Chapter 1. Introduction

1.1 The species problem

Species are the fundamental units of biology, biological classification and taxonomy, yet there is no single species concept applicable to define life in all of its forms (e.g. Darwin 1859; Stuessy 1990). Various species concepts have been derived to answer basic questions about how many species there are and understand their relationships. Even within the seemingly well-known and 'natural' groups, such as the Angiosperms, different species concepts have been developed and applied, yet no single definition has emerged (Judd *et al.* 2002). In the absence of consensus about species limits, the classification of species remains more contentious than one might expect.

Philosophical and practical questions about species are dealt with through the field of systematics (Stuessy 1990; Judd *et al.* 2002). The basic aims of systematics are to:

- work out species limits.
- reconstruct phylogeny, and from these
- develop classification schemes.

The main aims of biological classification are to group related organisms together, to allow for the application of names, and assign relative rank to each named entity. Ideally the resulting classifications are robust and relatively stable when new information is made available, have predictive value and incorporate the best estimates of evolutionary relationships of species (Stuessy 1990; Judd *et al.* 2002).

1.2 Different species concepts

Different species concepts have been developed over time (Stuessy 1990). The more commonly encountered and applied concepts are summarized below:

1.2.1 The morphological species concept

The morphological species concept has a long history of use in biological science (Darwin 1859; Stuessy 1990). It is such a pervasive idea that the authors of flora treatments do not always state that it is the framework behind their decision making (McDade 1995; Henderson 2005). The morphological species concept is based on the idea that plants, represented by specimens, that share a suite of observable attributes, or characters, belong to the same species (Stuessy 1990). An essential part of the application of this species concept is the designation of type specimens (Quicke 1993). A type specimen is chosen at the time a new species is described and serves a fundamental role in fixing the application of a species name.

The application of the morphological species concept is based on characters, that is, observable traits belonging to the study group (Quicke 1993). Different types of characters exist and often need to be treated differently in analysis. Quantitative (or overlapping) characters comprise direct measurements from an Operational Taxonomic Unit (OTU), such as leaf number or petal length. Quantitative characters may be discontinuous or continuous, that is they may occur as discrete states, such as the number of stamens in a flower, or be a part of a continuum, such as leaf length in a range of samples. Qualitative (or non-overlapping) characters are those in which two, or more, mutually exclusive categories, or character states, occur, such as pollen colour and plant growth form (Sokal and Rohlf 1969; Kitching *et al.* 1998).

Whilst the morphological species concept has been historically applied intuitively, recent advances in computing and software programs now exist to enable this to be done quickly and in a more objective way (Quicke 1993). Matrices of character state x OTU can be analysed by statistical analyses, particularly cluster analysis and ordination, i.e. in the field of phenetics pioneered by Sneath and Sokal (1973). Such advances in storing and analysing data, however, do not overcome the main problems with this species concept: of how many characters are needed to define a species, and the subjective nature of ascribing taxonomic rank to the taxa defined by this method (Darwin 1859).

1.2.2 The biological species concept

The biological species concept is based on the dual tenets that a species is a group of potentially interbreeding populations which are reproductively isolated from other groups (Mayr 1942; Mayr 1993). By focusing on reproduction, this concept has the advantage of linking taxonomy to the broader evolutionary framework of biology (Quicke 1993). Further, reproductive isolation ensures a lack of gene flow, which is essential for evolutionary independence of organisms. However, sufficient information about the reproductive biology of the organisms under question may be lacking for this species concept to be applied (Stuessy 1990). In addition, asexually reproducing organisms and allopatric taxa cannot be treated by this concept, and even infrequent hybrids have profound implications for the application of this concept. Growing evidence indicates that evolutionary divergence does not always result in an inability to interbreed (Ornduff 1969; Whitmore 1993; Zink and McKitrick 1995).

The biological species concept can only be applied to plants once the breeding system(s) of the study groups are known (Stuessy 1990). This information may be obtained by performing experimental pollinations to determine the potential mating capabilities of plants (Levin 1971; Kearns and Inouye 1993). Plants may be self-incompatible, where self-pollen placed on the stigmatic surfaces of their flowers is unable to produce viable and fertile progeny; only pollen from a different genetic individual will lead to pollination and seed set. A consequence of self-incompatibility is increased gene flow within a population, and thus increased genetic variation of that population. Self-compatible plants, in contrast, are able to produce viable seed and fertile offspring when self-pollen is placed on the stigmatic surfaces of their flowers. With increasing self-pollination, gene-flow within a population will decrease and the gene pool of the population will become less heterogeneous. The reduction in gene-pool heterogeneity will be accelerated if the plants develop an autonomous self-pollination mechanism: whereby the cost of reproductive assurance is paid for by limited inter-generational gene flow (Wendt *et al.* 2002).

The biological species concept encapsulates useful information about the evolutionary relationships between plants, but does not necessarily form a suitable basis for defining species limits (Mallet 1995; Snow 1997).

1.2.3 The genetic species concept

The genetic species concept is based on genetic differences and distance between taxa and assumes that such differences are a consequence of a cessation of gene flow and reproductive isolation (Stuessy 1990). Rapid advances have been made in the fields of DNA extraction, amplification of selected segments, rapid and accurate reading of base pairs, and in editing the resulting sequences (Soltis and Soltis 1998). Molecular data has the advantage of providing a large number of characters (particularly base pairs) to be analysed (in a similar manner to that used for morphological data). Molecular data is not always easy to interpret, and so it is preferable to use it for corroboration and comparison with other types of data, such as morphology, when resolving phylogenetic problems (Stuessy 1990).

Advances in molecular techniques, such as DNA extraction, Polymerase Chain Reaction (PCR) amplification and sequencing have all revolutionized access to molecular data. This has been matched by the increase in processing power and availability of personal computers, which has led to the greater ability to store, edit and analyse molecular data, particularly molecular sequence data (Quicke 1993). There are now many computer programs available for phenetic and cladistic analysis of molecular data, e.g. Parsimony Analysis Using Parsimony (PAUP*) (Swofford 2001), to investigate molecular differences and evolutionary relationships between samples. Whilst differences in molecular sequences between species often correspond with different morphological characters, this is not always the case, for different genes may evolve at different rates, even between closely related taxa (Stace 2005). Analysis of a single molecular sequence may infact map the evolution of that molecular sequence, rather than the organisms from which the sequences have been obtained. Targeting several molecules, preferably in different parts of the cell, may provide more confidence that the analysis is able to better estimate evolutionary relationships of the taxa (Stuessy 1990; Soltis and Soltis 1998).

1.2.4 The phylogenetic species concept

The phylogenetic species concept (Cracraft 1983) is based on the idea of species as evolutionary lineages. Evidence for membership of such lineages is determined by the presence of diagnostic morphological, molecular, and behavioural or biochemical

characters (Nixon and Wheeler 1990). However, caution is needed to distinguish similar characters, particularly apomorphies, that have arisen through convergent evolution, or homoplasy (Quicke 1993; Dover 1995).

In practice, the phylogenetic species concept applies at the population scale (Nixon and Wheeler 1990; Snow 1997). As a consequence the application of the phylogenetic species concept usually results in the recognition of a greater number of species, including paraphyletic species, than of other concepts (Crisp and Chandler 1996; Snow 1997).

1.2.5 Cryptic species

Cryptic species are defined as populations considered to belong to the same species, due to strong morphological similarity until genetic evidence reveals they are separated by reproductive isolating mechanisms (Stebbins 1950). Once identified, morphological characters may indeed be found that enable previously cryptic species to be readily identified (Paris *et al.* 1989), but this task is made difficult by intra-population variation (Speer and Hilu 1998). Cryptic species therefore are 'cryptic' when the morphological species concept is applied. However, they may merit species status when the genetic, biological, or other species concepts are applied.

1.3 Phenetic analysis

Phenetic analysis involves statistical analyses of character x OTU data to group OTUs together based on an overall similarity (Stuessy 1990; Belbin 1995). Whilst objective and repeatable techniques are used, subjectivity cannot be totally removed as this is often intrinsic to the character selection process. Prior to analysis it is important to ensure that the characters are weighted equally, so as to remove bias from the analysis. Multi-state characters in particular need to be down weighted in proportion to the number of character states in them, so that influence of the total character is equivalent to that of a discrete quantitative character (Belbin 1995).

Clustering and ordination analyses are commonly employed in phenetic analysis (Quicke 1993). Cluster analysis works by successively grouping the most similar

OTUs together (agglomerative fusion) (Stuessy 1990). The output of cluster analysis is a branching tree diagram, or phenogram. The OTUs are presented as one axis, and a coefficient of association (a measure of similarity or dissimilarity) is presented on the other axis, and the relationship of OTUs is depicted as a series of branching lines (e.g. see Figure 12). The most commonly used ordination analyses simultaneously optimize OTU structure in multi-dimensional ordination space. Ordination provides a means to identify groups of OTUs in the data (e.g. see Figure 13). Where OTUs form tight and distinct groups in ordination space, due to co-varying character states, then more confidence may be placed in those groups of OTUs presenting different taxa.

Phenetics is therefore an appropriate technique to use to test species limits prior to phylogenetic analysis (Doyen and Slobodchikoff 1974; Crisp and Weston 1993).

1.4 Cladistic analysis

Cladistics is a field of science that began with Hennig (1950; 1965). Unlike phenetics, cladistics is based on the idea that classifications should reflect the evolutionary history, and that evolutionary relationships may be estimated by analysing character transformation, gain or loss between related entities (Stuessy 1990; Quicke 1993). Hennig (1965) identified several different states of character; those that were ancestral, or 'plesiomorphic', and those that were derived, or 'apomorphic'. Such terms are relative to the study group. Organisms are grouped on the basis of shared derived features, or 'synapomorphies'. Derived characters found only in one species or lineage are 'autapomorphies'. A fundamental principle behind cladistics analysis is that the characters used are homologous, that is, that the suites of characters studied are structurally and developmentally the same, and that these homologous attributes are inherited from a common ancestor (Stuessy 1990). Homoplastic attributes represent superficial similarity rather than evolutionary affinity, and are discounted in cladistic analysis.

Cladistic analysis is conducted applying one or more models of character transformation to a character x terminal taxon data matrix. Character transformation models are used to dictate the way in which character transformations can take place

(Stuessy 1990). Terminal taxa are linked together in tree diagrams, or cladograms, based on synapomorphy or homology.

1.5 Species concepts applied to flowering plants and *Drosera* L. in particular

Different species concepts have been applied to flowering plants to answer slightly different questions. The morphological species concept has been the most widely applied species concept used for taxonomic work (McDade 1995), although the genetic and phylogenetic species concepts are now widely used due largely to easy access to DNA sequencing technology (Stuessy 1990). The biological species concept is perhaps more applicable to studies of populations, but still provides information that relates directly to the morphological and phylogenetic species concepts.

1.5.1 The genus *Drosera* L. and the Droseraceae

The Droseraceae comprise three insectivorous genera: the monotypic genus *Dionaea,* with *Dionaea muscipula* Ellis., which is restricted to the coastal plain of North and South Carolina in the United States (Schnell 1974), the monotypic genus *Aldrovanda*, with *Aldrovanda vesiculosa* L., found in unpolluted fresh water habitats in the Old World (Marchant and George 1982), and the large and cosmopolitan genus *Drosera* (Diels 1906; Schlauer 1996). *Drosera* has a centre of diversity in the southwestern corner of Western Australia (Marchant and George 1982; Lowrie 1987; Lowrie 1989; Lowrie 1998). A fourth monotypic, insectivorous genus, *Drosophyllum lusitanicum* Link, from the south western Iberian Peninsula and northern Morocco was, until recently, also included in the Droseraceae but has been now placed in the Dioncophyllaceae based largely on molecular analysis of *rbcL* and *trnK* intron sequence data (Fay *et al.* 1997; Meimberg *et al.* 2000).

Phytochemistry, morphology and molecular data suggest Droseraceae is considered closely related to Plumbaginaceae (Albert *et al.* 1992; Williams *et al.* 1994; Stevens 2001 onwards; Rivadavia *et al.* 2003). Sequence data, *rbcL* and 18S

rDNA supports monophyly of the family and of the genus *Drosera* (Rivadavia *et al.* 2003).

Taxonomic treatments of species of *Drosera* have largely been conducted using morphology (de Candolle 1824; Diels 1906; Marchant and George 1982; Seine and Barthlott 1994; Schlauer 1996), cytology (Kondo 1969; Kondo 1976; Kondo *et al.* 1976; Kondo and Oliver 1979; Kondo and Lavarach 1984; Kondo and Segawa 1988; Hoshi and Kondo 1998a; Hoshi and Kondo 1998b; Hoshi 2002; Hoshi *et al.* 2002; Rivadavia *et al.* 2005) and, particularly more recently, using molecular data (Albert, *et al.* 1992; Meimberg *et al.* 2000; Rivadavia *et al.* 2002; Williams 2002; Rivadavia *et al.* 2003). Anatomical characters (DeBuhr 1977), phytochemistry (Culham and Gornall 1994), seed germination patterns (Conran *et al.* 1997), leaf gland type (Conran *et al.* 2007), and pollen microstructure (Takahashi and Sohma 1982) have also been used, with varying degrees of success at elucidating fine-scale relationships among species.

All species of *Drosera* are characterized by the development of motile glandular hairs on the leaf adaxial surface which are involved in the capture and digestion of prey (Darwin 1875; Diels 1906; Lloyd 1942). Subgeneric classification of *Drosera* has seen some dramatic changes in ideas of the relationships between different members of the genus (Table 1). Some recent studies did not include all species in the genus, due to geographic constraints (Marchant and George 1982), or the lack of samples of key species within the genus (Conran *et al.* 1997; Conran *et al.* 2007). Whilst many subgenera within the genus were subsequently found to be paraphyletic, and have been revised, *Drosera* subgenus *Ergaleium* has proved to a natural and monophyletic group that has been recognized since de Candolle(1824).

Drosera subgenus *Ergaleium*, which is almost exclusive to Australia, and with a centre of endemism in south western Australia, contains about 57 species and is therefore one of the largest subgenera in the genus (Planchon 1848; Diels 1906; Marchant and George 1982; Lowrie 1987; Schlauer 1996). This subgenus comprises species that form a tuber to which the plants seasonally aestivate. Subgenus *Ergaleium* was divided into three sections: section *Erythrorhiza* with 12 species that form flat rosettes; section *Stolonifera* with 10 species possessing typically flabellate cauline leaves that are either borne alternately or in whorls (DeBuhr 1977; Lowrie

2005), and section *Ergaleium* with 35 species (Table 1) which are made up of caulescent plants with typically peltate leaves arranged alternately up the stem (Marchant and George 1982; Seine and Barthlott 1994; Schlauer 1996; Conran *et al.*1997). Members of *Drosera* subgenus *Ergaleium* section *Ergaleium* are colloquially referred to as "Rainbow Sundews" due to the refraction of light that may occur as sunlight passes through the colourless drops of mucin on the ends of the glandular hairs (Erickson 1978, p. 16).

All names in *Drosera* presented by Australian Plant Name Index (1991 onwards), International Plant Names Index (2004) and the Carnivorous Plant Database (1993 onwards) relevant to the study group have been considered. The taxonomic treatment of the genus *Drosera* by Schlauer (1996) is used in this thesis since it most closely matches the inferred phylogeny of the genus as indicated by Rivadavia *et al.* (2003), based on molecular and morphological data. However, where Schlauer (1996) is in conflict with Marchant and George (1982), in the composition of *Drosera* subgenus *Ergaleium*, I follow the latter for Australia taxa.

Table 1 Subgeneric classification of *Drosera* over time. Taxa are hierarchical and indentation signifies lower ranked taxa (see text for details).

Conran *et al.* (1997)	Schlauer (1996)	Seine and Barthlott (1994)	Marchant and George (1982)	Diels (1906)	Planchon (1848)	de Candolle (1824)
107 taxa	176 taxa		61 taxa	84 taxa	89 taxa	32 taxa
Drosera	Thelocalyx	Drosera	Drosera	Rorella	a11, a16:	Rorella
a1: Arachnopus	a5: Thelocalyx	a1, a2, a11,a13:	a1: Arachnopus	a11: Psychophila	Psychophila	a2, a3, a5, a14,
a2: Drosera	Arcturia	Drosera	a4: Phycopsis	a18: Bryastrum	a11: Arcturia	a18 Acaules
a3: Lasiocephala	a11, a16: Arcturia	a10, a 18: Bryastrum	a2: Drosera	a10: Lamprolepis	a5: Thelocalyx	a1, a2, a6, a14
a4: Phycopsis	Stelogyne	a9: Coelophylla	a5: Thelocalyx	a5: Thelocalyx	a2: Rossolis	Caulescents
a5: Thelocalyx	a13: Stelogyne	a3: Lasiocephala	a3: Lasiocephala	a9: Coelophylla	a2: Cripterisma	Ergaleium
Ergaleium	Meristocaules	a17: Meristocaules	Ergaleium	a1: Arachnopus	a1: Arachnopus	a6: Caulescents
a6: Ergaleium	a17: Meristocaules	a4: Phycopsis	a6: Ergaleium	Rossolis	a9: Coelophylla	a4: Acaules
a7: Erythrorhiza	Regiae	a14: Ptycnostigma	a9: Stolonifera	a2: Eurossolis	a10: Lamprolepis	
a8: Stolonifera	a15: Regiae	a5: Thelocalyx	a7: Erythrorhiza	a3: Lasiocephala	a18: Bryastrum	
Rorella	Coelophylla	Ergaleium	Rorella	a13: Stelogyne	a3: Lasiocephala	
a9: Coelophylla	a9: Coelophylla	a6: Ergaleium	a13: Stelogyne	a4: Phycopsis	a4: Phycopsis	
a10: Lamprolepis	Lasiocephala	a9: Stoloniferae	a11: Psychophila	Ptycnostigma	a14: Ptycnostigma	
a11: Psychophila	a3: Lasiocephala	a7: Erythrorhizae	a9: Coelophylla	a14: Ptycnostigma	Ergaleium	
a12: Rorella	Drosera	Regiae	a18: Rorella	Ergaleium	a6: Scuttelifere	
a13: Stelogyne	a1: Prolifera	a15: Regiae	a10: Lamprolepsis	a6: Polypeltes	a6: Lunifere	
Ptycnostigma	a1: Arachnopus			a7:, a8:	Erythrorhiza	
a14: Ptycnostigma	a14: Ptycnostigma			Erythrorhiza	a8: Stromifere	
Regiae	a2, a3: Oosperma				a7: Rosulatae	
a15: Regiae	a2: Drosera				a14, a7: Unplaced	
	Bryastrum				taxa	
	a18: Bryastrum					
	a10: Lamprolepsis					
	Phycopsis					
	a4: Phycopsis					
	Ergaleium					
	a6: Ergaleium					
	a8: Stolonifera					
	a7: Erythrorhiza					

Table 2. Accepted taxa within *Drosera* subgenus *Ergaleium* section *Ergaleium* based on Marchant and George (1982). Taxa studied for this thesis are underlined.

Drosera andersoniana W. Fitzg. Ex Ewart & Jean White
Drosera bicolor A. Lowrie & S. Carlquist
Drosera bulbigena Morrison
Drosera erythrogyne N.G. Marchant & A. Lowrie
Drosera gigantea Lindl. subsp. *gigantea*
Drosera gigantea subsp. *geniculata* N.G. Marchant & A. Lowrie.
Drosera graniticola N.G. Marchant
Drosera heterophylla Lindl.
Drosera huegelii Endl.
Drosera insolita Taton
Drosera intricata Hook ex Planch.
Drosera macrantha Endl. subsp. *macrantha*
Drosera macrantha Endl. subsp. *eremaea* N.G. Marchant & A. Lowrie
Drosera macrantha subsp. *planchonii* (Planch.). N.G. Marchant
Drosera marchantii DeBuhr subsp. *marchantii*
Drosera marchantii subsp. *prophylla* N.G. Marchant & A. Lowrie
Drosera menziesii R.Br. Ex DC. subsp. *menziesii*
Drosera menziesii subsp. *basifolia* N.G. Marchant & A. Lowrie
Drosera menziesii subsp. *penicillaris* (Diels) N.G. Marchant & A. Lowrie
Drosera menziesii subsp. *thysanosepala* (Diels) N.G. Marchant
Drosera microphylla Endl.
Drosera modesta Diels
Drosera moorei (Diels) Lowrie
Drosera myriantha Planch.
Drosera neesii Lehm. subsp *neesii*
Drosera neesii subsp. *borealis* N.G. Marchant
Drosera pallida Lindl.
Drosera peltata Thunb. subsp. *peltata*
Drosera peltata subsp. *auriculata* (Planch.) Conn
Drosera radicans N.G. Marchant
Drosera salina N.G. Marchant & A. Lowrie
Drosera stricticaulis (Diels) O. Sarg. subsp. *stricticaulis*
Drosera subhirtella Planch.
Drosera sulphurea Lehm.
Drosera zigzagia A. Lowrie

1.5.2 The *Drosera peltata* Thunb. complex (Droseraceae)

The *Drosera peltata* complex belongs to subgenus *Ergaleium* and occurs in south-western Australia as well as eastern Australia. It also extends east to New Zealand, and north into Asia. In Asia it occurs in the Indonesian archipelago, the Philippines, and Indochina, southern China to southern Japan and South Korea. From Indochina, *Drosera peltata* also extends to the west, through the Indian Subcontinent, including Sri Lanka and Nepal, and reaches its north-western range in the Hindu Kush mountains of Pakistan, Afghanistan and Tajikistan (Figures 2 and 7). There is also a disjunct species in the *Drosera peltata* complex, *D. insolita*, from central Africa (Taton 1951).

The *Drosera peltata* complex is composed of tuberous-rooted, erect-growing herbs usually with dimorphic leaves (Figure 1). Individual plants may initially develop a rosette of spathulate leaves before forming a stem with cauline, peltate crescentic leaves, or may bypass the rosette stage and commence stem formation immediately upon emergence above ground. The stem terminates in a raceme, rarely a panicle, of pentamerous, bisexual flowers with glabrous to glandular hirsute sepals, with an entire, variably toothed or ciliate margin. Each flower has a three-lobed ovary with three carpels, and is surmounted by three styles that are variably divided. Many of the flowers per inflorescence are subtended by a bract. The fruit is a capsule filled with many ovoid to tabular seeds with reticulate surface vernation (Marchant and George 1982; Lowrie 1987; Lowrie 1989; Salmon 2001).

This thesis is concerned with the systematics of the *Drosera peltata* complex at the species level. In particular, this thesis examines the species limits within the species complex and phylogenetic relationships among species. Within this study, the *Drosera peltata* complex includes *Drosera auriculata, D. peltata s. str, D. bicolor* and the taxa that have been reduced to synonymy with *D. peltata* by Diels (1906) and Walker (1993 onwards) (Table 3). A number of undescribed putative taxa, or entities, are included in the analyses presented in this thesis. In order to assess the relative similarity of members of the *D. peltata* complex a number of other species within *Drosera* subgenus *Ergaleium* section *Ergaleium* were included in this study. These species were *D. andersoniana, D. gigantea* subsp. *gigantea, D. graniticola, D. microphylla* and *D.* salina. In addition there were representatives from *Drosera*

Ergaleium section *Stolonifera*: *D. purpurescens* and *D. porrecta*, as well as from other parts of the genus: *D. regia*, *D. binata* and *D. cistiflora*.

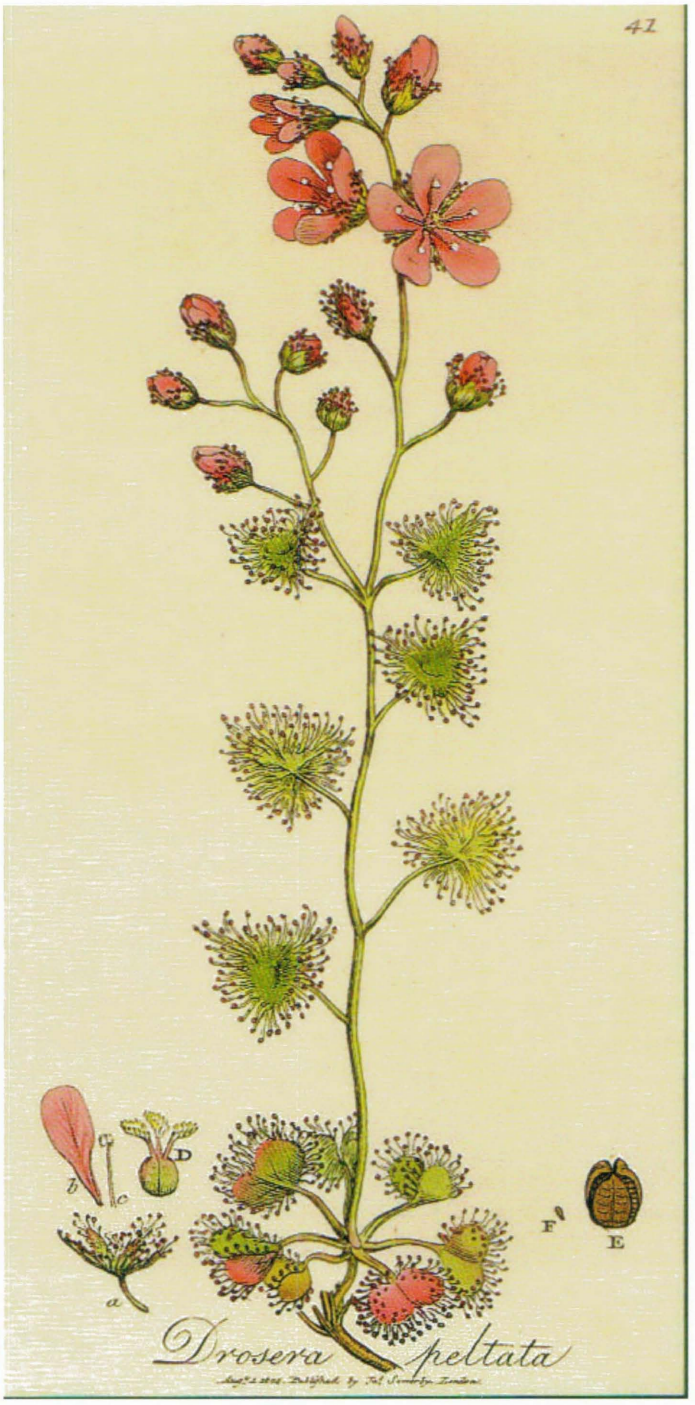
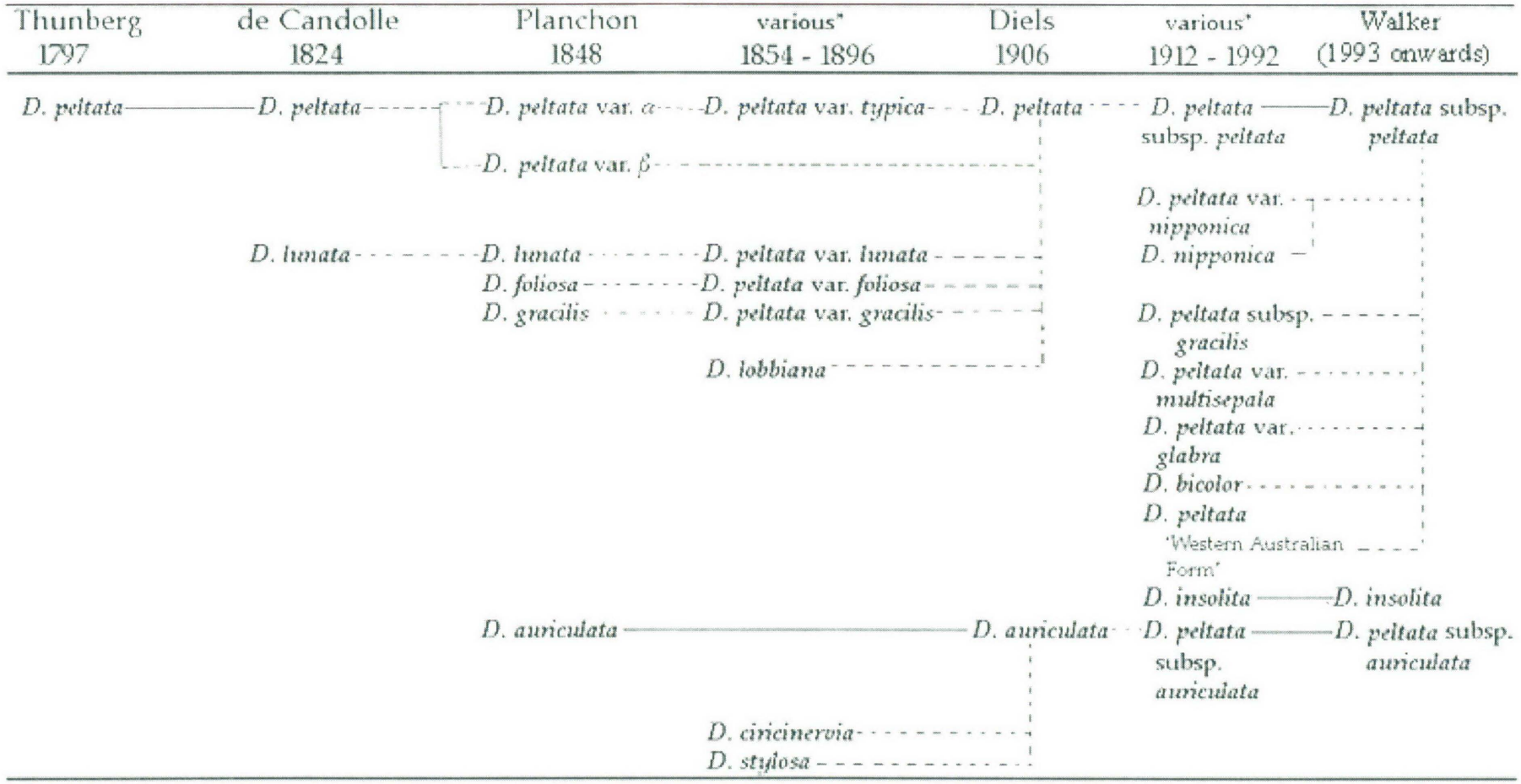


Figure 1 The first colour illustration of a member of the *Drosera peltata* complex. This illustration was drawn by James Sowerby from plants at Port Jackson, New South Wales and published in Smith's (1804) *Exotic Botany*, as Tab. 41. This entity appears to match *D. peltata* 'Black Mountain, A.C.T.' (see Figure 5).

Table 3 Summary of nomenclature history of the *Drosera peltata* complex. * denotes periods of years when various authors contributed to the taxonomy of the *D. peltata* complex (See text for discussion). Solid lines indicate acceptance of the name and status between authors, dashed lines indicate taxonomic changes.



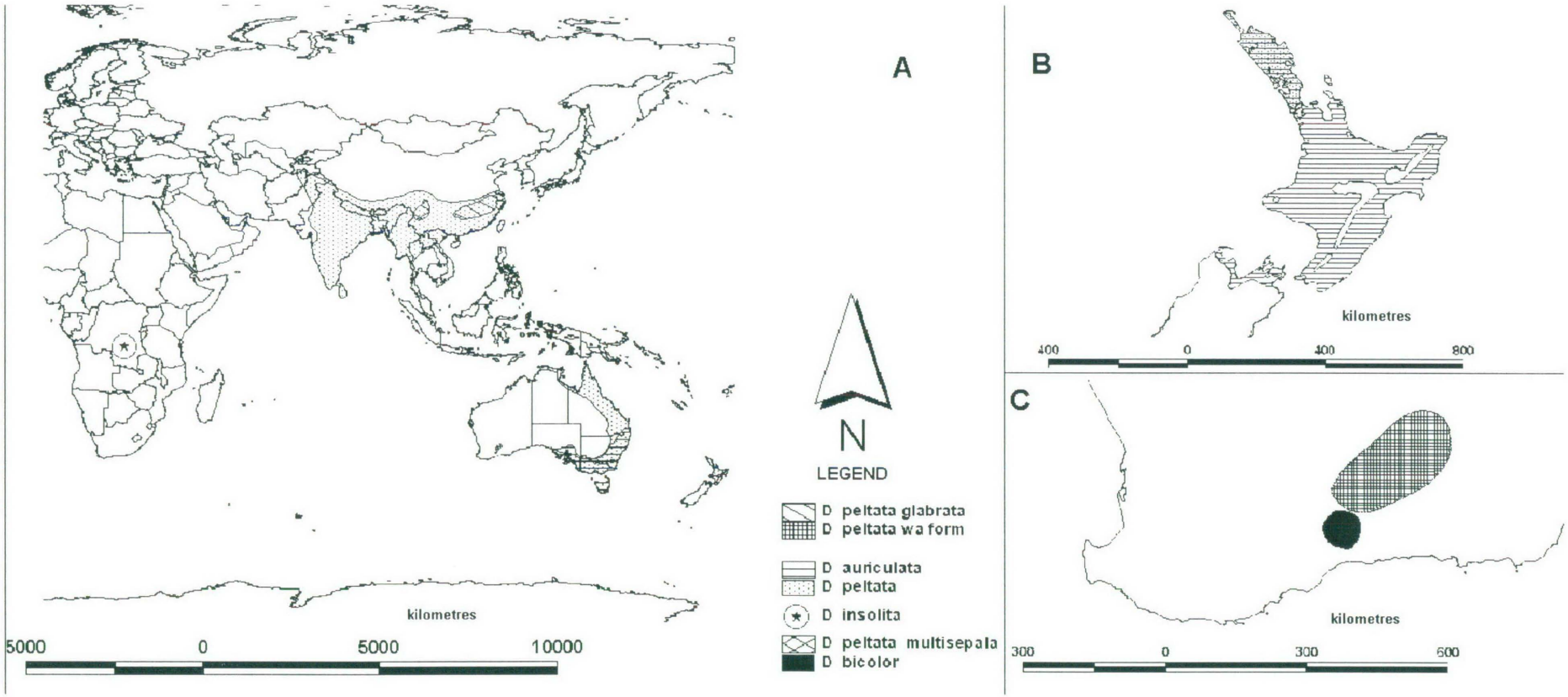


Figure 2 (A) Total distribution map of the *Drosera peltata* complex (Droseraceae), with detailed maps for (B) New Zealand and (C) south-western Australia, based on Diels (1906), Marchant and George (1982), Taton (1951), van Steenis (1953), van Royen (1973), Lowrie and Carlquist (1992) and Salmon (2001).

1.5.3 Historical overview of the *Drosera peltata* complex

The *Drosera peltata* complex has a long and complex history in which 12 species names have been applied to different entities in the complex over the last 209 years. The nomenclature history of the *D. peltata* complex is summarised in Table 3.

Thunberg (1797) described *Drosera peltata* from a specimen held at the J. E. Smith Herbarium (LINN). This specimen was reportedly collected at Port Jackson, New South Wales, Australia in 1793. Conn (1981, p. 92) attributed this collection to a Dr. W. White [sic]. However, in 1793 the Surgeon General at Port Jackson was a Dr. John White, who actively sent botanical specimens to England, including to Sir James Edward Smith (Anderson 1933).

Sir James Edward Smith published his monumental *Exotic Botany* in 1804. This volume included a description of *Drosera peltata* from Port Jackson, New South Wales, Australia. Smith (1804) included the first colour illustration of *Drosera peltata* (Figure 1), which was produced by a James Sowerby, and sent by Dr. White in Port Jackson to Smith in England. For the next 177 years, Smith was incorrectly attributed as the author of *Drosera peltata* by many authors, from de Candolle (1824) to Ruan (1981). This mistake was corrected by Conn (1981).

De Candolle (1824) presented the first systematic revision of the genus dividing the 32 species then recognised into two sections: *Rorella*, with simple two to three lobed styles, style lobes entire with subcapitate apices, and *Ergaleium*, with multiply divided capillary styles. Each section was further divided into two series, based on stem presence or absence. *Drosera lunata* from eastern India was circumscribed in this revision (Table 1).

Planchon (1848) included 88 species in his treatment of the genus *Drosera* (Table 1). He divided the genus into eight sections. Section *Ergaleium* (*sensu* de Candolle 1824) was retained and its members defined as having 'Stamina 5 (rarissime 7 - 8) hypogyna. Styli 3 (rarissime 2) in lacinias tenuissimas confervoideas, penicillato-congestas soluti. Capsula polysperma'. The 21 species then recognized within section *Ergaleium* were placed into two series based upon leaf shape and the arrangement of leaves at each node. *Drosera auriculata,* from south eastern Australia, including Tasmania, and New Zealand, and *D. gracilis* and *D. foliosa* from Tasmania

were circumscribed. These new taxa, in addition to *Drosera peltata* were placed in series *Lunifere* of *Drosera* section *Ergaleium*.

Turczaninow (1854) circumscribed *Drosera lobbiana* from herbarium specimens incorrectly attributed to have come from Singapore (Conn 1981). At the end of the description Turczaninow acknowledged the close morphological similarity of *D. lobbiana* to *D. lunata* and he questioned whether this new taxon may not in fact be a variant of *D. lunata*. These two species were said to differ in the longevity of the basal rosette during the growing season, sepal width, and the length and development of marginal sepal hairs, and style division details (Turczaninow 1854).

Clarke (1879) described two varieties of *Drosera peltata* from southern Asia: var. '*typica*' and var. '*lunata*. *Drosera peltata* var. '*typica*' from the Malay Peninsula was defined according to the characters of 'rosulate leaves persistent, sepals very fimbriate'. *Drosera peltata* var. '*lunata*', from throughout India, was defined according to the characters of 'rosulate leaves early deciduous, sepals erose or but slightly fimbriate'. Clarke (1879) arrived at a similar conclusion to Turczaninow (1854) in that he also recognized variation in sepal morphology and basal rosette longevity within the *Drosera peltata* complex from southern Asia, and placed taxonomic significance on these character states.

In New Zealand, Colenso described two species in this complex; *Drosera circinervia* (Colenso 1894) from the Taupo area of the North Island, and *D. stylosa* (Colenso 1896) from the Ruahine Mountain Range in the eastern North Island. Both species were separated from *D. auriculata* by minor morphological characters. *Drosera circinervia* was distinguished by its development of a basal rosette and in some sepal details (Colenso 1894). *Drosera stylosa* was characterized by its branched stem, the nature of bracts on the raceme, 'broad laciniate sepals' and 'very peculiar styles' (Colenso 1896; p. 594). Both descriptions lacked Latin descriptions and thus both circumscriptions are illegitimate according to the International Code of Botanical Nomenclature (Stafleu 1978).

Diels (1906) published a monograph on the genus *Drosera* (Table 1). He described 84 species that he placed in three subgenera, 12 sections and two series. The infrageneric subdivision was based on flower structure, root system and the

development or not of a stem. Diels reduced *D. lunata, D. gracilis* and *D. foliosa* to synonymy with *D. peltata* and reduced *D. circinervia* and *D. stylosa* to synonymy with *D. auriculata*. Diels (1906) also formally divided subgenus *Ergaleium* into two sections; *Polypeltes*, for caulescent plants with cauline leaves, and section *Erythrorhizae* for rosulate and acaulescent taxa.

Early in the 20th century several taxa were described from Japan. *Drosera lunulata* was described by Matsumune (1912). Masamune (1932) first described *Drosera nipponica* from southern Japan. In the following year (Masamune 1933), he provided a formal Latin description of *D. nipponica*, and reduced *Drosera peltata* var. *lunata* and *D. lunulata* to synonymy with *D. nipponica*.

Taton (1951) described *Drosera insolita* from a single collection, with a single specimen, that was reported to have been made in central Africa (Figure 3). He commented on the similarity of this species to *Drosera peltata* but on the basis of its reported African origin it was ascribed as a distinct species.

Ohwi (1953) reduced *Drosera nipponica* to the synonymy of *Drosera peltata* var. *nipponica*. Ohwi (1965) provided no reason for this change, stating that *D. peltata* var. *nipponica* occurs in central and southern Japan and China whilst '[t]he typical phase occurs in India, Australia and e. [sic] Asia' (Ohwi 1965, p. 73).

DeBuhr (1977) circumscribed *Drosera fimbriata* from south-western Western Australia. Additionally, in this paper, he revised Diel's (1906) two-fold subdivision of subgenus *Ergaleium* into a three-fold classification by installing section *Stolonifera* for species with typically fan-shaped leaves, which are arranged in whorls.

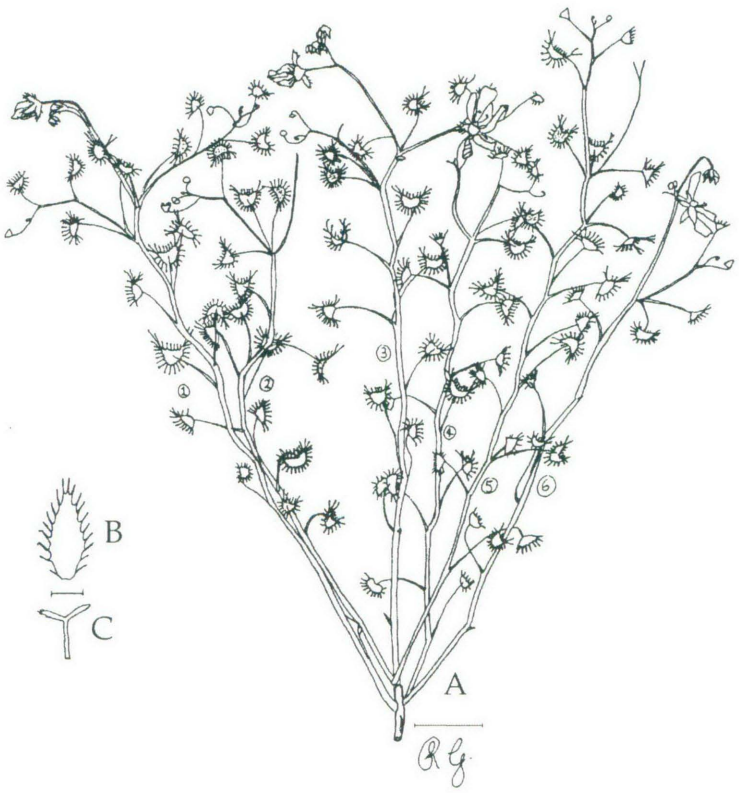


Figure 3 Sketch of Homblé 169 (BRU), the type specimen of *D. insolita* Taton, reportedly collected in Africa (Figure 2). (A) The only plant of the collection has multiple branches (numbered 1 to 6) and lacks a basal rosette. (B) The sepals are glabrous with a fimbriate margin. (C) The most accessible bract on the sample, from stem number 4, is bifid. The scale bar for (A) = 10 mm, the scale bar for (B) and (C) = 1 mm.

Conn (1981) presented an argument, based of a study of herbarium specimens of *D. peltata* and *D. auriculata* from across their ranges, for the reduction of *D. auriculata* to subspecific status of *D. peltata.* He argued that *Drosera peltata* was a widespread but variable species. In addition, Conn (1981) resolved a long-standing historical error on the authority for *D. peltata*, which had been incorrectly attributed to Smith, and a new holotype, Thunberg 7720 (UPS) was allocated. Conn (1981, p. 95) concluded that:

> 'The best solution, based on an assessment of the wide range of variation within populations (e.g. as found in Australia and New Guinea) and accounting for the existence of distinctive sympatric populations (e.g. as found in Australia) in parts of the geographical range, is to recognize two infraspecific taxa on a combination of characters. The morphological differences observed between these two taxa represent infraspecific variation. Accordingly, *D. auriculata* is here reduced to a subspecies of *D. peltata*.'

Also in 1981, Ruan described *Drosera peltata* var. *glabrata* and *D. peltata* var. *multisepala*, from southern China (Ruan 1981) (Figures 2 and 4). The author recognized the trivial nature of the variations by the low taxonomic rank provided.

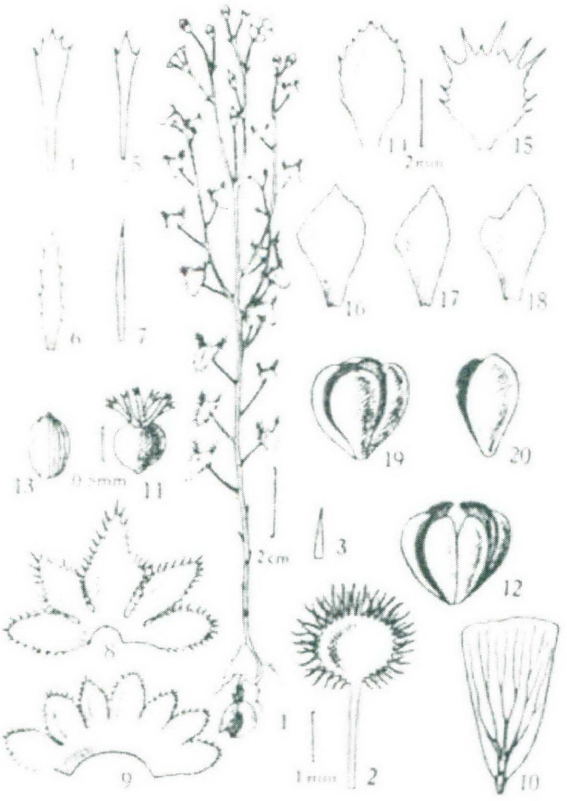


图 2 1—13. 茅膏菜 **Drosera peltata** Smith var. **multisepala** Y. Z. Ruan 1.植株和花序; 2.基叶; 3.退化基叶; 4—6.花序下部苞片; 7.花序上部苞片; 8—9.花萼展开; 10.花瓣; 11.雌蕊; 12.蒴果(示果瓣 6); 13.种子; 14—20. **光萼茅膏菜 D. peltata** Smith var. **glabrata** Y. Z. Ruan 14—18. 萼片(示各种萼形); 19—20.蒴果 (示果瓣 2 和 4)。
(余汉平绘)

Fig. 2 1. Habitus; 2—3. Folia basalia; 4—7. Bracteae; 8—9. Calyx; 10. Petalum; 11. Gynaeceum; 12. Capsula; 13. Semen. 14—18. Sepala; 19—20. Capsula (valvae 2 et 4).

Figure 4. *Drosera peltata* var. *multisepala* and *D. peltata* var. *glabrata* from Ruan (1981). There is variation in bracteole morphology. The protologue of *D. peltata* is incorrectly attributed to (Sir James Edward) Smith.

Marchant and George (1982) presented a review of the genus *Drosera* in the *Flora of Australia*. They presented a new infrageneric classification across the genus, modified from Diels (1906), based on stipule morphology and flower structure.

Following the new classification all species then known within Australia were described. In this treatment, *D. peltata* and *D. auriculata* were kept as separate species. The work of Conn (1981) was discussed but the two species were retained due to reported consistent different characters. Marchant and George (1982), presented an illustration of *D. peltata* (Figure 5), and also alluded to a variant of *D. peltata* with glabrous sepals from Queensland.

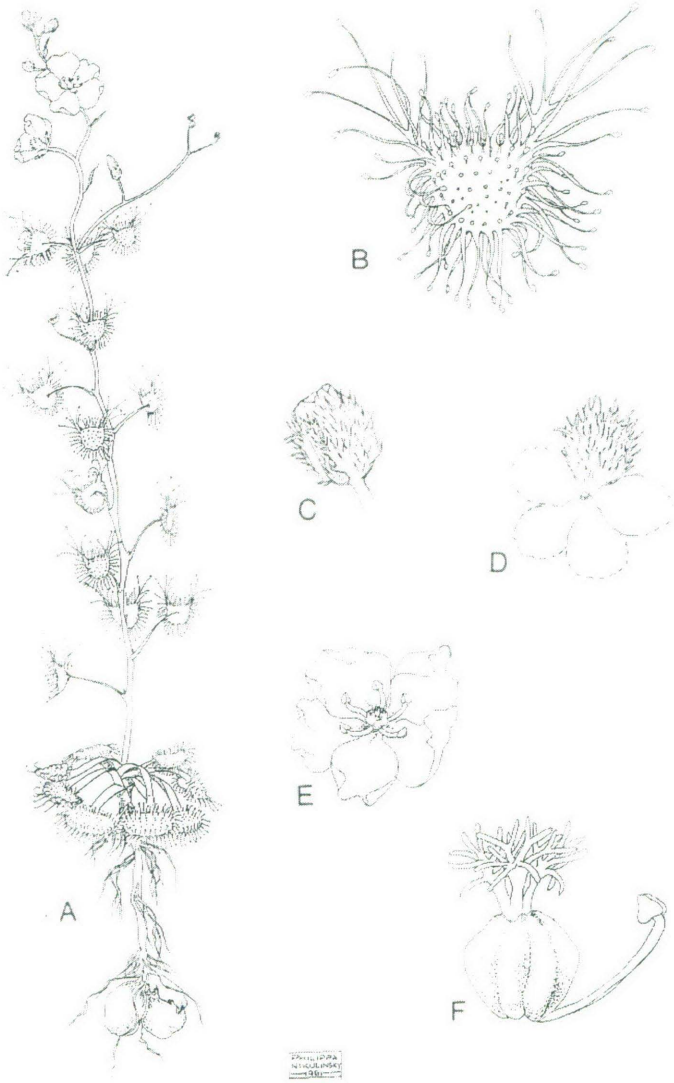


Figure 6. *Drosera peltata*. **A**, flowering plant, ×0.5. **B**, leaf lamina, ×3.5. **C**, bud, ×2.5. **D**, sepal, ×2.5. **E**, flower, ×2.5. **F**, ovary, styles and 1 stamen, ×6. (Black Mountain, A.C.T., A. S. George, PERTH).

Figure 5 Illustration of a member of the *Drosera peltata* complex, from Marchant and George (1982, p. 23). This entity is referred to as *D. peltata* 'Black Mountain, A.C.T.' in this thesis.

Lowrie and Carlquist (1992) circumscribed *Drosera bicolor* from sandplains in the south west of Western Australia. In the preceding few years this taxon had been informally called *D. peltata* 'Hammersley' because of its resemblance to *D. peltata* by virtue of its rosette of spathulate leaves, crescentic and peltate cauline leaves and hirsute sepals. However it was retained as a distinct species based on the autapomorphies of unique style architecture and petal coloration (Figures 6 and 31).

Seine and Barthlott (1994) presented a review of the genus *Drosera* based on pollen morphology, root system architecture, stem development and leaf shape (Table 1). They retained the infrageneric subdivision of Diels (1906) and added a new subgenus, *Regiae*, and a new section, *Meristocaulis*, based on the description of two species with many novel characters: *Drosera regia* (Stephens 1926) and *D. meristocaulis* (Maguire and Wurdach 1957).

Schlauer (1996) presented a new dichotomous key for the genus *Drosera* in which there were 11 subgenera and ten sections (Table 1). Many of the new subgenera were made by raising the taxonomic status of sections of earlier authors, particularly those of Diels (1906). Schlauer also changed the taxonomic status of many taxa, reducing many to subspecific or varietal ranking, often without explanation. He adopted the subspecific ranking of *D. peltata* and *D. auriculata* by Conn (1981) but retained *D. bicolor* and *D. insolita* as separate species. However, he subsequently reduced *D. bicolor* to synonymy with *D peltata* (Walker 1993 onwards), in which Dr. Schlauer provides the taxonomic update to this database.

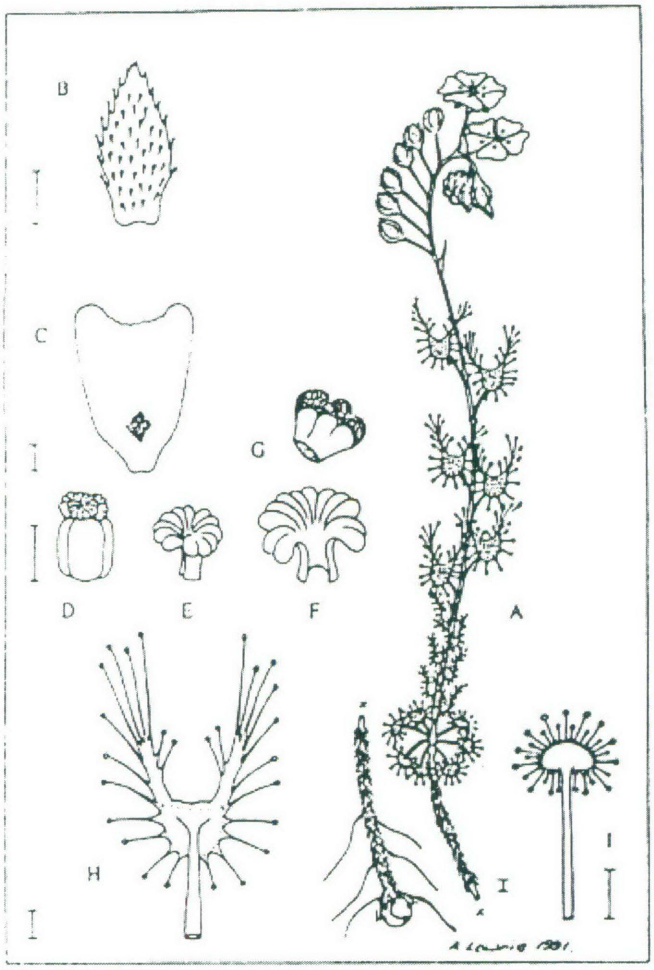


Figure 6 *Drosera bicolor* illustration from Lowrie and Carlquist (1992). "A. Habitat of plant in flower. B. Sepal. C. Petal. D. Ovary with styles. E. Styles and stigmas. F. Style and stigmas enlarged, dissected. G. Stigmas and style segments, enlarged. H. Lamina and adjacent petiole portion of cauline leaf. I. Lamina and adjacent petiole portion of basal leaf. Scales = 1 mm."

Conran *et al.* (1997) presented phylogeny reconstruction of the Droseraceae based on an analysis of seedling germination patterns (Table 1). They sampled 109 taxa of *Drosera* in 4 subgenera and 13 sections of the genus, represented by one sample per taxon and used the classification of Marchant and George (1982). They also included the monotypic *Dionaea muscipula*, *Aldrovanda vesiculosa* and *Drosophyllum lusitanicum* in their study. They were able to demonstrate that species in the subgenus *Ergaleium* and *Drosera* subgenus *Drosera* section *Lasiocephala*, *Drosera* subgenus *Rorella* sections *Coelophylla, Rorella* and *Lamprolepsis* shared the character of cryptocotylar germination. In cryptocotylar germination, the cotyledons are largely retained within the testa of the germinating seed. Characters of the cotyledons and first leaves were also investigated. The study of seedling characters

proved to have some use at estimating phylogeny within the genus when compared with independent studies using other characters. The classification used did not account for all of the results, indicating either that the genus was paraphyletic, or that the set of characters studied are prone to homoplasy. From this study, it was concluded that subgenus *Ergaleium* was monophyletic.

In all cases, except Conn (1981), taxonomy of members of the *Drosera peltata* complex has been applied intuitively. Henderson (2005) identified such intuitive taxonomy as a common problem within biology.

1.6 Selection of the study group

The *Drosera peltata* complex was chosen for this project due to my long-standing interest in the group (Gibson 1992; Gibson 1993a; Gibson 1993b). This group has a long and complex taxonomic history (Conn 1981; Marchant and George 1982) and is one of several species complexes in the genus *Drosera* in which species limits are poorly known (Schlauer 1996). This study also utilizes experimental pollinations to test species limits within this complex. Species limits within the *Drosera peltata* complex require clarification as the current classification of the complex does not appear to adequately describe the observed variation within the complex. These issues need to be addressed using analytical methods, including phenetic analysis, molecular sequence analysis, experimental pollinations and cladistic analysis.

1.7 Aims of the thesis

The aims of this project were to:

- Explore and set the species limits within the *Drosera peltata* complex.
- Study the breeding system of members of the *Drosera peltata* complex and investigate cross-compatibility relationships between taxa.
- Estimate the phylogeny of the *Drosera peltata* complex, using morphological, molecular and breeding system data.
- Incorporate this estimate of phylogeny into classification of the complex.

1.8 Outline of the thesis

This chapter reviews the literature of systematics in general and higher classification, the taxonomic history of the *Drosera peltata* complex, and sets out the aims of this thesis.

Chapter two presents a phenetic analysis of a morphological study of the *D. peltata* complex and some of the comparator species.

Chapter three comprises a phylogenetic analysis of nuclear gene (ITS1 and ITS2 with the 5.8S gene in between) and chloroplast gene (*trnL*) data.

Chapter four presents an analysis of experimental pollinations conducted between selected members of the complex from south-eastern Australia and some taxa from Western Australia.

Chapter five presents a synthesis of the three data chapters and presents the findings in relation to the often-confusing nomenclature of the complex.

Chapter six presents the general conclusions of the thesis, outlines the limitations of the study, and provides suggestions for future research into the *D. peltata* complex and the genus *Drosera* in general.