera in the subtribe, further divisions were proposed (Jones *et al.* 2002). The following two segregate genera were split off from *Arthrochilus*: *Phoringopsis*, to account for those species with linear lanceolate leaves, and reverse position of the labellum callus, represented by *P. byrnesi* and *P. dockrillii*; and *Thynninorchis* for the semi-mycrohetrotrophic species, *T. hunteriana*, that inhabits the southern mountain regions of south-eastern Australia isolated from the remaining species. Jones and Clements (2005) later recognised and segregated a small group of species from *Chiloglottis*, as *Myrmecchila*. This group of species can be distinguished by its winter to spring flowering, suberect to erect flowers, very short sepaline osmophores and suberect to erect labella.

Most of these proposed changes of traditional established genera have, in general, not been well received and adopted throughout the botanical community, both in Australia and overseas. A major objection to these proposed changes was their destabilising effect on traditional orchid nomenclature and classification (Hopper and Brown 2006, 2007; Hopper 2009). There were also objections about methods used, as almost all were exclusively morphologically based, without any cladistic or morphometric analyses of the data to support the proposed changes. Considering the high levels of current uncertainty surrounding the classification of taxa within Drakaeinae and the lack of a published robust phylogeny of the group, one of the main aims of the present paper was to address this situation. A secondary aim was to test the monophyly of all traditional and recently proposed genera. We hypothesise that some of the characters used to define these genera were autapomorphies for subgroups within genera, rather than being synapomorphies for the entire genus. We discuss the clades and important taxonomic characters, test alternative classifications and propose a classification based on our results.

Materials and methods

Taxon sampling

DNA sequences for the nuclear rDNA ITS were obtained from 55 species, including representatives of all traditional or recently recognised higher taxa within Drakaeinae (Jones *et al.* 2002,

2006), and outgroups from *Calochilus*, *Cryptostylis*, *Epiblema* and *Thelymitra*. Successful analysis, based only on ITS data, has previously allowed establishment of viable, acceptable taxonomic outcomes, from which the results of further multigene analyses have deviated little. For example, Cox *et al.* (1997) on the phylogeny of the slipper orchids, and recent publications on Brassicaceae (Warwick *et al.* 2010), provided evidence of the utility of results from ITS sequence phylogenetic analysis. Details of source material and provenance, and GenBank accession numbers used are listed in Table 2. Reference vouchers for collections used in the study are housed either at CANB or CHR. Taxa were chosen on the basis of previous broader-level studies by Cameron *et al.* (1999), Clements *et al.* 2002), Cameron (2004), Salazar *et al.* (2003, 2009) and Górniak *et al.* (2010).

DNA isolation, amplification and sequencing

Genomic DNA was extracted from 10–100 mg of fresh or silica gel-dried leaf tissue, or from herbarium material, using the DNeasy Plant Mini Kit (Qiagen, Melbourne, Vic., Australia) either individually or in the 96-well plate format. The complete ITS region of the 18S–26S nrDNA was amplified by polymerase chain reaction (PCR), following methods outlined in Clements *et al.* (2002). The following primer pairs from Sun *et al.* (1994) were used: ITS4–ITS5, 17SE–26SE or 17SE–ITS4.

Phylogenetic analyses

Contiguous sequences were assembled and edited using *Sequencher* v.3.0 (Gene Codes Corp., Ann Arbor, MI, USA) and manually aligned in *BioEdit* sequence alignment editor v.4.8.6 (Hall 1999). Sequence alignments and Nexus formatted files are available in TreeBase (accession number 15661) and all sequences are lodged in GenBank (see Table 2). Any uncertain base positions, generally located close to priming sites, and highly variable regions with equivocal sequence homology, were excluded from phylogenetic analysis. Individual base positions were coded as unordered multistates and potentially informative insertions/deletions (indels) were manually coded as additional binary characters.

Bayesian analyses were performed using MrBayes version 3.1.2. (Ronquist and Huelsenbeck 2003). The GTR+I+gamma model was applied to the ITS alignment. Indel characters were included as a separate partition and a standard (morphology) discrete state model with a gamma-shape parameter was applied to this partition. The Markov chain Monte Carlo search was run for 20 million generations with trees sampled every 50 000 generations. MrBayes performed two simultaneous analyses starting from different random trees (Nruns = 2), each with six Markov chains. In total 25% of the trees were discarded and the run ended with an average standard deviation of split frequencies of <0.005. A Bayesian consensus phylogram with posterior probability values plotted was calculated in MrBayes. Maximum parsimony analyses were performed with the heuristic search option (excluding uninformative characters) in PAUP* 4.02 (Swofford 2003). A two-step search method for multiple islands was performed with 10 000 random replicates with tree bisection reconnection (TBR) on, and saving only one of the

Table 2. List of specimens examined

Reference vouchers of the Australian collections are housed in CANBR and the New Zealand collections are housed in CHR. Abbreviations: ORG, Orchid Research Group; H, herbarium specimen; Can, Canberra; Ncc, New South Wales (NSW) Central Coast; Nct, NSW Central Tablelands; Nnc, NSW northern coast; Nnt, NSW Northern Tablelands; Nsc, NSW southern coast; Nst, NSW Southern Tablelands; Qco, Queensland (Qld) Cook; Qdd, Qld Darling Downs; Qle, Qld Leichhardt; Tas, Tasmania; Vgi, Victoria (Vic) Gippsland; Vwh, Vic western highlands; Wav, Western Australia (WA) Avon; Wcv, WA Carnarvon; Wda, WA Darling; Wey, WA Eyre; AU, Australia; NZ, New Zealand

Species	Collection number	Provenance	GenBank number
<i>Arthrochilus prolixus</i> D.L.Jones	Perkins & Weston s.n.	—	AF321581
<i>Arthrochilus rosulatus</i> D.L.Jones	ORG 2565	AU: Qco; Double Barrel Pinch (near Cooktown)	AF391763
<i>Arthrochilus dockrillii</i> Lavarack	ORG 2116	AU: Qco; Little Forks	AF347982
<i>Arthrochilus oreophilus</i> D.L.Jones	ORG 2044	AU: Qco; Mount Poverty	AF347984
<i>Caleana lyonsii</i> Hopper & A.P.Br.	Evans (ORG 2742)	AU: Wcv; 90 km N of Galena Bridge	KF539926 ^A
<i>Caleana major</i> R.Br.	Perkins & Weston s.n.	—	AF321585
<i>Caleana minor</i> R.Br.	Perkins & Weston s.n.	—	AF321586
<i>Caleana minor</i>	Simpson (Richards 2060)	AU: Vgi; Loch Sport	KF539925 ^A
<i>Caleana minor</i>	Crane 2232	AU: Qle; Carnarvon Gorge	AF348050
<i>Caleana major</i> R.Br.	Clements 9718	AU: Nst; Mount Jerrabomberra	AF347996
<i>Caleana nigrita</i> Lindl.	French 1296	AU: Wda; Bernbrooke Pl cul de sac, Wellesly N Rd	AF348051
<i>Calochilus paludosa</i> R.Br.	Clements 9732	AU: Nsc; Nowra, Flat Rock Creek	AF348000
<i>Chiloglottis</i> aff. <i>Formicifera</i>	Mant 151	AU: Nnt; Tenterfield	AY042155
<i>Chiloglottis pluricallata</i> D.L.Jones	Mant 220	AU: Nnt; Barrington Tops	AY042158
<i>Chiloglottis</i> aff. <i>formicifera</i>	Bower (Jones 12491)	AU: Nnt; Bald Rock NP	KF539938 ^A
<i>Chiloglottis</i> aff. <i>pluricallata</i>	Mant 218	AU: Nnt; Barrington Tops	AY042159
<i>Chiloglottis chlorantha</i> D.L. Jones	Mant 180	AU: Nct; Kanangra–Boyd NP	AY042157
<i>Chiloglottis cornuta</i> Hook.f.	Clements 10627	AU: Tas; Mount Wellington	KF539929 ^A
<i>Chiloglottis cornuta</i>	Molloy 015/98	NZ: Hamner	KF539928 ^A
<i>Chiloglottis diphylla</i> R.Br.	Riley s.n.	AU: Nnc; Nelson Bay	AF348001
<i>Chiloglottis formicifera</i> Fitzg.	Mant 161	AU: Ncc; Dharug National Park	AY042154
<i>Chiloglottis grammata</i> G.W.Carr	Mant 188	AU: Tas; Mount Wellington	AY042162
<i>Chiloglottis gunnii</i> Lindl.	ORG 1807	AU: Tas; Peggs Beach, near Rocky Cape	KF539930 ^A
<i>Chiloglottis longiclavata</i> D.L.Jones	Jones 9285	AU: Qle; Blackdown Tableland	KF539935 ^A
<i>Chiloglottis palachila</i> D.L.Jones	Jones 12773	AU: Nnt; Mount Kaputar	KF539927 ^A
<i>Chiloglottis platyptera</i> D.L.Jones	Mant 173	AU: Nnt; Barrington Tops	AY042156
<i>Chiloglottis platyptera</i>	Jones 5093	AU: Nnt; Barrington Tops	KF539936 ^A
<i>Chiloglottis reflexa</i> (Labill.) Druce	Mant s.n.	AU: Nct; Mount Wilson	AY042148
<i>Chiloglottis reflexa</i>	Richards 6	AU: Vgi; Croydon	AY042148
<i>Chiloglottis seminuda</i> D.L. Jones	Mant 231	AU: Ncc; Kurrajong	AY042149
<i>Chiloglottis sphyrnoides</i> D.L.Jones	Mant 103	AU: Nnt; Nowendoc	AY042151
<i>Chiloglottis sylvestris</i> D.L. Jones et M.A. Clem.	Mant 104	AU: Nnt; Washpool NP	AY042150
<i>Chiloglottis trapeziformis</i> Fitzg.	Mant 160	AU: Nct; Orange	AY042153
<i>Chiloglottis trapeziformis</i>	Clements 9713	AU: Nst; Braidwood–Bungandor road	KF539937 ^A
<i>Chiloglottis triceratops</i> D.L.Jones	Mant 190	AU: Tas; Mount Wellington	AY042160
<i>Chiloglottis trilabra</i> Fitzg.	Mant 106	AU: Nnt; Ebor	AY042147
<i>Chiloglottis truncata</i> D.L.Jones et M.A.Clem.	Mant 155	AU: Qdd; Toowoomba	AY042152
<i>Chiloglottis truncata</i>	Crane 1226	AU: Qdd; Crowsnest	KF539940 ^A
<i>Chiloglottis valida</i> D.L.Jones	Molloy 016/98	NZ: Hamner	KF539932 ^A
<i>Chiloglottis valida</i>	Molloy 243/00	NZ: Iiwatahi	KF539933 ^A
<i>Chiloglottis valida</i>	Jones 16325	AU: Nst; Thredbo area	KF539934 ^A
<i>Chiloglottis valida</i>	Clements 9737	AU: Can; Gibraltar Falls	KF539931 ^A
<i>Chiloglottis valida</i>	Mant 181	AU: Nct; Kanangra–Boyd NP	AY042161
<i>Cryptostylis ovata</i> R.Br.	French 1302	AU: Wda; Devlin Road	AF348014
<i>Cryptostylis subulata</i> (Labill.) Rchb.f.	Jones 16061a	AU: Tas; Black Bulls Scrub	AF348015
<i>Cryptostylis subulata</i>	Molloy 118/99	NZ: Northland	KF539921 ^A
<i>Cryptostylis erecta</i> R.Br.	Clements 10571	AU: Ncc; Castlecrag	KF539920 ^A
<i>Drakaea micrantha</i> Hopper & A.P.Br.	ORG1696	AU: Wda; Mount Lindesay, Penelup	KF539924 ^A
<i>Drakaea thynniphila</i> A.S.George	ORG 1694	AU: Wda; Mount Lindesay, Penelup	KF539923 ^A
<i>Drakaea glyptodon</i> Fitzg.	ORG 1693	AU: Wda; Mount Lindesay, Penelup	AF348027
<i>Epiblema grandiflorum</i> R.Br.	ORG 1958	AU: Wda; Albany	AF238029
<i>Spiculaea ciliata</i> Lindl.	Evans (ORG 2057)	AU: Wav; Parkville	AF348063
<i>Thelymitra antennifera</i> (Lindl.) Hook.f.	Jones 15801	AU: Vwh; Stuart Mill Flora Reserve	KF539922 ^A
<i>Thynninorchis huntianus</i> (F.Muell.) D.L.Jones et M.A. Clem.	Perkins & Weston s.n.	—	AF321582
<i>Thynninorchis huntianus</i>	Clements 9830	AU: Can; Brindabella Range	AF347983

^ANewly submitted sequence.

shortest trees per replicate. The saved trees were then swapped to completion, saving all shortest-length trees. Support for internal branches was evaluated by the heuristic bootstrap method with 10 000 bootstrap replicates, each with 10 random-addition sequences with TBR and MULPARS activated (Felsenstein 1985).

Results

The aligned ITS dataset comprised 55 DNA sequences, with a matrix length of 762 nucleotide sites. There was a total of 396 shared polymorphisms. Six indels were scored. The parsimony analyses identified 143 equal-length trees of 1320 steps (consistency index (CI)=0.60, rescaled consistency index (RCI)=0.50).

The Bayesian analysis of the ITS region resolved a phylogenetic tree with moderate support for the monophyly of Drakaeinae (posterior probability, PP=0.83), and *Spiculaea cilata* sister to the rest of the Drakaeinae. The parsimony analysis (not shown) was congruent with the Bayesian analysis, except that *Spiculaea* was not supported as part of the Drakaeinae, rather it was supported in a clade containing all the outgroups as sister to the Drakaeinae. A clade containing *Thynninorchis* and *Arthrochilus* (with *Phoringopsis*) (PP=1.0, bootstrap values, BV=80) was sister to a clade containing *Caleana*, *Drakaea* and *Chiloglottis*. *Arthrochilus s.lat.* was well supported, as were each of the internal clades, namely, *Thynninorchis*, (PP=1.0, BV=100) and a clade (PP=1.0, BV=97) comprising *Arthrochilus* (PP=1.0, BV=100) and *Phoringopsis* (*Arthrochilus dockrillii*, Fig. 1). *Caleana s.lat.* was sister to a clade containing *Drakaea* and *Chiloglottis s.lat.*

Caleana s.lat. was well supported (PP=1.0, BV=100) and showed support for monophyletic *Caleana* (PP=0.97) and *Paracaleana* (PP=98, BV=69). *Drakaea* (PP=1.0, BV=100) was strongly supported but showed very little differentiation among species. *Chiloglottis s.lat.* (PP=1.0, BV=100) was also well supported, with strong support on short branches for *Simpliglottis* (PP=1.00, BV=99) and *Myrmecchila* (PP=1.00, BV=100), whereas *Chiloglottis s.s.* was unresolved.

Discussion

Although it is recognised that the present study was based on the use of a single marker region, ITS, nevertheless it has provided an important analysis of the group. Our results, which are based on analysis of 32 species, increase the representation of all genera within Drakaeinae compared with previous studies (Fig. 1). The results are highly congruent with the previously published nuclear (Clements *et al.* 2002; Górniak *et al.* 2010) and plastid gene phylogenies (Kores *et al.* 2001; Cameron 2004), which were based on small samples of species in each genus. Our Bayesian results confirmed the monophyly of Drakaeinae consistent with outcomes of other broader based studies of the Diurideae (Weston *et al.*, in press).

There are areas of incongruence between the previously published nuclear tree of Clements *et al.* (2002) and our current results. In particular, *Arthrochilus s.lat.* (including *Thynninorchis*) is sister to *Drakaea* and *Chiloglottis*, and

the remainder of the Drakaeinae (*Spiculaea*, *Caleana* and *Paracaleana*), the latter forming a clade. However, there is little bootstrap support for phylogenetic relationships in this part of the backbone of the phylogeny. In the previous study, where the overall structure and phylogeny of the tribe was the focus, and no particular subtribe was investigated in detail (Clements *et al.* 2002), only 10 species were used as representatives of Drakaeinae. In the present study, we have expanded the range of collections, including several newly described species and additional material from disparate locations of some critical species, such as *Caleana major* and *C. (Paracaleana) minor*. The inclusion of sequence data from *Caleana (Paracaleana) lyonsii*, a species from south-western Western Australia, proved decisive in the assessment of that genus. *C. (Paracaleana) lyonsii* with a multiflowered inflorescence and erect, narrow lanceolate leaf is sister to the rest of *Paracaleana*. *C. (Paracaleana) nigrita*, with its single flower and reptant, broadly ovate to ovate lanceolate leaf, is embedded within and not isolated from that clade.

Spiculaea (Fig. 2A), as originally described (Lindley 1840b), is a monospecific genus, endemic to the inland south-west of Western Australia. Phylogenetically, it is sister to the rest of the Drakaeinae, but not well supported. Its inclusion in the Drakaeinae, therefore, is equivocal. *Spiculaea* is characterised by a single relatively broad, glabrous basal leaf, with a thin, wiry scape narrower at the base and fleshy, resupinate, yellowish-brown, sequentially developing flowers. The fleshy scape contains sufficient nutrients and water to enable flowers and capsules of pollinated flowers to develop to maturity, even when the basal stem dries during the extreme heat of late spring and early summer. *Spiculaea* is also characterised by several autapomorphies, including the prominent basal labellum stalk hinged to a very short column foot, a fleshy insectiform labellum callus, with strap-like apical appendage, and prominent, sickle-like column wings that are serrated along the inner margin.

Historically, *Arthrochilus* has been linked or confused with *Drakaea* and *Spiculaea* (Reichenbach 1871; von Mueller 1889; Schlechter 1926), and comprises three morphologically distinct groups. These groups were segregated by Jones and Clements (2005) into the following three genera, based primarily on differences in plant habit, but also on floral morphology: the dimorphic *Arthrochilus* (10 spp.), the monomorphic *Phoringopsis* (3 spp.) and mycoheterotrophic *Thynninorchis* (2 spp.).

Arthrochilus (Fig. 2C) predominantly inhabits the Australian tropical and temperate coastal woodlands and heathlands, extending along the eastern coast as far south as Sydney. Plants occur in colonies as rosettes or as multi-flowered racemes. Flowers are non-resupinate, greenish with inconspicuous sepals and petals and a prominent intricately insectiform, delicately hinged labellum that dangles like a fishing lure, and column with two unequal pairs of projecting column wings.

Phoringopsis (Fig. 2D) is distributed disjunctly in northern tropical Australia and south-eastern Papua New Guinea and was segregated from *Arthrochilus* (Jones *et al.* 2002) on the basis of possession of one or two elongate, distichous basal leaves, inflorescence emerging with the leaves, smooth, non-papillate

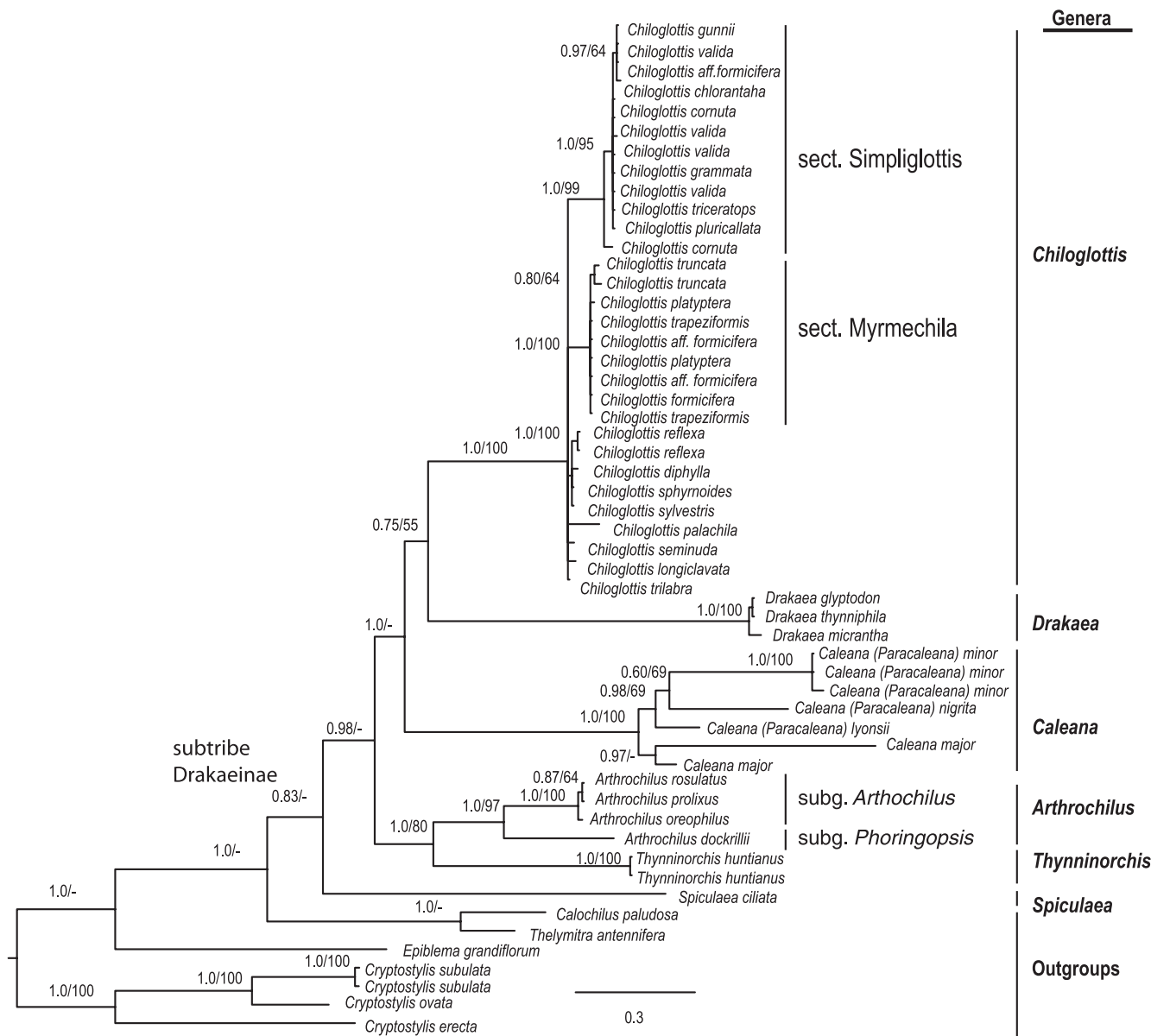


Fig. 1. Internal transcribed spacer (ITS) Bayesian consensus tree, with branch lengths of Drakaeninae (Orchidaceae). Numbers above branches indicate the Bayesian posterior probability, followed by bootstrap values.

column foot and sepal bases, labellum attached basally (not via a peltate stalk), and the callus fungiform and ornamented with penicillate calli.

Thynninorchis (Fig. 2B) comprises two leafless species that inhabit the montane eucalypt forests of south-eastern Australia, including Tasmania. These are the only fully mycoheterotrophic species of Drakaeinae and Jones and Clements (2005) erected the genus on account of this plant habit, but also because of possession of a hinged, insectiform labellum ornamented with long, multi-layered, barbed, caudiform cells, with the main head deeply divided into two lobes, each ending in a swollen, knob-like structure that hangs at the end of a long, narrow column foot, and column with two pairs of similar-sized, projecting, column wings that are reminiscent of those present in *Spiculaea*.

Sister to *Thynninorchis* is the clade containing *Arthrochilus* (10 species and the segregate genus *Phoringopsis* (3 species)). *Phoringopsis* is distinguished from *Arthrochilus* by possession of one or two narrow, erect, linear, lanceolate leaves and similarity of leaf morphology in flowering and sterile plants, flowers with smooth tepal bases, labellum hinge attached in the centre of the column foot, labellum lacking a peltately attached supporting stalk and the strongly swollen, fungi-like callus ornamented with long, thin, penicillate glands. *Phoringopsis* has a scattered disjunct distribution across northern Australia and one species, *P. lavarackiana*, also inhabits sites in the *Melaleuca*-dominated savanna woodlands of southern New Guinea.

Arthrochilus inhabits coastal, sandy heathlands and woodlands or mountain woodlands along the eastern coast of

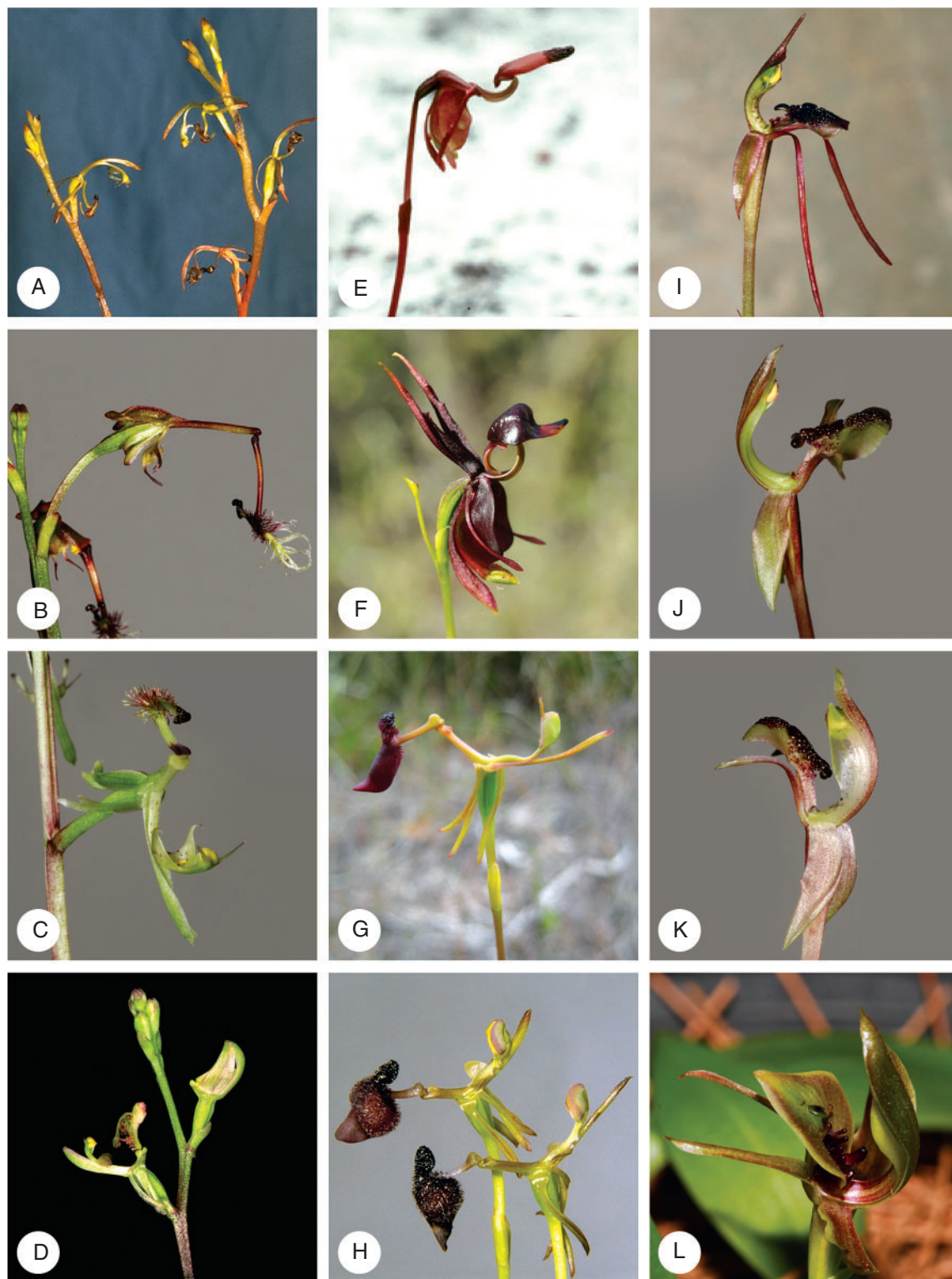


Fig. 2. Representative of genera within Drakaeinae (Orchidaceae). A. *Spiculaea ciliata*, The Humps, Western Australia (WA); B. *Thynninorchis hunteriana*, Mount Bollard, New South Wales (NSW); C. *Arthrochilus prolixus*, Bulahdelah, NSW; D. *A. (Phoringopsis) dockrillii*, Little Forks, Queensland (Qld); E. *Caleana triens*, Dale State Forest, WA (G. Brockman); F. *C. major*, Mount Jerrabomberra, NSW (Z. Groeneveld); G. *Drakaea thynniphila*, Walpole, WA (C. Busby); H. *D. glyptodon*, Bayonet Head, WA (R. Heberle); I. *Chiloglottis diphylla*, Bulahdelah, NSW; J. *C. (Myrmechila) formicifera*, Mill Creek, NSW; K. *C. (Myrmechila) platyptera*, Barrington Tops, NSW; L. *C. (Simpliglottis) jeanesii*, Toorongo, Victoria.

Australia from Sydney to north Cape York and some Torres Strait islands, with an isolated disjunct species, *A. latipes*, in Arnhem Land in the Northern Territory. Both *Arthrochilus* and *Phoringopsis* are colony-forming species, found in small clusters or in great numbers in some areas. Flowering occurs with or without leaves in *Arthrochilus*, depending on the species involved. Morphologically, these taxa have much in common despite these noted differences, particularly in plant habit.

The older (Blaxell 1972) and more recent treatment of *Phoringopsis* as *Arthrochilus* *s.lat.* (Szlachetko 2003) is possibly more appropriate than the recognition of these taxa as separate genera. *Thynniorchis* is distinctive, supported by a long branch with the nrDNA ITS data, but the possession of several unique vegetative and floral characters makes it difficult to identify synapomorphies shared by it and *Arthrochilus* and *Phoringopsis*. Clearly, these DNA data can be interpreted to recognise alternative classifications. Features and characteristics that facilitate ready recognition of and isolation of *Thynniorchis* from *Arthrochilus* are the mycoheterotrophic leafless plant habit, presence of protocorm or protocorm-like structures and absence of true tubers, labellum hinged to the end of a long narrow column foot and dangled like a fishing lure, labellum lamina simple, unlobed, with a long, peltately attached basal stalk, a callus intricately insectiform and dominating the labellum lamina, ornamented with long, multi-layered, barbed caudiform cells, with a main head that is deeply divided into two lobes, each lobe ending in a swollen knob-like structure, along with being distributed in tall wet forests throughout mountainous regions of south-eastern Australia. On this basis, we support a classification that recognises both *Arthrochilus* and *Thynniorchis* (Fig. 1).

A clade containing a monophyletic *Caleana* (Fig. 2F) and a monophyletic *Paracaleana* (Fig. 2E) is strongly supported. *Caleana major* (Fig. 2F), the type of that genus, is sister to representatives of *Paracaleana* (and *Sullivania*); however, both of these groups are on shorter branches than is the combined *Caleana*–*Paracaleana* clade. *Caleana*, the unmistakable flying duck orchid, is a south-eastern Australian species with disjunct outliers in the Mount Lofty Ranges in South Australia and Carnarvon Gorge–Blackdown Tableland region in central Queensland. *P. minor* often occurs sympatrically and has a distribution similar to that of *C. major*, although also occurring on the North island of New Zealand (St George 1999). However, the greatest number of *Paracaleana* species (11 spp.) inhabit areas in the south-west of Western Australia (Hopper and Brown 2006; Brown *et al.* 2008; Hoffman and Brown 2011). All are colony-forming species.

Caleana (Fig. 2F) is distinct from *Paracaleana* (Fig. 2E) on morphological grounds. This is reflective of the pollination syndrome and associated development of morphological features, such as tuberculate labella surface, first identified by Blaxell (1972) when describing the genus (Hopper and Brown 2006). Possession of a glabrous labellum or the apparent lack of glands on the labellum of *C. major* is attributable to the pollination syndrome, where flowers are visited by males of the long-tailed sawfly, *Lophyrotoma leachii* (Kirby), that land cross-wise on the smooth labellum surface (Cady 1965; Bates 1989; Bower 2001). All other species are apparently pollinated by male thynnine wasps (*Erione* spp.: Tiphidae) that are attracted to the flower by

allomones and pseudocopulate with the insectiform labellum (Hopper and Brown 2006). Possession of a hinged labellum sensitive to touch is characteristic for all species in this major clade and this is the only group in Drakaeinae with this character. Column wings are also highly developed, extending the whole length of that organ, forming a cup-like structure that temporarily holds the insect in place during pollination. From the results of our study, we conclude that *Paracaleana* (and *Sullivania*) are synonymous with *Caleana*, as originally proposed by Clements (1989).

The three sampled species representative of the genus *Drakaea* (Fig. 2G, H) form a strongly supported clade. These unique hammer orchids of south-western Western Australia possess several synapomorphies and the genus is now recognised as containing at least 10 species (Hopper and Brown 2006). Their separation from all other members of Drakaeinae belies past confusion surrounding their recognition as a distinct genus. Recent research (Phillips *et al.* 2011) has suggested that most species inhabit highly specialised microhabitats in open areas of sandy ground and that each species is associated with a single specific mycorrhizal fungus. All species are reported as being pollinated by thynnine wasps (*Zaspilothynnus* spp.) during attempted pseudocopulation with the highly specialised insectiform labellums (Hopper 2009). Column wings are more or less vestigial in all species and the anther is very prominent. In addition, *Drakaea* is characterised by possession of a single, short, reinform, spongy, glabrous leaf, a thin, wiry, glabrous scape that gradually widens towards the apex, and a one-flowered inflorescence, with a labellum stalk basally hinged and able to pivot on the hinge, returning to its original position.

Chiloglottis *s.lat.* comprises the final clade. Our results suggested that although species attributed to both *Myrmecchila* (represented by *C. truncata*, *C. platyptera*, *C. trapeziformis* and *C. formicifera*) (Fig. 2J, K) and *Simpliglottis* (represented, for example, by *C. cornuta*, *C. valida*, *C. chlorantha*) (Fig. 2L) are monophyletic (PP = 1.00, BV = 100), on short branches, the rest of *Chiloglottis* (*Chiloglottis* *s.s.*) (Fig. 2I) is unresolved within *Chiloglottis* *s.lat.* Analysing a combined matrix of both ITS and *trnL*–*trnF* cpDNA intergenic spacer sequences, Mant *et al.* (2002) found strong support for the monophyly of two groups, where *Chiloglottis* *s.str.* was sister to *Myrmecchila*, and these combined were sister to *Simpliglottis*, contrary to what was found here. These conflicting results are likely to be the result of ITS being a faster-evolving locus than *trnL*–*F* in these taxa. The arrangement of taxa where the *Simpliglottis* clade is sister to the remainder of *Chiloglottis* is also reflected in possession of a simpler, less elaborate floral morphology found in species of *Simpliglottis*. The nature of these conflicting results and the minimal nature of the morphological differences among taxa, in particular *Myrmecchila* and *Chiloglottis* *s.s.*, and the difficulty in applying this taxonomic segregation in practice, suggest that the original decision by Szlachetko (2001) and follow-up decisions by Jones and Clements (2005) to split *Chiloglottis* *s.lat.* were unnecessary. We, therefore, argue that Robert Brown's original concept of a single *Chiloglottis*, supported by most subsequent authors, is the best taxonomic interpretation of these data.

Chiloglottis (Fig. 2I–L) is distributed throughout south-eastern Australia, including Tasmania, as well as occurring in

New Zealand where it reaches as far south as the Auckland Island, where *C. cornuta* was first discovered and described by Hooker (1844–1847). *Chiloglottis* is characterised by possession of the following: two subequal, opposed leaves; a one (rarely two) flowered, fleshy, ephemeral inflorescence arising from the centre of the two leaves; flowers suberect to horizontal; sepals with cylindrical, apical osmophores; a prominent rhomboid-trapeziform, caudate, stiffly, hinged labellum with a wide lamina and prominent columnar; and stalked calli, weakly or strongly insectiform; and column wings extending the length of the column.

Conclusions

Although only based on analysis of ITS nuclear rDNA sequences, our results provided sufficient basis for a reinterpretation of generic circumscription within subtribe Drakaeinae. These results are supported by those generated using both nuclear and chloroplast genes (Weston *et al.*, *in press*), where the position and status of Drakaeinae, relative to the remainder of Diurideae, is the subject of further consideration. Given the very high levels of support and degree of genetic divergence, coupled with possession of readily definable morphological synapomorphies for each major clade, the Drakaeinae require significant taxonomic changes to conform to a monophyletic interpretation of the tribe and its genera. A reclassification of all the species involved, including some reallocation of taxa to appropriate genera, is provided (Appendix 1).

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Appendix 1. Taxonomic enumeration of the subtribe Drakaeinae

!, type seen; Dist., distribution, codes follow Table 1

Drakaeinae Schltr., *Bot. Jahrb. Syst.* 45: 381 (1911). Type: *Drakaea* Lindl

Tribe Geoblasteae Barb. Rodr. Subtribe Chiloglottidinae Szlach., *Fragm. Flor. Geobot.*, Suppl. 3: 23 (1995). Type *Chiloglottis* R.Br.

Tribe Geoblasteae Barb. Rodr. Subtribe Caeanae Szlach., *Fragm. Flor. Geobot.*, Suppl. 3: 24 (1995). Type *Caeana* R.Br.

Tribe Geoblasteae Barb. Rodr. Subtribe Drakaeinae (Schltr.) Szlach., *Fragm. Flor. Geobot.*, Suppl. 3: 24 (1995).

Arthrochilus F.Muell., *Fragm.* 1: 42 (Jun. 1858). Type species: *Arthrochilus irritabilis* F.Muell.

Drakaea Lindl. sect. *Akaedra* Schltr., *Bot. Jahrb. Syst.* 45: 383 (1911).

Type species: *Drakaea irritabilis* F.Muell. and *D. hunterianan* F.Muell.

Subgen. **Arthrochilus**

Arthrochilus apectus D.L.Jones, *Orchadian* 14(8): Suppl. i, ii (June 2004)

Type: Queensland: Cook District; old slaughterhouse area, Heathlands Reserve, Cape York Peninsula, 25 Jan. 1992, *D.L.Jones 8940* and *C.H.Broers* (CBG 9220228) (holo CANB!).

Dist: Qco.

Arthrochilus aquilus D.L.Jones, *Orchadian* 14(8): Suppl. ii, iii (June 2004)

Type: Queensland: Cook District; old slaughterhouse area, Heathlands Reserve, Cape York Peninsula, 25 Jan. 1992, *D.L.Jones 8941* and *C.H.Broers* (CBG 9220229) (holo CANB!).

Dist: Qco.

Arthrochilus corinnae D.L.Jones, *Orchadian* 14(8): Suppl. iii, iv (June 2004)

Type: Queensland: Cook District; swamp on south bank of Dulhunty River, Old Telegraph Road crossing, Cape York Peninsula, 23 Jan. 1992, *D.L.Jones 8888* and *C.H.Broers* (CBG 9220175) (holo CANB!; iso BRI!, MEL!).

Dist: Qco.

Arthrochilus irritabilis F.Muell., *Fragm.* 1: 43 (1858)

Drakaea irritabilis (F.Muell.) Rchb.f., *Beitr. Syst. Pflanzenk.* 68 (1871); *Spiculaea irritabilis* (F.Muell.) Schltr., *Repert. Spec. Nov. Regni Veg. Beih.* 17: 81 (1921).

Type: 'Moreton Bay', *W.Hill and F.Mueller s.n.* (holo MEL!; iso K-LINDL!).

Dist: Ncc, Nnc, Qmo, Qwb, Qkn, Ddg.

Arthrochilus latipes D.L.Jones, *Austral. Orch. Res.* 2: 8, 9, f. 7 (1991)

Type: Northern Territory: Radon Gorge, Mount Brockman, 12°45'S, 132°53'E, 7 Dec. 1978, *C.R.Dunlop 5044* (holo DNA, iso DNA).

Dist: Ddg.

Arthrochilus oreophilus D.L.Jones, *Austral. Orch. Res.* 2: 9, 10, f. 8 (1991)

Type: Queensland; Cook District; Herberton Range, 17°24'S, 142°20'E, 22 Jan 1988, *L.Lawler 24* (holo CANB!; iso BRI!, CANB!).

Dist: Qco.

Arthrochilus prolixus D.L.Jones, *Austral. Orch. Res.* 2: 10, f. 9 (1991)

Type: New South Wales; Bellangry, NW of Wauchope, 31°21'S, 152°37'E, 9 Dec. 1985, *D.L.Jones 2228*, *L.Barton and T.D.Jones* (holo CANB!; iso BRI!, CANB!, NSW!).

Dist: Ncc, Nnc, Qmo.

Arthrochilus rosulatus D.L.Jones, *Austral. Orch. Res.* 2: 10, 11, f. 10 (1991)

Type: Queensland; Cook District; Double Barrel Pinch, Shipton's Flat Road, ~8 km from Big Forks junction, S of Cooktown, 15°45'S, 148°15'E, 6 June 1990, *L.Lawler 83* (holo CANB!; iso BRI!, CANB!).

Dist: Qco.

Arthrochilus sabulosus D.L.Jones, *Austral. Orch. Res.* 2: 11, 12, f. 11 (1991)

Type: Queensland; Horn Island, ~4.5 km W of airstrip towards jetty, 10°35'S, 142°15'E, 9 Feb. 1989, *D.L.Jones 3558*, *B.Gray, P.S.Lavarack and J.R.Clarkson* (holo CANB!; iso BRI!, CANB!, MEL!, NSW!).
 Dist: Qco.

Arthrochilus stenophyllus D.L.Jones, *Austral. Orch. Res.* 2: 12, 13, f. 12 (1991)

Type: Queensland; Sunday Creek, south of Cardwell, 18°30'S, 146°10'E, 12 Dec. 1988, *P.S.Lavarack 3624* (holo CANB!; iso CANB!).
 Dist: Qkn.

Subgen. *Phoringopsis* (D.L.Jones & M.A.Clem.) Szlach., *Richardiana* 3(2): 97

Basionym: *Phoringopsis* D.L.Jones et M.A.Clem., *Orchadian* 13(10): 457 (Feb. 2002).

Type species: *Arthrochilus byrnesii* Blaxell.

Arthrochilus byrnesii Blaxell, *Contr. New South Wales Natl. Herb.* 4: 278 (1972)

Phoringopsis byrnesii (Blaxell) D.L.Jones et M.A.Clem., *Orchadian* 13(10): 457 (Feb. 2002).

Type: 'Waterfall Creek, South Alligator River, Northern Territory', 2 Apr. 1969, *N. Byrnes 1530* (holo NSW!; iso DNA!).
 Dist: Ddg, Wga.

Arthrochilus dockrillii Lavarack, *Proc. Roy. Soc. Queensland* 86(25): 155, f. 1 (1975)

Phoringopsis dockrillii (Lavarack) D.L.Jones et M.A.Clem., *Orchadian* 13(10): 457 (Feb. 2002).

Type: 'Kurrimine, near Innisfail, North Queensland', 17 July 1972, *P. Lavarack N.P. [National Park number series] 1691* (holo BRI!; iso NSW!).
 Dist: Qkn, Qco.

Arthrochilus lavarackiana (D.L.Jones) Lavarack, *Austrobaileya* 7(20): 385 (2006)

Phoringopsis lavarackiana D.L.Jones, *Orchadian* 14(8): Suppl. xi (2004).

Type: Queensland. Cultivated Australian National Botanic Gardens, 16 May 1990, ex 'Moa Island, ~1 km NE of airport, Kubin', *D.L.Jones 6006 (CBG 9010305)* (holo CANB).
 Dist: Qco; PG.

Caleana R.Br., *Prod.* 329 (1810)

Type species: *Caleana major* R.Br., *fide* Blaxell (1972).

Caleya R.Br. in W.Aiton et W.T.Aiton, *Hort. Kew.* (Ed. 2) 5: 204 (1813) (orth. var.).

Sullivania F.Muell., *J. Proc. Roy. Soc. New South Wales* 15: 229 (1882), syn. nov.

Type species: *Caleya sullivanii* F.Muell., *fide* Jones and Clements (2005).

Paracaleana Blaxell, *Contr. New South Wales Natl. Herb.* 4: 281 (1972). *Paracaleana* Blaxell subgen. *Paracaleana*, *Orchadian* 13(10): 458 (2002).

Type species: *Caleana minor* R.Br.

Sullivania subgen. *Sullivania* D.L.Jones et M.A.Clem., *Orchadian* 15(1): 36 (2005)

Basionym: *Paracaleana* Blaxell subgen. *Tanychila* D.L.Jones et M.A.Clem., *Orchadian* 13(10): 458 (2002); *Sullivania* subgen. *Tanychila* (D.L.Jones et M.A.Clem.) D.L.Jones et M.A.Clem., *Orchadian* 15(1): 36 (2005).

Type species: *Paracaleana nigrita* (J.Drummond ex Lindl.) Blaxell.

Paracaleana Blaxell, *Contr. New South Wales Natl. Herb.* 4: 281 (1972).

Type species: *Caleana minor* R.Br. (*Paracaleana minor* (R.Br.) Blaxell).

Caleana alcockii (Hopper & A.P.Br.) M.A.Clem., *comb. nov.*

Basionym: *Paracaleana alcockii* Hopper & A.P.Br., *Aust. Syst. Bot.* 19(3): 222, 223, f.2, 6, 7 (map) (30 June 2006).

Type: NW Coastal Highway, 14 km N of Galena Bridge (over the Murchison River), 27°42'39"S, 114°40'35"E, 9 Sep. 2005, *s.d.Hopper 8660*, *A.Brown, G.Brockman and R.Phillips* (holo PERTH; iso: MEL).
 Dist: Wir.

Caleana brockmanii (Hopper & A.P.Br.) M.A.Clem., *comb. nov.*

Basionym: *Paracaleana brockmanii* Hopper & A.P.Br., *Aust. Syst. Bot.* 19(3): 222, 223, f. 223–225, figs 2, 8, 9 (map) (30 June 2006).

Type: Extension of Douglas Road into Victoria Dam catchment MARTIN, 450 m N of locked Water Corp. gate, E side of track, 32°04'16"S, 116°04'04"E, 23 Nov. 2004, *G.Brockman 1471* (holo PERTH 06945643).

Dist: Wda.

Caleana disjuncta (D.L.Jones) M.A.Clem., *comb. nov.*

Basionym: *Paracaleana disjuncta* D.L.Jones, *Orchadian* 14(5): 226–228, f. (2003); *Sullivania disjuncta* (D.L.Jones) D.L.Jones et M.A.Clem., *Orchadian* 15(1): 36 (2005).

Type: South Australia; Coxs Scrub Conservation Park, 29 Oct. 1995, *D.E.Murfet 2292B and R.L.Taplin* (holo CANB!; iso AD).

Paracaleana aff. *nigrita* R.J.Bates et J.Z.Weber, *Orchids of South Australia* 61–62, t. 73 (1990).

Paracaleana linearifolia Hopper & A.P.Br. in N.Hoffman et A.P.Br., *Orchids South-West Austral.* (Ed. 2), 210, t. (1992) & (Ed. 2), Rev. Suppl. 439 (1998), *nom. inval.*, *fide* Hopper & A.P.Br. (2006: 227).

Paracaleana sp. aff. *nigrita* (Horsham) J.H.Ross et N.G.Walsh (2003), *A Census of the Vascular Plants of Victoria* (Ed. 7): 20, 23 (2003).

Paracaleana aff. *nigrita* W.R.Barker, R.M.Barker, J.Jessop et H.Vonow, *Census of South Australian Vascular Plants*: 198 (2005).

Dist: Wda, Wey, Wro, Ski, Sls, Vwh.

Caleana dixonii (Hopper & A.P.Br.) M.A.Clem., *comb. nov.*

Basionym: *Paracaleana dixonii* Hopper & A.P.Br., *Aust. Syst. Bot.* 19(3): 228, 229, f. 2, 12, 13 (map) (2006).

Type: Leeman Road on both the N and S sides, 17 Nov. 1987, *A.Brown 781* (holo PERTH 1256912).

Paracaleana dixonii Hopper & A.P.Br. in N.Hoffman et A.P.Br., *Orchids South-West Austral.* (Ed. 2), 213, t. (1992) & (Ed. 2, Rev. and Suppl.) 213 (1998), *nom. inval.*

Dist: Wda.

Caleana gracilicordata (Hopper & A.P.Br.) M.A.Clem., *comb. nov.*

Basionym: *Paracaleana gracilicordata* Hopper & A.P.Br., *Aust. Syst. Bot.* 19(3): 229, 230, f.2, 14, 15 (map) (2006).

Type: Granite rock 1.5 km SE of Blue Rock, Jarrahdale–Albany Highway road, 32°20'01"S, 116°07'58"E, 21 Oct. 2003, *G.Brockman 1117* (holo PERTH 06734693).

Dist: Wda.

Caleana granitica (Hopper & A.P.Br.) M.A.Clem., *comb. nov.*

Basionym: *Paracaleana granitica* Hopper & A.P.Br., *Aust. Syst. Bot.* 19(3): 230–232, f.2, 16, 17 (map) (2006).

Type: Sullivan Rock on Albany Highway, 32°23'S, 116°15'E, 26 Nov. 1986, *s.d.Hopper 5835* (holo PERTH 904309).

Dist: Wda.

Caleana hortiorum (Hopper & A.P.Br.) M.A.Clem., *comb. nov.*

Basionym: *Paracaleana hortiorum* Hopper & A.P.Br., *Aust. Syst. Bot.* 19(3): 232–234, f. 2, 18, 19 (map) (2006).

Type: Flynn State Forest, Deefor Road, York. 350 m W of Surrey Road, 32°1'58"S, 116°28'42"E, 11 Oct. 2003, *F.Hort & J. Hort 2053* (holo: PERTH 06639674).

Dist: Wda.

Caleana lyonsii (Hopper & A.P.Br.) M.A.Clem., *comb. nov.*

Basionym: *Paracaleana lyonsii* Hopper & A.P.Br., *Aust. Syst. Bot.* 19(3): 219–221, f. 4, 5 (map) (2006).

Type: 15.7 km E of the North West Coastal Highway along fenceline, ENE of Nerren Nerren Station, 27°07'17"S, 114°46'44"E, 28 Sep. 1994, *A.P.Brown 1131* (holo PERTH 03926044; iso AD, CBG[CANB]!).

Paracaleana lyonsii Hopper & A.P.Br. in N.Hoffman et A.P.Br., *Orchids South-West Austral.* (Revised ed. 2), 439, t. (1998), *nom. inval.*, *ined.*

Dist: Wir, Wau, Wco.

Caleana major R.Br., Prod. 329 (1810)

Caleya major (R.Br.) R.Br. in W.Aiton et W.T.Aiton, *Hort. Kew.* (ed. 2) 5: 204 (1813).

Type: '(J) v.v.' [Port Jackson; Bennelong Point', Sep. 1803, *R.Brown s.n.*] (lectotype specimen (a) BM!; isolectotype E!, FI!, K!, K-LINDL!, P!), *fide* Clements (1989).

Dist: Sls, Ski, Sse, Vwp, Vwh, Vgi, Veh, Tas, Nsc, Nst, Ncc, Nct, Nnc, Qmo, Qdd, Qle.

Caleana minor R.Br., Prod. 329 (1810)

Caleya minor (R.Br.) Sweet, *Hort. Brit.* 385 (1827)

Paracaleana minor (R.Br.) Blaxell, *Contr. New South Wales Natl. Herb.* 4: 281 (1972); *Sullivania minor* (R.Br.) D.L.Jones et M.A.Clem., *Orchadian* 15(1): 36 (2005).

Type: '(J.) v.v.' [Port Jackson; Sandy ground between brickfields and Barclay Lagoon, Oct.–Nov. 1803, *R.Brown s.n.*] (lectotype specimen (a) BM!; isolectotype E!, G!, K!, K-LINDL!, P!), *fide* Clements (1989).

Caleya sullivanii F.Muell., Chem. & Druggist, *Aust. Suppl.* 4: 44 (1882); *Caleana sullivanii* (F.Muell.) E.E.Pescott, *Victorian Naturalist* 43: 228 (1926); *Paracaleana sullivanii* (F.Muell.) Blaxell, *Contr. New South Wales Natl. Herb.* 4: 282 (1972).

Type: 'Near Mt. Zero, Grampians in Victoria', Jan. 1882, *D.Sullivan s.n.* (holo MEL!).

Caleana nublingii Nicholls, *Victorian Naturalist* 48: 15 (1931).

Type: 'New South Wales, Bell, Blue Mountains, 27 Dec.1930, *E.Nubling s.n.* (holo AD!).

Dist: Sls, Sse, Vwp, Vwh, Veh, Vgi, Tas, Nsc, Nst, Can, Ncc, Nct, Nnc, Ncs, Qmo, Qdd, Qwb, Qle; NZ.

Caleana nigrita J.Drummond ex Lindl. in Edwards's, *Bot. Reg.* 1–23: Swan Riv. Append. liv (1840)

Paracaleana nigrita (J.Drummond ex Lindl.) Blaxell, *Contr. New South Wales Natl. Herb.* 4: 282 (1972); *Sullivania nigrita* (J.Drummond ex Lindl.) D.L.Jones et M.A.Clem., *Orchadian* 15(1): 36 (2005).

Type: 'Swan River', 1839, *J.Drummond s.n.* (holo K-LINDL!; iso E!, G!, K!).

Dist: Wda, Wey.

Caleana parvula (Hopper & A.P.Br.) M.A.Clem., *comb. nov.*

Basionym: *Paracaleana parvula* Hopper & A.P.Br., *Aust. Syst. Bot.* 19(3): 237, 238, f. 2, 23, 24 (map) (2006).

Type: Mount Ragged track, 4.2 km N of Fisheries Road, E of Esperance, 33°43'06"S, 123°07'13"E, 30 Oct. 2004, *G.Brockman 1449* (holo PERTH 06945686).

Dist: Wey.

Caleana terminalis (Hopper & A.P.Br.) M.A.Clem., *comb. nov.*

Basionym: *Paracaleana terminalis* Hopper & A.P.Br., *Aust. Syst. Bot.* 19(3): 239–240, f. 2, 25, 26 (map) (2006).

Type: Z Bend Gorge, Kalbarri National Park, 27°39'S, 114°28'E, 21 Aug. 1984, *A.Brown s.n.* (holo PERTH 929158).

Paracaleana terminalis Hopper & A.P.Br. in N.Hoffman et A.P.Br., *Orchids South-West Austral.* (Ed. 2), 212, t. (1992), *nom. inval.*

Dist: Wir.

Caleana triens (Hopper & A.P.Br.) M.A.Clem., *comb. nov.*

Basionym: *Paracaleana triens* Hopper & A.P.Br., *Aust. Syst. Bot.* 19(3): 240–242, f. 2, 27, 28 (map) (2006)

Type: Cut Hill, W of York, 31°54'23"S, 116°43'11"E, 15 Sep. 1907, *O.H.Sargent s.n.* (holo PERTH 00337307).

Paracaleana triens Hopper & A.P.Br. in N.Hoffman et A.P.Br., *Orchids South-West Austral.* (Ed. 2), 211, t. (1992), *nom. inval.*

Dist: Wda, Wav, Wro.

Chiloglottis R.Br., Prod. 322, 323 (1810)

Type species: *Chiloglottis diphylla* R.Br.

Chiloglottis R.Br. subgen. *Chiloglottis*, *Orchadian* 13(10): 459 (2002).

× *Chilosimpliglottis* Jeanes, *Muelleria* 16: 81 (2002). *syn nov.*

Chiloglottis anaticeps D.L.Jones, *Austral. Orch. Res.* 2: 37, f. 44 (1991)

Type: New South Wales; ~2 km SE of Forbes River crossing, Hastings Forest Way, W of Wauchope, 31°09'S, 152°22'E, 9 Dec. 1985, *D.L.Jones 2229, L.Barton and T.D.Jones* (holo CANB!; iso CANB!, NSW!).

Dist: Nnt.

Chiloglottis diphylla R.Br., *Prod.* 323 (1810)

Caladenia diphylla (R.Br.) Rehb.f., *Beitr. Syst. Pflanzenk.* 67 (1871).

Types: '(J) v.v.' [Port Jackson; Sydney and Parramatta, Mar. 1805, *R.Brown s.n.*] (lectotype specimen (a) BM!; isolectotype E!, K!, K-LINDL!, P!), *fide* Clements (1989); Syntype: '(J) v.v.' [Port Jackson, 1804, *R.Brown s.n.*] (AD!).

Dist: Nsc, Ncc, Nct, Nnc, Ncs, Nnt, Qmo, Qdd, Qwb, Qbn, Qle.

Chiloglottis longiclavata D.L.Jones, *Austral. Orch. Res.* 2: 38–39, f. 46 (1991)

Type: Queensland; Cook District; SFR 194, Parish of Western, Herberton Range, 17°20'S, 145°25'E, 100 m, 26 April 1987, *B.Gray 4455* (holo CANB!; iso CANB!).

Dist: Qle, Qks, Qkn, Qco.

Chiloglottis palachila D.L.Jones, *Austral. Orch. Res.* 2: 39, f. 47 (1991)

Type: 'New South Wales; Barrington Tops, 31°59'S, 151°58'E, 8 Dec. 1985, *D.L.Jones 208, L.Barton and T.D.Jones* (holo CANB!; iso BRI!, CANB!, MEL!, NSW!).

Dist: Ncs, Nnt.

Chiloglottis reflexa (Labill.) Druce, *Rep. Bot. Exch. Cl. Brit. Isles Suppl.* 2: 614 (1917)

Basionym: *Epipactis reflexa* Labill., *Nov. Holl. pl.* 2: 60, t. 211 (1806).

Type: Van Diemen, *J. Labillardiere s.n.* (lecto FI!; illustration only!), *fide* Clements (1989).

Acianthus bifolius R.Br., *Prod.* 322 (1810), *nom. illeg.*

Type: Van Diemen, *J. Labillardiere s.n.* (lecto FI!; illustration only).

Dist: Vwp, Vwh, Vgi, Veh, Tas, Nsc, Ncc, Nnt.

Chiloglottis seminuda D.L.Jones, *Austral. Orch. Res.* 2: 41, f. 50 (1991)

Type: 'New South Wales; Penrose State Forest, 34°40'S, 150°13'E, 14 Mar. 1990, *D.L.Jones 5745 and C.H.Broers* (holo CANB, iso CANB, NSW, MEL, AD, BRI).

Dist: Ncc, Nst, Nct.

Chiloglottis sphaerula D.L.Jones, *Austral. Orchid. Res.* 5: 73, 74, f.3.7 (21 Dec. 2006)

Type: New South Wales. Barrington Tops, 5 Feb. 1993, *R.Tunstall, D.Herd. G.Hillman and J.Riley (D.L.Jones 11282)* (holo CANB 677939!).

Dist: Nnt.

Chiloglottis sphyrnoides D.L.Jones, *Austral. Orch. Res.* 2: 41, 42, f. 51 (1991)

Type: Queensland; Pat's Bluff, Lamington National Park, 28°16'S, 153°07'E, 1 Apr. 1988, *C.Harman 3* (holo CANB!; iso BRI!, CANB!, NSW!).

Dist: Nnc, Qmo.

Chiloglottis sylvestris D.L.Jones et M.A.Clem., *Proc. Roy. Soc. Queensland* 98: 123–4, f. 1 (1987)

Type: 'Queensland Springbrook', 12 Jan. 1986, *D.L.Jones 2231* (holo BRI!; iso AMES!, BRI!, CANB!, K!, MO!, NSW!, PERTH!, US!).

Dist: Ncc, Nnc, Qmo.

Chiloglottis trilabra Fitzg., *J. Bot.* 21: 204 (1883)

Type: 'Mount York, Blue Mountains, N.S.W.', *R.D.Fitzgerald s.n.* (holo BM!).

Chiloglottis dockrillii Rupp, *Victorian Naturalist* 70: 54, f. (1953).

Type: 'Barrington Tops, New South Wales', Feb. 1953, *A.W.Dockrill s.n.* (holo NSW!; iso MEL!), *fide* Clements (1989).

Dist: Tas, Vgi, Veh, Nst, Can, Nct, Nnt.

Sect. *Myrmechila* (D.L.Jones et M.A.Clem.) M.A.Clem., *comb. et stat. nov.*

Basionym: *Myrmechila* D.L.Jones et M.A.Clem., *Orchadian* 15(1): 36, 37 (2005).

Type species: *Chiloglottis formicifera* Fitzg.

Chiloglottis formicifera Fitzg., *Austral. Orch.* 1(3): [t. 9] (1877)

Myrmechila formicifera (Fitzg.) D.L.Jones et M.A.Clem., *Orchadian* 15(1): 37 (2005).

Type: 'Liverpool', Sep.–Oct., *C. King s.n.* (holo not found; lectotype Fitzgerald's plate!), *fide* Clements (1989).

Dist: Nsc, Ncc, Nct, Nnc, Nnt, Qdd; NZ.

Chiloglottis platyptera D.L.Jones, *Austral. Orch. Res.* 2: 39, 40, f. 48 (1991)

Myrmechila platyptera (D.L.Jones) D.L.Jones et M.A.Clem., *Orchadian* 15(1): 37 (2005).

Type: New South Wales; N of Dingo Gate, Barrington Tops, 31°55'S, 151°21'E, 26 Sep. 1989, *C. Bower s.n.* (*D.L.Jones 5093*) (holo CANB!; iso CANB!, NSW!).

Dist: Nnt., Nnc.

Chiloglottis trapeziformis Fitzg., *Austral. Orch.* 1(3): [t. 9] (1877)

Myrmechila trapeziformis (Fitzg.) D.L.Jones et M.A.Clem., *Orchadian* 15(1): 37 (2005).

Basionym: Type: 'New South Wales, Liverpool', *C. King s.n.* (holo BM!).

Dist: Sse, Vgi, Veh, Tas, Nst, Can, Nss, Ncc, Nct, Ncs.

Chiloglottis trullata D.L.Jones, *Austral. Orch. Res.* 2: 42, 43, f. 52 (1991)

Myrmechila trullata (D.L.Jones) D.L.Jones et M.A.Clem., *Orchadian* 15(1): 37 (2005)

Type: Queensland; Rainbow Falls, Blackdown Tableland, 23°39'S, 149°04'E, 18 July 1989, *E. Pederson s.n.* (*D.L.Jones 4552*) (holo CANB, iso BRI).

Dist: Qle.

Chiloglottis truncata D.L.Jones et M.A.Clem., *Proc. Roy. Soc. Queensland* 98: 124, f. 2 (1987)

Myrmechila truncata (D.L.Jones et M.A.Clem.) D.L.Jones et M.A.Clem., *Orchadian* 15(1): 37 (2005).

Type: 'Queensland, Anduramba, W of Toogoolawah', Aug. 1984, *D.L.Jones s.n.* (holo BRI!; iso AMES!, CANB!, K!, MO!, NSW!).

Dist: Qdd, Qle.

sect. *Simpliglottis* (Szlach.) M.A.Clem., *sect. et stat. nov.*

Basionym: *Simpliglottis* Szlach., *Polish Bot. J.* 46(1): 13 (2001).

Type species: *Simpliglottis valida* (D.L.Jones) Szlach. (*Chiloglottis valida* D.L.Jones).

Chiloglottis R.Br. subgen. *Simpliglottis* (Szlach.) D.L.Jones et M.A.Clem., *Orchadian* 13(10): 459 (2002).

Chiloglottis chlorantha D.L.Jones, *Austral. Orch. Res.* 2: 37–38, f. 45 (1991)

Simpliglottis chlorantha (D.L.Jones) Szlach., *Polish Bot. J.* 46(1): 13 (2001).

Type: New South Wales; Jamberoo Mountain SW of Wollongong, 34°38'S, 150°44'E, Oct. 1988, *R.G. Tunstall s.n.* (holo CANB!; iso CANB!, MEL!, NSW!).

Dist: Ncc.

Chiloglottis cornuta Hook.f., *Fl. \Antarct.* 1: 69 (1844)

Simpliglottis cornuta (Hook.f.) Szlach., *Polish Bot. J.* 46(1): 13 (2001).

Type: 'Campbell Islands', *Lyll s.n.* (holo K!).

Chiloglottis muelleri Fitzg., *Austral. Orch.* 2(2): [t. 6] (1885).

Type: 'Loddon, Victoria', Nov., *C. French ex F. Mueller s.n.* (holo not found; lectotype Fitzgerald's plate!), *fide* Clements (1989).

Dist: Sse, Veh, Tas, Nst; NZ.

Chiloglottis grammata G.W.Carr, *Indig. Fl. & Fauna Assoc. Misc. Paper* 1: 20, 21 (1991)*Simpliglottis grammata* (G.W.Carr) Jeanes, *Muelleria* 16: 82 (2002).Type: Tasmania, Jackeys Marsh, 20 Nov. 1982, *G.W. Carr s.n.* (holo MEL 223596!; iso CANB, HO, K, NSW).*Chiloglottis* × *pescottiana* auct. non R.S.Rogers; Messmer in W.M. Curtis, *Student's Fl. Tas.* 4A: 86 (1979), *fide* Jones (1998).

Dist: Tas.

Chiloglottis gunnii Lindl., *Gen. sp. orchid. pl.* 387 (1840)*Caladenia gunnii* (Lindl.) Rchb.f., *Beitr. Syst. Pflanzenk.* 67 (1871)*Simpliglottis gunnii* (Lindl.) Szlach., *Polish Bot. J.* 46(1): 13 (2001).Type: 'Tasmania, Circular Head', Nov. 1837, *R.Gunn 913* (holo K-LINDL!; iso K!, P!).*Chiloglottis platychila* G.W.Carr, *Indig. Fl. & Fauna Assoc. Misc. Paper* 1: 21 (1991).Type: Tasmania, western city limits of Hobart at foot of Mt Wellington, 20 Dec. 1984, *G.W.Carr 10055* (holo MEL!; iso AD, CANB, HO, K, NSW), *fide* Jones (1998).

Dist: Tas.

Chiloglottis jeanesii D.L.Jones, *Muelleria* 10: 63–67, f.1 (1997)*Simpliglottis jeanesii* (D.L.Jones) Jeanes, *Muelleria* 16: 82 (2002).Type: Victoria, Torongro, 14 Jan. 1995, *C. Bower (D.L.Jones 13809)* (holo CANB!; iso AD!, BRI!, MEL!, NSW!).

Dist: Veh.

Chiloglottis pluricallata D.L.Jones, *Austral. Orch. Res.* 2: 40, f. 49 (1991)*Simpliglottis pluricallata* (D.L.Jones) Szlach., *Polish Bot. J.* 46(1): 13 (2001).Type: New South Wales; Point Lookout, New England National Park, 30°29'S, 152°25'E, 7 Dec. 1989, *D.L.Jones 5538 and C. Broers* (holo CANB!; iso BRI!, CANB!, MEL!, NSW!).

Dist: Nn, Nnc, Ncc, Nct.

Chiloglottis triceratops D.L.Jones, *Aust. Orch. Res.* 3: 66, 67, f. 3.3 (1998)*Simpliglottis triceratops* (D.L.Jones) Jeanes, *Muelleria* 16: 82 (2002).Type: Tasmania; Coquette Ck., Scottsdale Road, 7 Nov. 1990, *D.L.Jones 7060, C.H.Broers and J. Campbell* (holo CANB!; iso AD, CANB, HO, MEL, NSW).

Dist: Tas.

Chiloglottis turfosa D.L.Jones, *Austral. Orch. Res.* 2: 43, f. 53 (1991)*Simpliglottis turfosa* (D.L.Jones) Szlach., *Polish Bot. J.* 46(1): 13 (2001).Type: New South Wales; ~7 km along Tantangara Dam Road, Kosciusko National Park, 35°52'S, 148°38'E, ~1000 m, 16 Dec. 1989, *D.L.Jones 5571, B.E.Jones and T.D.Jones* (holo CANB, iso CANB).

Dist: Nst.

Chiloglottis valida D.L.Jones, *Austral. Orch. Res.* 2: 43, 44, f. 54 (1991)*Simpliglottis valida* (D.L.Jones) Szlach., *Polish Bot. J.* 46(1): 13 (2001).Type: Australian Capital Territory; track from Ginini Flats to Stockyard Arboretum, 35°32'S, 148°47'E, 3 Dec. 1989, *D.L.Jones 5453 and B.E.Jones* (holo CANB!; iso CANB!, NSW!, MEL!).

Dist: Vwh, Vwp, Vgi, Veh, Tas, Nst, Can.

Chiloglottis* × *pescottiana R.S.Rogers, *Proc. Roy. Soc. Victoria* (new ser.), 30: 139, t. 25 (1918)× *Chilosimpliglottis pescottiana* (R.S.Rogers) Jeanes, *Muelleria* 16: 81 (2002).Type: 'Cravensville near Tallangatta', 8 Oct. 1917, *A.B.Braine s.n.* (holo AD!; iso MEL!).Notes: a natural hybrid between *Chiloglottis gunnii* and *C. trapeziformis*.

Dist: Veh, Nst.

Drakaea Lindl. in Edwards's, *Bot. Reg.* 1–23: *Swan Riv. Append.* lv (1840)

Type species: *Drakaea elastica* Lindl., *fide* Pfeiffer (1874).

Drakaea Lindl. Sect. *Eu-Drakaea* Schltr., *Bot. Jahrb. Syst.* 45: 383 (1911).

Drakaea andrewsiae Hopper & A.P.Br., *Austral. Syst. Bot.* 20: 261, 262, f., 3, 7, 8 (2007).

Type: 'Gnowangerup', 7 Sep. 1930, *P.Andrews s.n.* (holo AD97034193).

Dist: Wda.

Drakaea concolor Hopper & A.P.Br., *Austral. Syst. Bot.* 20: 262–264, f., 3, 9, 10 (2007)

Type: 'Kalbarri National Park', 21 Aug. 1984, *A.P.Brown s.n.* (holo PERTH 0929190).

Drakaea concolor Hopper & A.P.Br. in N.Hoffman et A.P.Br., *Orchids South-West Austral.* (ed. 2), 202, t. (1992), *nom. inval.*

Dist: Wir.

Drakaea confluens Hopper & A.P.Br., *Austral. Syst. Bot.* 20: 264–266, f., 3, 11, 12 (2007)

Type: 'Boyup Brook area', 6 Oct. 1983, *s.d.Hopper 3461* (holo PERTH 00228893; iso AD, CANB!, K, MEL).

Drakaea confluens Hopper & A.P.Br. in N.Hoffman et A.P.Br., *Orchids South-West Austral.* (Ed. 2), 199, t. (1992), *nom. inval.*

Dist: Wda.

Drakaea elastica Lindl. in Edwards's, *Bot. Reg.* 1–23: *Swan Riv. Append.* lvi (1840)

Type: 'Swan River', *J.Drummond s.n.* (lectotype one flower in a packet (b) and the illustration on the sheet in Lindl.'s herbarium (c) K-LINDL!; isolectotype K!), *fide* Clements (1989).

Drakaea lucida J.Drummond in Hooker's, *London J. Bot.* 1: 628 (1842).

Type: 'Swan River', *J.Drummond s.n.* (lectotype specimen (a) K-LINDL!; isolectotypes E!, FI!, G!, K!, K-LINDL!), *fide* Clements (1989).

Drakaea jeanensis R.S.Rogers, *Trans. & Proc. Roy. Soc. South Australia* 44: 322–327, t.XIII 1–3 (1920) & *Trans. & Proc. Roy. Soc. South Australia* 47: 340 (1923).

Type: 'Found in sandy soil at Ravenswood, near Pinjarra, Western Australia', 1 Oct. 1919, *J.S.Rogers s.n.* (holo AD!).

Dist: Wda.

Drakaea glyptodon Fitzg., *Gard. Chron.* (new ser.), 17: 494 (1882)

Type: 'Dardanup and Albany' [Bunbury], Sep., *R.D.Fitzgerald s.n.* (holo BM!; iso BM!, NSW!).

Dist: Wir, Wda, Wav, Wro, Wey.

Drakaea gracilis Hopper & A.P.Br., *Austral. Syst. Bot.* 20: 271–273, f., 3, 17, 18 (2007)

Type: 'Stirling Range National Park, 3 km ENE of Mondurup Peak, 34°24'S, 117°51'E, 7 Oct. 1983, *s.d.Hopper 3508* (holo PERTH 00232270!; iso AD, CANB!, MEL).

Drakaea gracilis Hopper & A.P.Br. in N.Hoffman et A.P.Br., *Orchids South-West Austral.* (Ed. 2), 198, t. (1992), *nom. inval.*

Dist: Wda.

Drakaea isolata Hopper & A.P.Br., *Austral. Syst. Bot.* 20: 273–275, f., 3, 19, 20 (2007)

Type: 'near Pingrup', 12 Sept. 1985, *s.d.Hopper 4548* (holo PERTH 00902217; iso CANB!).

Drakaea isolata Hopper & A.P.Br. in N.Hoffman et A.P.Br., *Orchids South-West Austral.* (Ed. 2), 200, t. (1992), *nom. inval.*

Dist: Wav.

Drakaea livida J.Drummond in Hooker's, *London J. Bot.* 1: 628 (1842)

Type: 'Swan River', *J.Drummond s.n.* (lectotype K!; isolectotype K!).

Drakaea fitzgeraldii Schltr., *Repert. Spec. Nov. Regni Veg. Beih.* 17: 81 (1921).

Type: 'Perth, Western Australia', Sep., *R.D.Fitzgerald s.n.* (holo BM!; icon Fitzgerald's plate).

Drakaea elastica sensu Fitzg., *Austral. Orch.* 2(1): [t. 4] (1884), *non* Lindl. (1840).

Dist: Wda, Wav.

Drakaea micrantha Hopper & A.P.Br., *Austral. Syst. Bot.* 20: 278–280, f., 3, 23, 24 (2007)

Type: 'Nannup area', 10 Oct. 1983, *s.d.Hopper 3566* (holo PERTH 00231762; iso AD, CANB!).

Drakaea micrantha Hopper & A.P.Br. in N.Hoffman et A.P.Br., *Orchids South-West Austral.* (Ed. 2), 203, t. (1992), *nom. inval.*

Dist: Wda

Drakaea thynniphila A.S.George, *Nuytsia* 5(1): 60, f. 3, F–K (1984)

Type: 'Gull Rock Road, E of Oyster Harbour, Western Australia', 1 Oct. 1971, *A.S.George 11099* (holo PERTH!; iso CANB!).

Dist: Wda.

Spiculaea Lindl. in *Edwards's, Bot. Reg.* 1–23: *Swan Riv. Append.* lvi (1840)

Type species: *Spiculaea ciliata* Lindl.

Spiculaea ciliata Lindl. in *Edwards's, Bot. Reg.* 1–23: *Swan Riv. Append.* lvi (1840)

Drakaea ciliata (Lindl.) Rehb.f., *Beitr. Syst. Pflanzenk.* 68 (1871).

Type: 'Swan River', *J.Drummond 325* (holo K-LINDL!; iso BM!, FI!, G!, K!).

Dist: Wda, Wav, Wro, Wey, Wco.

Thynninorchis D.L.Jones et M.A.Clem., *Orchadian* 13(10): 457 (Feb. 2002)

Type species: *Drakaea huntiana* F.Muell. (*Arthrochilus huntianus* (F.Muell.) Blaxell).

Thynninorchis huntiana (F.Muell.) D.L.Jones et M.A.Clem., *Orchadian* 13(10): 457 (Feb. 2002)

Basionym: *Drakaea huntiana* F.Muell., *Victorian Naturalist* 5: 174 (1889); *Spiculaea huntiana* (F.Muell.) Schltr., *Repert. Spec. Nov.*

Regni Veg. Beih. 17: 81 (1921); *Arthrochilus huntianus* (F.Muell.) Blaxell, *Contr. New South Wales Natl. Herb.* 4: 277 (1972).

Type: Tingerinji Mountain, [New South Wales], 2 Mar. 1889, *W.Baeuerlen 175* (holo MEL!; iso NSW!).

Dist: Vwp, Vwh, Vgi, Tas (Flinders Island), Nst, Can, Ncc, Nct.

Thynninorchis nothofagicola (D.L.Jones) D.L.Jones et M.A.Clem., *Orchadian* 13(10): 457 (Feb. 2002)

Basionym: *Arthrochilus huntianus* (F.Muell.) Blaxell subsp. *nothofagicola* D.L.Jones, *Austral. Orch. Res.* 3: 4, f. 1.1, t.2 (1998).

Type: Tasmania, behind Needles Picnic area, Gordon River Road, 24 Feb. 1994, *A.Garner and D.Ziegler (Jones 12812A)* (holo CANB!).

Dist: Tas.