

Chapter 6. Conclusions about the phylogeny and composition of the *Drosera peltata* complex (Droseraceae)

6.1 Introduction

This chapter presents a summary of the general conclusions of the thesis. The levels of support of the different datasets are discussed. The limitations of the study are examined, and recommendations for further research are made.

6.2 Summary

Phenetic analysis of OTUs of the *Drosera peltata* complex resolved the group into three species: the narrow endemic *D. bicolor*, the widespread and morphologically variable *D. peltata*, and an undescribed cryptic species that is informally known as *D. peltata* ‘Western Australian Form’ (Table 25). This latter group includes the entity *D. auriculata* which Conn (1981) had relegated to a subspecies of *D. peltata*. This study suggests that Conn (1981) did not go far enough.

Phylogenetic reconstruction of cpDNA and nrDNA sequences reveal that the *D. peltata* complex is paraphyletic. It comprises a monophyletic group of entities from along the western Pacific Ocean margin. But *D. peltata* ‘Western Australian Form’ is a clade with the morphologically distinct Western Australian species *D. microphylla* and *D. graniticola*. Whilst horizontal gene transfer has not yet been ruled out, and a unique suite of apomorphic characters has yet to be found, although there are some differences in style architecture (Figure 33), I argue that *D. peltata* ‘Western Australian Form’ is a cryptic species.

Table 25. Taxa in the *D. peltata* complex before and after this study

Taxa before this study	Taxa after this study
<i>D. auriculata</i>	<i>D. peltata</i>
<i>D. bicolor</i>	<i>D. bicolor</i>
<i>D. circinervia</i>	<i>D. peltata</i>
<i>D. foliosa</i>	<i>D. peltata</i>
<i>D. gracilis</i>	<i>D. peltata</i>
<i>D. insolita</i>	<i>D. peltata</i>
<i>D. lunata</i>	<i>D. peltata</i>
<i>D. lunulate</i>	<i>D. peltata</i>
<i>D. nipponica</i>	<i>D. peltata</i>
<i>D. peltata</i>	<i>D. peltata</i>
<i>D. peltata</i> var. α <i>genuine</i>	<i>D. peltata</i>
<i>D. peltata</i> var. β <i>Gunniana</i>	<i>D. peltata</i>
<i>D. peltata</i> subsp. <i>auriculata</i>	<i>D. peltata</i>
<i>D. peltata</i> subsp. <i>nipponica</i>	<i>D. peltata</i>
<i>D. peltata</i> var. <i>glabrate</i>	<i>D. peltata</i>
<i>D. peltata</i> var. <i>lunata</i>	<i>D. peltata</i>
<i>D. peltata</i> var. <i>multisepala</i>	<i>D. peltata</i>
<i>D. peltata</i> var. <i>typical</i>	<i>D. peltata</i>
<i>D. peltata</i> ‘Western Australian Form’	<i>D. sp.</i> WA (S. Moore 95, K)*
<i>D. stylosa</i>	<i>D. peltata</i>

* The intended type for this putative new species

The members of the *Drosera peltata* complex studied have high self-, intra-entity and inter-entity fertility (Chapter 4). The eastern Australian entities studied have an efficient delayed autonomous self-pollinating mechanism for reproductive assurance and each fruit produces many small seeds that appear to be easily dispersed. The findings of high inter-entity fertility between members of this complex appear to be at odds with the results of phylogenetic analysis (Chapter 3). This is so where terminal taxa grew sympatrically and yet formed clades on the basis of *a priori* taxonomic entity instead of geography. There may yet be a number of factors operating that would reduce gene flow between entities:

- Not all entities in the complex grow sympatrically, and those that do, do so rarely.
- Entities flower at different times of the year, e.g. *D. peltata* ‘*gracilis*.’ and *D. peltata* ‘Isla Gorge, Qld.’ usually flower in summer whilst the other entities typically flower in spring.

- A greater proportion of seed set in populations may result from self-pollination, including autonomous self-pollination, than from cross-pollination.
- Pollination vectors may show high fidelity to the flowers of one entity of the *D. peltata* complex than others in sympatric situations (Levin 1971).
- Hybrids, when produced, may be less fit than either parent (e.g. Ramsey *et al.* 2003).

Phylogenetic analysis of the complex suggested that some entities were consistently closer to each other than others, particularly the pairs comprising *D. peltata* 'Black Mountain, A.C.T.' with *D. peltata* 'foliosa' and *D. peltata* 'gracilis' with *D. peltata* 'Red Rosette' (Figures 23, 25 and 28). However neither pair were as genetically distinct as *D. peltata* 'Western Australian Form'. When viewed with the results of the phenetic analysis (Chapter 2) and experimental pollinations (Chapter 3), it appears that there is still sufficient gene flow, albeit rare, within members of the complex in eastern Australia, and insufficient time has passed for distinct lineages to have yet emerged.

6.3 Considerations

Considering the results of both the phenetic and phylogenetic analyses there is strong evidence for *D. peltata* 'Western Australian Form' as a cryptic species (see also Figures 25 and 27). Molecular sequences from three samples of this entity, from two populations 70 km apart form monophyletic groups in all analyses (Chapter 3). Considering the phylogenetic evidence alone (Chapter 3) and geography, there is evidence under the phylogenetic species concept for recognition of *D. peltata* 'Western Australian Form' as a distinct species.

Phenetic analysis using herbarium specimens only has the advantage of being able to include type specimens which is therefore useful for the correct applications of names. However, it has the disadvantage that not all characters are available for study – they were either not developed on the plants at the time of collection, or they are present, but only available through destructive sampling.

Care is needed in collecting plant samples of members of the *D. peltata* complex — plants may break above ground level and thus information about the development of a basal rosette and nature of lower cauline leaves may be lost. The flowers are open for only a few hours, and for future studies it would be a great benefit to have samples with pressed open flowers. Ideally plants should be collected when they have both open flowers and ripe seeds available, which happens only over at most a few weeks and not for all plants. It is acknowledged that plants may not be at this ideal stage of growth when encountered in the field.

The pressing process often distorts leaves on the herbarium sample. To provide access to undistorted leaves, it would be ideal for some specimens in any collection to be preserved in liquid, such as FAA (by volume 40% formaldehyde 1: glacial acetic acid 1: 95% alcohol 8: water 10) or even 70% ethanol. In addition, some clean and fresh plant tissue could be preserved in 95% ethanol, for the possibility of conducting molecular analysis on such tissue in the future.

6.4 Limitations of the current study

Limitations of the current study can be summarized as follows:

- The phenetic analysis included morphological data from all but two members of the *D. peltata* complex, viz. *D. peltata* var. *glabrata* and *D. peltata* var. *multisepala*. For completeness it would have been useful to have included these Chinese taxa in the study, however, specimens were not readily available.
- The experimental pollinations were limited to members of the *D. peltata* complex from south-eastern Australia. Whilst this region has the greatest diversity of variation within the complex, it would have been useful to have included entities from south Asia and the ‘Western Australian Form’ in this study. The latter part of the project coincided with drought conditions which meant that plants, even in cultivation, had an abbreviated flowering period. These two entities also proved to be difficult to grow well in the greenhouse conditions provided. Future studies would benefit from growing plants in an environment where plants are protected from desiccating conditions so that the flowering period can be maximized.

- DNA was not successfully extracted from either *D. bicolor* or *D. salina*, and there was insufficient material of *D. andersoniana* at hand to include this species in the study. Therefore, it was not possible to explore the relationships of these morphologically similar species with the *D. peltata* complex in this study.

6.5 Recommendations for further work

The species status and veracity of the classification of the remaining members of *Drosera* subgenus *Ergaleium* section *Ergaleium* remain untested and controversial (Schlauer 1996). The results from this study show that phenetic analysis can help to resolve the status of entities in a group by either highlighting names that denote discrete entities (in this case *D. bicolor* and *D. peltata*) and also reveal names that are best rejected (such as *D. auriculata*). For best results, measurements would be preferentially taken from samples with open flowers, ripe seeds and undistorted leaves.

Not all members of the *D. peltata* complex were included in the molecular analysis. It is recommended that the range of entities is increased, to include *D. bicolor*. This would enable the molecular differences to be compared with the morphological differences discovered from the phenetic analysis.

Drosera peltata ‘Western Australian Form’ appears to be a cryptic species based on molecular data (Chapter 3), style characters and its highly disjunct distribution from the rest of the complex. Whilst this entity may be included in future experimental pollinations there is no guarantee that reproductive isolating mechanisms with other members of the complex will have evolved due to their widely allopatric distributions. If these entities proved to be highly interfertile when artificially cross-pollinated then the argument for *D. peltata* ‘Western Australian Form’ qualifying as a cryptic species would still be strong due to the phylogenetic analysis of this project. Further examination of other datasets, such as cytology, phytochemistry or anatomical features would be useful particularly if they reveal additional differences between the ‘Western Australian Form’ and the rest of the *D. peltata* complex. Even if that did not prove to be the case, other species have been described upon molecular sequence differences alone (e.g. Molina *et al.* 2004).

Delayed autonomous self-pollination was documented for the first time in *Drosera* subgenus *Ergaleium* in this study. Whilst the mechanism for movement in other parts of *Drosera* plants have been studied, in relation to trapping prey, it would be interesting to know if the same physiological mechanisms are involved in the inflexing of filaments of flowers of *D. peltata* that facilitate reproductive assurance.

The reproductive biology of most species in this large (ca. 150 taxa) genus remains unknown. To date, there have been few systematic studies on the reproductive biology of a few species (e.g. Murza and Davis 2005). Field observations in places where species of *Drosera* with variable and often colourful flowers grow sympatrically (e.g. Goldblatt *et al.* 1998; Lowrie 2001), suggest that the different species rely on different guilds of pollinators, or means of reproductive assurance. The field is ripe for further study, particularly for sundews native to Southern Africa and Australia where floral diversity is highest in the genus (Goldblatt *et al.* 1998).

6.6 The *Drosera peltata* complex offers a model system to test the biological and phylogenetic species concept.

The *Drosera peltata* complex appears to be at an interesting stage of its evolution, due to the balance between potential gene-flow between entities (where they occur sympatrically), and genetic divergence of lineages in allopathic populations, and as a result of self-pollination. Morphological and reproductive limits of different entities appear not yet to have been set. The complex appears to be currently in a phase of range expansion, and on the threshold of speciation, and so offers scope for evolutionary ecology study. In addition, the complex offers a great chance to study a novel means of autonomous self-pollination in a group of plants in which the breeding system is poorly known. All of these factors contribute to the *D. peltata* complex as being an excellent group to test different ideas about the species concept.

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