

Phyloclimatic Modeling: Combining Phylogenetics and Bioclimatic Modeling

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Abstract.—We investigate the impact of past climates on plant diversification by tracking the “footprint” of climate change on a phylogenetic tree. Diversity within the cosmopolitan carnivorous plant genus *Drosera* (Droseraceae) is focused within Mediterranean climate regions. We explore whether this diversity is temporally linked to Mediterranean-type climatic shifts of the mid-Miocene and whether climate preferences are conservative over phylogenetic timescales. Phyloclimatic modeling combines environmental niche (bioclimatic) modeling with phylogenetics in order to study evolutionary patterns in relation to climate change. We present the largest and most complete such example to date using *Drosera*. The bioclimatic models of extant species demonstrate clear phylogenetic patterns; this is particularly evident for the tuberous sundews from southwestern Australia (subgenus *Ergaleium*). We employ a method for establishing confidence intervals of node ages on a phylogeny using replicates from a Bayesian phylogenetic analysis. This chronogram shows that many clades, including subgenus *Ergaleium* and section *Bryastrum*, diversified during the establishment of the Mediterranean-type climate. Ancestral reconstructions of bioclimatic models demonstrate a pattern of preference for this climate type within these groups. Ancestral bioclimatic models are projected into palaeo-climate reconstructions for the time periods indicated by the chronogram. We present two such examples that each generate plausible estimates of ancestral lineage distribution, which are similar to their current distributions. This is the first study to attempt bioclimatic projections on evolutionary time scales. The sundews appear to have diversified in response to local climate development. Some groups are specialized for Mediterranean climates, others show wide-ranging generalism. This demonstrates that Phyloclimatic modeling could be repeated for other plant groups and is fundamental to the understanding of evolutionary responses to climate change. [Ancestral state reconstruction; bioclimatic modeling; Droseraceae; palaeo-climates; phylogenetics.]

The prospect of global climate change has focused many people's interest towards the impact of the environment on floral and faunal distribution, speciation and extinction (Davies et al., 2004; Perry et al., 2005; Thomas et al., 2004). Studying evolutionary responses to historical climate shifts will help to give us an insight into current and potential future changes.

It is difficult to demonstrate cause and effect concerning lineage diversification. However, it is possible to make estimates of diversification times and climate preferences for both current and ancestral lineages, and to compare these with our knowledge of present-day and historical climates. These studies can reveal important evolutionary patterns and show us the “footprint” of climate change on a phylogenetic tree.

A popular method to investigate species response to climate is by constructing bioclimatic models (Nix, 1986). These establish the climate preferences of a given species based on its known distribution and provide a model of the climate parameters correlating with this. There are many methods of bioclimatic modeling, including Bioclim (Nix, 1986), SPECIES (Pearson et al., 2002), and GARP (Stockwell and Peters, 1999); for a comparison of methods see Elith et al. (2006). Once built, the models can be projected into the present-day climate to estimate current distributions (Raxworthy et al., 2003; Robertson et al., 2001), future climate scenarios to predict extinction risk (Peterson et al., 2002; Thomas et al., 2004; Yesson & Culham, 2006), and the past to estimate historical distributions (Hilbert et al., 2004; Hugall et al., 2002; Peterson et al., 2004).

Interest is mounting in the application of these models across evolutionary time scales (Graham et al., 2004; Hardy and Linder, 2005; Peterson et al., 1999). Peterson et al. (1999) suggest that bioclimatic envelopes are

statistically more similar among sister species and that they are conserved across evolutionary time. This is supported by Martinez-Meyer et al. (2004) who used species-level bioclimatic models to successfully predict the distribution of sister species for seven *Passerina* birds. It is also supported by Davies et al. (2004), who suggest that climate-related factors such as environmental energy explain a significant amount of species richness amongst the angiosperms.

These studies have paved the way for a new area of investigation, which we have termed “Phyloclimatic Modeling” and could be described as the study of species evolution in tandem with their climatic preferences.

As yet there are still few studies that have begun to exploit the potential of phyloclimatic modeling. Hugall et al. (2002) used bioclimatic models in conjunction with an mtDNA haplotype phylogeny to investigate past distributions of snails over the last 20,000 years, although they examined the climate models from an evolutionary perspective, the timescale was short in evolutionary terms. Graham et al. (2004) examined climate preference characteristics on a phylogeny of five dendrobatid frogs. They optimized these characteristics across the phylogeny and reconstructed ancestral bioclimatic models. These models were projected into the present-day climate to produce a map of the climatically optimal areas, but not the relevant palaeo-climate, although they do suggest these models should ideally be applied to the relevant time frame. Although projecting into the present serves to demonstrate the differences between the models for ancestral nodes and extant species, it is trivial to note that some climate change may have occurred in the millions of years of evolutionary time from the diversification of these ancestral lineages.

Hardy and Linder (2005) have investigated relative merits of phylogenetic optimization techniques for continuous values of annual mean precipitation and temperature for use in ancestral ecology reconstruction. However, they did not project the resulting models into the climate of either the present or the past. Hoffmann (2005) used mean temperature and precipitation to reconstruct ancestral bioclimatic models for *Arabidopsis* species. He demonstrated a core climate zone shared by all species in the genus, but did not examine the ancestral distribution that his models would predict. Hoffmann suggested a link between some sections of the *Arabidopsis* phylogeny with historic climate change events, but did not temporally calibrate the phylogeny.

The data required for studies of bioclimatic envelopes in conjunction with evolutionary histories is becoming ever more available. The spread of molecular phylogenetics means evolutionary history is available for many species. The digitisation of herbarium specimen labels and plant distribution data (<http://www.gbif.org>) is proceeding apace, providing locality data for species. Data on global climate is now widely available to biologists, from organizations such as the Hadley Climate Centre (<http://www.metoffice.com/research/hadleycentre/>) and the BRIDGE project (<http://www.ggy.bris.ac.uk/research/bridge/index.html>). In particular, developments in palaeo-climate modeling (Valdes, 2000) permit historical studies on evolutionary timescales.

The path is now clear for phyloclimatic studies on a large scale that examines climate preference characteristics across a time-calibrated phylogeny, reconstructs ancestral bioclimatic models, and uses these to investigate ancestral areas.

The charismatic carnivorous plant group, the sundews (the genus *Drosera* L. within Droseraceae L.) is an ideal candidate for this study. *Drosera* is a widely studied group of c. 150 species with a global distribution (Rivadavia et al., 2003; Williams et al., 1994). The genus has its main center of diversity in southwestern (SW) Australia (approx 1/3 of all species) (Lowrie, 1987) but is well represented in Africa and the Americas. The Mediterranean-type climate of SW Australia is thought to be a key factor in the radiation of *Drosera*, particularly when linked with key innovations such as the tuber of subgenus *Ergaleium* DC., or the stout roots of section *Phycopsis* Planch. (Lowrie, 1987, 1989, 1998; Rivadavia et al., 2003).

The climate of SW Australia, characterized by hot, dry summers and cooler, wetter winters, is thought to have arisen 15 to 10 million years ago (Mya) (Christophel and Greenwood, 1989; Greenwood, 1994; Willis and McElwain, 2002). This provides the opportunity to investigate the impact of a localized climate-change event on the diversification of a large genus that is well represented across a wide range of biomes.

METHODS

Tree Searching

The species sampled by Rivadavia et al. (2003) were used to search for distribution data, and those with suffi-

cient data were used for bioclimatic modeling. Our sampling of *Drosera* contains representatives from each of the major subclades and geographic regions of *Drosera* diversity. The monospecific genera *Dionaea* and *Aldrovanda* are the only other members of the Droseraceae and are used as the outgroups for our analyses. See Appendix 1 for a full list of accession numbers and taxa used in this analysis. The published *rbcL* sequences were reanalyzed using the original alignment (data matrix available at <http://www.treebase.org>, accession M2812). A parsimony analysis was conducted by means of a heuristic search in PAUP*4b10 (Swofford, 2002). Characters were equally weighted, all minimal-length trees were saved, using the TBR branch swapping algorithm and 10,000 replicates of random taxon addition. A Bayesian analysis was also conducted using MrBayes V3.0B4 (Ronquist and Huelsenbeck, 2003). The model of evolution selected by MrModelTest (Nylander, 2004) was the GTR model with rates set to "invgamma." The analysis used 10,000,000 generations, sampling every 1000. Stationarity was reached after 650,000 iterations. Branch lengths were saved for subsequent dating. A majority-rule consensus tree of the sampled iterations from the point of stationarity was created to determine posterior probabilities of clades (Huelsenbeck et al., 2001).

Tree Dating

The data do not fit a molecular clock according to the likelihood-ratio test (Felsenstein, 1988). The tree topologies saved from the Bayesian analysis were ranked according to their probability using the "sumt" command in MrBayes v3.0 (Ronquist and Huelsenbeck, 2003). Four topologies were selected as equally most probable. Two of these topologies were randomly selected for further analysis. Both the selected topologies were represented by three different phylograms amongst the Bayesian replicates. For both the chosen topologies, the phylogram with the highest likelihood from the three alternatives was selected for dating. Phylogenetic dating was performed in r8s (Sanderson, 2004) using the penalized likelihood method (Sanderson, 2002). This is felt superior to other techniques such as nonparametric rate smoothing as it allows tuning of rate variation via a cross-validation procedure (Sanderson, 2004). The split between *Drosera* and *Aldrovanda* L. was fixed to 50 Mya, and a minimum age constraint of 40 Mya set for *Drosera glanduligera* Lehm. (see Fossil Calibration). The outgroup (*Dionaea* Ellis) was removed prior to rate smoothing as recommended in the r8s manual (Sanderson, 2004).

Confidence intervals, based on the effect of substitution noise (Sanderson and Doyle, 2001), were calculated via bootstrapping using Torsten Eriksson's r8s-bootkit (Clement et al., 2004). One thousand bootstrap replicates of the original data matrix were made. These matrices were used to produce 1000 trees, fixed by an optimal topology from the Bayesian analysis, branch lengths were assigned using the same GTR model selected before the initial Bayesian analysis. Cross-validation was carried out for each replicate. In the instances when cross-validation failed due to zero-length branches, a default

smoothing score of 10 was used, which was the smoothing value selected for the original data. These replicates were used to produce 95% confidence intervals using r8s-bootkit.

Confidence intervals based on both topological uncertainty and model variation (Sanderson and Doyle, 2001) were calculated using a procedure essentially the same as bootstrapping, but substituting the Bayesian replicates for the bootstrap replicates (Lavin et al., 2005). One thousand replicates were selected from the saved trees of the Bayesian analysis, keeping the original branch lengths. Each replicate was dated using penalized likelihood following same methodology outlined above. These replicates have potentially different tree topologies, so confidence intervals for any node can only be calculated from the replicates containing that node. Ninety-five percent confidence intervals were calculated for each node from the first and second most probable topologies.

Fossil Calibration

Fossil calibration is potentially a major source of error when dating phylogenetic trees (Magallon, 2004; Sanderson et al., 2004). The fossil record for *Drosera* is generally poor in comparison with *Aldrovanda*, which is also within the Droseraceae. *Drosera* fossils are mostly restricted to the pollen record (Truswell and Marchant, 1986). In contrast, the aquatic, monospecific genus *Aldrovanda* has an excellent fossil record (Cameron et al., 2002; Degreaf, 1997; Yakubovskaya, 1991) based on both pollen (Muller, 1981) and seeds (Yakubovskaya, 1991). Chanda (1965) recognized that each genus of Droseraceae has a characteristic pollen type, and the fossilized seeds are sufficiently distinct for Yakubovskaya (1991) to recognize two distinct *Aldrovanda* lineages amongst 13 named fossil species. *Aldrovanda* seeds show records from the Pleistocene, Pliocene, Miocene, and Oligocene through to the Eocene (Yakubovskaya, 1991). At present, the oldest seeds of *Aldrovanda* date from the early to middle Eocene (Chandler, 1961; Reid, 1926), although Degreaf (1997) talks of the uncertainty in determining the exact ages of the geological layers where fossils are found. Fossil *Aldrovanda* pollen also dates back at least as far as the early Eocene (Krutzsch, 1970).

Cameron et al. (2002) and Meimberg et al. (2000) speculate a Gondwanan origin for *Drosera*. Meimberg et al. (2000) support this based on current transcontinental distributions, whereas Cameron et al. (2002) suggest this dating is supported by the fossil record, but does not refer to any observations earlier than the Eocene. Knobloch and Mai (1984) described the genus *Palaeoalldrovanda* from seed fragments from the end of the Cretaceous (85 to 75 Mya), suggesting its similarities with *Aldrovanda*, but they do not place this within the Droseraceae.

Given the uncertainty surrounding the age of the Droseraceae, we have fixed the base of the *Aldrovanda*/*Drosera* split at 50 Mya, in accordance with the oldest unambiguous pollen date (Krutzsch, 1970), and slightly older than the oldest *Aldrovanda* seed fossils

(Chandler, 1961; Reid, 1926). This date is in agreement with the dating of *Drosera* in Wikstrom et al. (2001). This is a conservative estimate, and as with all phylogenetic dating any age estimates should be regarded as minimum ages subject to revision if older fossils are discovered.

Truswell and Marchant (1986) report fossil pollen of *Fischeripollis halensis* Truswell and Marchant from the middle to late Eocene (approximately 40 Mya). This pollen matches that of *Drosera glanduligera* closely. The pores scattered evenly across the proximal surface of each tetrad (Takahashi and Sohma, 1982) are highly distinctive and occur only in this species amongst all extant *Drosera* (Culham, 1993). We use this as an internal calibration for the phylogeny giving a minimum age for the *D. glanduligera* lineage at 40 Mya.

Climate Scenarios

Climate data for bioclimatic modeling was provided by Professor Paul Valdes from the BRIDGE project (<http://www.ggy.bris.ac.uk/research/bridge/index.html>). These climate models include scenarios for the present day, mid Miocene and other time frames. This set of climate scenarios are run using the same underlying algorithms and record the same set of variables at the same resolution. These scenarios are therefore unusual in allowing direct comparison across evolutionary time scales (Paul Valdes, personal communication).

Present-day model details are available at <http://www.paleo.bris.ac.uk/ummodel/standard.html/xakxu.html>. Details for the late Miocene model are available at <http://www.paleo.bris.ac.uk/ummodel/standard.html/xakft.html>. This model is one of a set of late Miocene scenarios each differing in detail, but empirical testing indicated similar outcomes for alternative scenarios. Past and present data were processed into biologically meaningful climate profile parameters (see Appendix 2 for full list) similar to those of Busby (1991) using the climate data processor plug-in developed by Tim Sutton as part of the Quantum GIS project (<http://www.qgis.org>).

Locality Data

Locality data were collected for each of the *Drosera* species analyzed in Rivadavia et al. (2003). Distribution data came primarily from online records available free of charge through <http://www.gbif.org>, from 24 institutions. This was supplemented with leased data, locality data extrapolated from published maps, and loans from herbaria. See Appendix 3 for a full list of institutions providing data. Points obtained via GBIF were excluded if they fell in an ocean or sea or did not coincide with current known distributions from the Carnivorous Plants Database (http://www.omnisterra.com/bot/cp_home.cgi). Exclusions were minimal, comprising less than 3% of the total collected, primarily being records from near coastlines with poor geographic resolution whose coordinates projected into the sea. Species with fewer than 10 observations were excluded from all subsequent analysis, following Graham et al. (2004), due to the

unreliability of bioclimatic models based on them. This process reduced Rivasdavia's original 59 *Drosera* to 45.

Data from the UK National Biodiversity Network for *D. rotundifolia* and *D. anglica* were excluded from the analysis as the extremely high resolution of these data would provide in excess of 10,000 locality points (more data than for all other *Drosera* from all other institutions combined). When including these data, the core areas of climatic suitability indicated by the bioclimatic models were misleadingly restricted to the UK. Data from the Atlas Florae Europaeae provided UK distribution data for these species at a resolution consistent with the rest of the data.

Present-Day Bioclimatic Models

Bioclim bioclimatic models were built using these locality data in the present-day climate scenario. The bioclimatic models were projected into this present-day scenario to identify all areas that are currently climatically suitable. Models were projected using the Bioclim algorithm of the openModeller software package version 0.3.2 (<http://openmodeller.sourceforge.net/>). At present, only Bioclim models have been used for ancestral state reconstruction. The independent treatment of each climatic variable permits each variable to be independently optimized across the phylogeny, these independently optimized variables can be easily combined into a Bioclim model, which is defined by the minimum and maximum (or 95% confidence intervals) for observed values. More recent, and more complex, algorithms do not permit this independent treatment of climate variables.

Character Optimization

The mean, standard deviation, and minimum and maximum values were collected for the 10 climatic parameters, for all species. Each value was independently optimized as a continuous character across the chosen phylogeny, using square change parsimony optimisation implemented in Mesquite (Maddison and Maddison, 2004). A table showing each of these optimized values for every node on the tree is provided in the supplementary material (available online at <http://systematicbiology.org>). The quantitative convergence index QVI (Ackerley and Donoghue, 1998) was calculated for each character. This measure is analogous to 1 minus the retention index for discrete characters and has been used to test continuous data for phylogenetic conservatism of ecological niches in higher plants (Prinzing et al., 2001). A randomization test of this value was performed following the methodology of Prinzing et al. (2001). A random shuffle of the terminal node values was optimized on the chosen topology with the same method as above and was repeated 100 times for each character. The observed QVI was compared with the distribution of the randomization replicates to test if the observed value is different from a random placement of data on the fixed phylogeny.

Ancestral Bioclimatic Models

The phylogenetically optimized climatic variables were combined to define a Bioclim bioclimatic model (Nix, 1986) for each node on the tree. This follows the methodology of Graham et al. (2004), described as the MinMax + SqCP method by Hardy and Linder (2005). These models were projected into palaeo-climate scenarios to identify the areas of the underlying palaeo-continent reconstruction with suitable climate for the relevant palaeo time frame.

Tests of Models

Similarity of bioclimatic models was assessed using interpretability calculations (Martinez-Meyer et al., 2004; Peterson and Vieglais, 2001). This was achieved by overlay of locality records of one species (species A) into the predicted area of another (species B). Similarity was measured as the percentage of points of A falling within the predicted area of the model of B, and vice versa (Martinez-Meyer et al., 2004). This method assumes that the suitable area predicted by a model built from the set of observed point localities should cover most or all of these points. Therefore we can regard the predicted proportion of another model's observed points as a measure of model similarity. This has the advantage of being a nonsymmetric measure and makes obvious the case where one model completely encompasses another. This measure can be applied to any model regardless of algorithm used.

The potential correlation of geographic overlap and bioclimatic model overlap was tested. Distribution data from the carnivorous plants database was transformed into the Taxonomic Database Working Group (TDWG) standard level four areas (http://www.nhm.ac.uk/hosted_sites/tdwg). The occupancy of the distribution of species A by species B was measured as the proportion of coincident TDWG4 areas for species B. This produces a nonsymmetric measure analogous to the model similarity measure. The *r*-squared correlation between geographic overlap and bioclimatic model overlap for all pairs was calculated.

RESULTS

The retained Bayesian replicates contained 8989 different topologies. The consensus tree of Figure 1 is topologically congruent with Rivasdavia et al. (2003), but several clades are more fully resolved (this tree is available on TreeBASE, accession S1562). However, some of these groups collapse in the maximum parsimony strict consensus, or have low bootstrap support. The main area of topological uncertainty surrounds the clade comprising *D. graminifolia* St. Hil., *D. chrysolepsis* Taub., *D. villosa* St. Hil., and *D. montana* St. Hil. Although this clade is positioned sister to the African clade of *D. aliciae* Raym.-Hamet to *D. madagascariensis* DC. in the majority of Bayesian replicates, there are a minority of cases where it appears sister to the African clade plus the clade comprising *D. esmeraldae* (Steyerm.) Maguire & Wurdack to *D. neocaledonica* Raym.-Hamet. Of the 12 topologies with

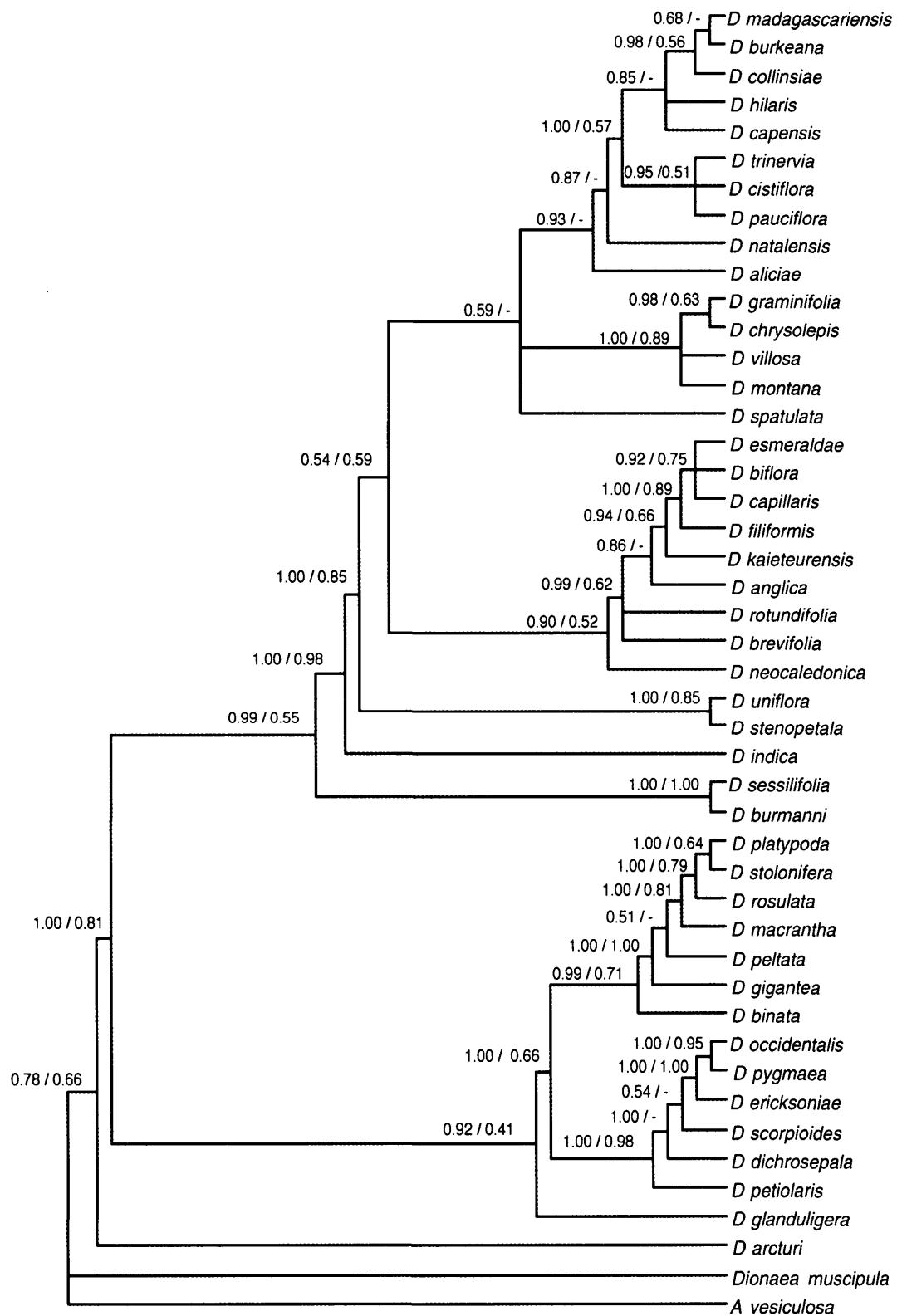


FIGURE 1. Majority rule consensus tree of Bayesian replicates (using sumt command in MrBayes). Posterior probabilities displayed at nodes before "/". Bootstrap support displayed after. Bootstrap replicates calculated in PAUP* using 100,000 replicates using the "fast" stepwise addition.

TABLE 1. Mean node ages based on (A) topological uncertainty replicates and (B) substitution noise replicates.

Node	(A) Topological uncertainty replicates				(B) Substitution noise replicates				Similar*	Significantly different
	Mean	SD	95% CI	N	Mean	SD	95% CI	N		
0	50.00	—	—	1000	50.00	—	—	1000	—	—
3	46.88	1.26	46.80–46.97	801	46.55	1.00	46.49–46.61	999	Yes	Yes
4	42.62	1.58	42.52–42.72	1000	42.29	0.84	42.24–42.34	1000	Yes	Yes
5	40.42	1.07	40.35–40.49	917	40.01	—	—	997	Yes	—
6	35.18	2.35	35.04–35.33	997	34.96	1.61	34.86–35.06	998	Yes	Yes
7	29.43	3.05	29.24–29.62	988	27.52	2.11	27.39–27.65	1000	Yes	Yes
8	13.51	2.86	13.33–13.69	1000	12.74	1.82	12.63–12.85	1000	Yes	Yes
9	8.54	2.56	8.38–8.70	999	10.50	1.77	10.38–10.62	879	Yes	Yes
10	5.42	1.95	5.30–5.54	1000	6.47	1.42	6.38–6.56	986	Yes	Yes
12	4.20	1.56	4.10–4.30	991	5.25	1.27	5.16–5.33	864	Yes	Yes
16	10.54	2.95	10.26–10.82	422	8.94	1.78	8.82–9.05	969	Yes	Yes
20	21.26	3.48	21.05–21.48	1000	21.65	2.63	21.49–21.81	1000	Yes	Yes
21	12.76	2.88	12.58–12.94	1000	11.25	1.95	11.13–11.37	1000	Yes	Yes
22	10.39	2.41	10.19–10.6	510	9.87	1.85	9.75–9.99	874	Yes	Yes
24	4.81	1.49	4.72–4.91	1000	4.25	1.29	4.17–4.33	1000	Yes	Yes
26	1.35	0.85	1.30–1.40	994	0.62	0.60	0.59–0.66	950	Yes	Yes
32	37.90	2.87	37.72–38.08	992	35.78	2.44	35.62–35.93	990	Yes	Yes
33	28.81	3.64	28.59–29.04	1000	24.75	2.44	24.60–24.90	1000	No	Yes
34	20.68	4.08	20.43–20.93	1000	15.35	1.96	15.22–15.47	1000	No	Yes
35	16.95	3.96	16.61–17.28	530	11.36	1.85	11.25–11.48	995	No	Yes
36	15.22	4.10	14.88–15.56	561	8.88	1.60	8.77–8.99	873	No	Yes
37	13.74	4.36	13.46–14.02	944	7.73	1.44	7.61–7.84	644	No	Yes
38	11.87	3.91	11.6–12.14	795	7.34	1.23	7.24–7.43	658	No	Yes
39	9.32	3.19	9.12–9.52	999	5.75	1.07	5.69–5.82	956	No	Yes
40	6.24	2.75	6.06–6.41	906	3.62	1.07	3.54–3.71	639	Yes	Yes
42	4.92	2.36	4.62–5.23	229	—	—	—	—	—	—
45	7.85	2.62	7.66–8.03	780	5.16	0.96	5.08–5.23	634	No	Yes
46	6.80	2.52	6.50–7.10	275	—	—	—	—	—	—
47	4.96	2.06	4.83–5.09	962	3.55	0.98	3.49–3.62	852	Yes	Yes
48	3.58	1.46	3.46–3.69	605	2.45	0.90	2.39–2.51	855	Yes	Yes
56	13.83	4.24	13.21–14.45	183	—	—	—	—	—	—
57	7.75	4.06	7.50–8.00	997	2.52	1.11	2.45–2.59	980	No	Yes
58	5.64	3.29	5.21–6.07	227	—	—	—	—	—	—
60	2.97	2.49	2.81–3.13	935	0.64	0.64	0.60–0.69	643	Yes	Yes
65	12.91	3.90	12.67–13.15	1000	7.86	1.54	7.76–7.96	982	No	Yes
67	9.28	3.19	9.08–9.48	995	5.82	1.29	5.73–5.90	953	No	Yes
68	5.20	2.69	4.91–5.49	329	3.36	1.34	3.26–3.47	645	Yes	Yes
71	6.85	2.43	6.69–7.01	861	5.23	1.14	5.15–5.32	648	Yes	Yes
72	5.64	2.04	5.51–5.77	923	4.39	1.01	4.33–4.46	859	Yes	Yes
74	3.15	1.24	3.07–3.22	1000	2.20	0.86	2.14–2.25	981	Yes	Yes
75	1.54	0.87	1.49–1.6	883	0.45	0.44	0.42–0.48	637	No	Yes
77	0.99	0.71	0.90–1.08	251	—	—	—	—	—	—
82	8.17	3.55	7.95–8.40	1000	7.87	2.10	7.74–8.00	992	Yes	Yes
86	10.66	5.00	10.35–10.97	1000	5.60	2.35	5.45–5.75	1000	No	Yes

*Similarity indicated when mean B is within 1 standard deviation of mean A. Significantly different indicates failure of the *t*-test of similarity of means at the 5% level. Values for set B are missing when the relevant node is collapsed in all replicates. Node numbers refer to those indicated on the chronogram in Figure 2. Nodes mentioned in the text are in bold.

highest posterior probability from amongst the Bayesian replicates, there were 2 with this grouping. All 12 are amongst the 1408 best parsimony trees of length 474 (CI = 0.639, RI = 0.842).

Time calibration was performed with and without the internal calibration point of *D. glanduligera*. With just the basal calibration this node was estimated at 37.6 to 37.1 Mya (95% confidence limits for 1000 replicates using the topological uncertainty method) or 34.7 to 34.4 Mya (95% confidence limits for 1000 replicates using the substitution noise method). This is in reasonable agreement with the approximate 40 million year old fossil evidence for this taxon. All subsequent dates have this internal calibration point applied.

The estimated ages for the replicates relating to topological uncertainty (Table 1) and those for substitution

noise (Table 2) show a significant difference for every node (using a *t*-test of the means). However, the majority of mean ages for nodes based on topological uncertainty are within one standard deviation of the equivalent mean age based on substitution noise. The exceptions are concentrated around the problematic clade *D. graminifolia*–*D. montana*, noted above, which shows significant topological variation amongst the Bayesian replicates.

It should be noted that initial confidence intervals were calculated using 100 replicates for both methods; however, it was shown that with 1000 replicates, there is a large reduction of the range of the 95% confidence interval (CI). For this data set the 1000 replicates CI ranges are 66% smaller than using 100 replicates ($N = 40$ nodes, $SD = 3\%$).

TABLE 2. Observed climatic tolerance for species based on herbarium locality data. Grouped by major nodes from Figure 2. Temperature (temp.) given in °C, precipitation (precip.) in mm. QVI of each character given in parentheses. *QVI value is less than the 99th percentile of randomization test.

Species	Node no.	Mean temp. (0.45)	Mean temp. in warmest month (0.47)	Mean daily precip. (0.23)*	Mean daily precip. in warmest month (0.23)*	Mean temp. in coolest month (0.47)*	Mean daily precip. in driest month (0.35)*	SD of mean precip. (0.34)*	Mean daily precip. in wettest month (0.29)*	Mean daily precip. in coolest month (0.36)	SD of mean temp. (0.47)
<i>D. madagascariensis</i>	37	20.21	23.58	2.54	3.60	15.94	0.20	2.38	6.68	0.47	2.78
<i>D. collinsiae</i>		13.56	18.49	2.28	4.19	6.98	0.23	2.01	5.68	0.40	4.39
<i>D. burkeana</i>		17.99	22.43	2.38	3.11	12.53	0.18	2.37	6.67	0.39	3.60
<i>D. hilaris</i>		16.43	19.01	1.07	0.82	13.93	0.56	0.52	1.88	1.39	1.89
<i>D. capensis</i>		16.14	19.53	1.07	0.88	12.85	0.49	0.57	1.98	1.25	2.49
<i>D. trinervia</i>		15.83	19.54	0.94	0.87	12.17	0.46	0.46	1.66	1.16	2.76
<i>D. cistiflora</i>		15.66	19.76	1.06	1.09	11.57	0.44	0.59	2.03	1.15	3.08
<i>D. pauciflora</i>		15.74	20.01	0.93	0.81	11.58	0.40	0.56	1.87	1.02	3.13
<i>D. natalensis</i>		17.81	21.98	2.14	3.90	12.50	0.25	2.02	5.77	0.40	3.48
<i>D. aliciae</i>		16.48	19.26	1.23	1.09	13.92	0.65	0.54	2.04	1.57	2.01
<i>D. graminifolia</i>	57	20.30	22.65	3.38	5.58	16.39	0.36	3.01	8.09	0.36	2.35
<i>D. chrysoplepis</i>		19.44	21.70	4.41	7.01	16.05	0.93	3.24	9.56	1.02	2.09
<i>D. villosa</i>		20.69	24.02	2.70	4.62	17.22	0.73	1.64	5.23	0.85	2.49
<i>D. montana</i>		18.32	21.00	3.53	5.50	14.56	0.45	2.86	7.77	0.76	2.37
<i>D. spatulata</i>		6.19	11.83	5.31	6.07	-0.33	3.39	1.07	6.58	3.43	4.34
<i>D. capillaris</i>	65	24.90	27.29	3.48	3.10	21.9	1.05	1.78	6.11	2.19	1.88
<i>D. biflora</i>		24.93	26.06	6.14	4.95	24.05	1.89	2.40	9.37	7.25	0.65
<i>D. esmeraldae</i>		24.70	25.73	6.79	5.75	23.82	2.24	2.50	10.13	8.55	0.61
<i>D. filiformis</i>		18.16	26.52	3.21	4.84	7.35	1.38	1.11	4.93	3.13	6.92
<i>D. kaieurensis</i>		23.27	24.51	4.06	2.10	22.08	1.28	2.57	9.15	2.71	0.75
<i>D. anglica</i>		3.69	14.53	2.76	2.63	-9.23	1.65	0.86	4.21	2.86	8.47
<i>D. rotundifolia</i>		3.35	14.56	2.20	2.26	-9.55	1.42	0.58	3.14	2.20	8.68
<i>D. brevifolia</i>		19.01	27.20	2.59	3.33	10.47	1.14	1.01	4.28	1.69	5.92
<i>D. neocaledonica</i>		23.56	26.11	2.77	4.11	21.11	1.00	1.53	5.59	2.49	1.88
<i>D. stenopetala</i>	82	7.38	12.12	5.05	5.64	2.04	3.31	0.93	6.13	3.31	3.60
<i>D. uniflora</i>		7.10	11.19	3.86	3.07	3.88	2.13	1.46	5.92	4.96	2.69
<i>D. indica</i>		23.93	28.72	2.25	3.11	18.76	0.20	2.65	7.61	0.48	3.50
<i>D. sessilifolia</i>	86	25.22	27.56	4.09	2.37	23.16	0.52	2.88	8.55	4.48	1.53
<i>D. burmanni</i>		24.23	28.09	2.94	3.66	19.98	0.61	3.04	8.79	1.04	2.85
<i>D. platypoda</i>	8	16.45	19.26	1.78	1.12	14.09	0.63	1.14	3.69	3.02	1.98
<i>D. stolonifera</i>		16.29	24.18	1.04	0.78	9.57	0.28	0.62	2.08	1.58	5.21
<i>D. rosulata</i>		15.46	23.18	0.99	0.59	8.91	0.31	0.56	1.92	1.55	5.08
<i>D. macrantha</i>		15.60	23.70	1.04	0.86	8.63	0.38	0.52	1.91	1.42	5.36
<i>D. gigantea</i>		15.96	23.68	1.06	0.69	9.44	0.31	0.62	2.06	1.66	5.09
<i>D. peltata</i>		14.58	20.99	2.10	2.43	8.58	1.18	0.76	3.41	1.99	4.46
<i>D. binata</i>		12.32	18.04	2.47	2.68	6.97	1.49	0.66	3.41	2.28	3.99
<i>D. occidentalis</i>	21	15.28	24.15	0.82	0.54	7.74	0.23	0.42	1.52	1.15	5.82
<i>D. pygmaea</i>		13.64	18.87	1.81	1.63	9.05	1.02	0.58	2.67	2.11	3.55
<i>D. ericksoniae</i>		17.61	25.45	0.93	0.63	10.88	0.19	0.62	1.97	1.58	5.22
<i>D. scorpioides</i>		15.73	20.34	1.37	0.99	11.65	0.50	0.79	2.75	2.06	3.17
<i>D. dichrosepala</i>		16.13	20.11	1.56	0.97	12.73	0.56	0.95	3.14	2.60	2.72
<i>D. petiolaris</i>		25.91	29.44	2.52	2.84	22.27	0.09	3.69	10.16	0.15	2.45
<i>D. glanduligera</i>		14.98	23.05	1.14	1.02	8.04	0.52	0.49	1.97	1.43	5.33
<i>D. arcturi</i>		12.39	17.12	2.03	1.89	8.33	1.22	0.47	2.64	2.29	3.20
<i>A. vesiculosa</i>		10.64	19.94	2.15	1.99	0.02	1.10	1.08	4.21	1.83	7.12

The estimated age for each node is shown in Table 1. The base of the genus *Drosera* is obviously highly constrained by the basal calibration of 50 Mya and the internal calibration of 40 Mya. The 95% confidence interval is relatively narrow at 46.97 to 46.8 Mya, which includes many replicates where *D. arcturi* Hook. is sister to *Aldrovanda*.

The groups identified by Rivadavia et al. (2003), where more than one species has been sampled, show the following dates of origin: subgenus *Ergaleium* (Tuberous sundews) (node 8) 13.69 to 13.33 Mya, section *Bryastrum* Planch. (Pygmy sundews) (node 21) 12.94 to 12.58 Mya, section *Thelocalyx* Planch. (node 86) 10.97 to 10.35 Mya. These clades show a period of stasis (minimum 9 million years for section *Bryastrum*, maximum 27 million years for section *Thelocalyx*) followed by diversification. This diversification occurs within the 15 to 10 Mya band when the Mediterranean climates are thought to have arisen (Fig. 2).

Other clades appear to have diversified during this time period, including the African clade (node 37) 14.02 to 13.46 Mya, and the American/European clade (node 65) 13.15 to 12.67 Mya. These clades do not share the long period of stasis prior to this diversification observed for the above groups, nor do they exhibit accompanying suites of morphological changes seen in subgenus *Ergaleium* and section *Bryastrum*.

Only section *Ptycnostigma* Planch. (node 39) at 9.52 to 9.12 Mya and section *Psycophila* Planch. (node 82) 8.4 to 7.95 Mya fall marginally outside this period, but it should be noted that section *Ptycnostigma* is not fully resolved, and has weak bootstrap support.

Table 2 shows the mean values for each of the climate variables for all the species under study (see supplementary material for minimum, maximum, and standard deviations). These data form the climatic profile of each species, and display phylogenetic patterns. The majority of characters display phylogenetic conservatism and

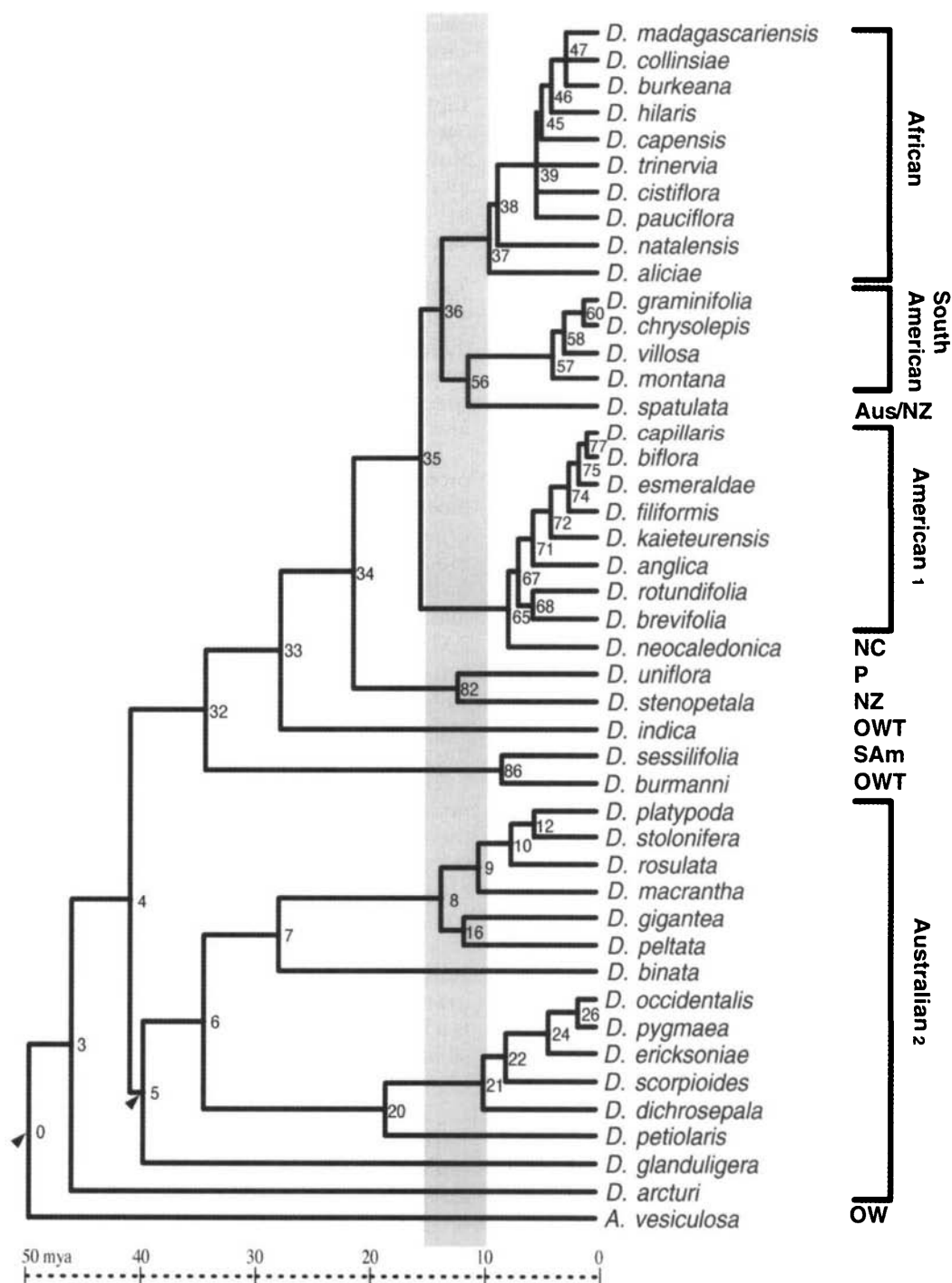


FIGURE 2. Chronogram of one of the optimal Bayesian replicates. This is also the topology used to construct the bootstrap replicates. Numbers at internal nodes refer to Table 3. Arrows indicate fossil calibration points. Some node ages on this tree are outside the 95% confidence intervals of Table 3. The grey bar shows 15 to 10 Mya origin of Mediterranean climate. Distribution is indicated for several clades (Note 1: *D. anglica* and *D. rotundifolia* are widespread throughout the northern hemisphere; Note 2: *D. peltata* has Australasian and East Asian distribution, *D. pygmaea* and *D. arcturi* also in New Zealand). Aus = Australia; NC = New Caledonia; P = Patagonia; NZ = New Zealand; OW = Old World; OWT = Old World Tropics and Australia; SAm = South America.

demonstrate low values of quantitative convergence index (QVI range from 0.23 to 0.47). More than half of these characters have QVI less than the 99th percentile of the randomization replicates. This is represented visually in Figures 3 and 4 which show a high degree of similarity

within some clades in parameters of precipitation and temperature.

Species of *D.* section *Bryastrum* and the African clade all demonstrate a very low maximum value for mean precipitation in the driest month, which indicates

an adaptation to drought (Fig. 3). The species from Mediterranean-type climates, subgenus *Ergaleium*, section *Bryastrum*, and many of the African species (*D. aliciae*, *D. capensis* L., *D. cistiflora* L., *D. hilaris* Cham. & Schlecht., *D. pauciflora* Banks ex DC., *D. trinervia* Spreng.) all demonstrate the seasonal variability of roughly doubling rainfall from the hottest to coldest month.

Extant species of section *Bryastrum* show a marked difference from their sister taxon *D. petiolaris* R.Br. ex DC. (Fig. 4). Mean temperature for *D. petiolaris* is 25.91°C, whereas the mean temperatures for section *Bryastrum* range from 13.64°C to 17.61°C. A similar contrast is evident for mean daily precipitation with *D. petiolaris* at 2.52 mm, and section *Bryastrum* ranging from 0.82 to 1.81 mm.

Species of subgenus *Ergaleium* also display a difference from their sister taxon, *D. binata* Labill. (Fig. 4). The mean temperature for *Ergaleium* ranges from 14.58°C to 16.45°C, in contrast with 12.32°C for *D. binata*.

Sections *Psycophila* and *Thelocalyx* each contain species pairs with disjunct trans-Pacific separation but each pair has very similar climatic preferences (Fig. 4). Species in section *Psycophila* share a low mean temperature (7.1°C to 7.3°C) and consistently high rainfall. *Thelocalyx* share high mean temperatures (24.23°C to 25.22°C), which are consistently high in the coolest month (19.98°C to 23.16°C).

The ancestral nodes of these clades (Table 3) have optimized climatic means that are, on the whole, similar to the terminal taxa within each clade. The mean values for the ancestral node of subgenus *Ergaleium* (node 8) are all within the ranges of means exhibited by the extant taxa of the subgenus. This is not quite the case for the ancestral node of Section *Bryastrum*, which has higher mean temperature and variation in precipitation.

Bioclimatic models, constructed for all taxa, were projected into the same global climate used in constructing the models. Focusing on subgenus *Ergaleium* (Fig. 5), we find that the models for *D. stolonifera* Endl., *D. rosulata* Lehm., *D. platypoda* Turcz., and *D. gigantea* Lindl. select only the Mediterranean-type climate evident at the southwestern tip of Australia, with the exception of the island of Corsica and part of the southern coast of France. *D. macrantha* Endl. and *D. peltata* Thunb. occur in both southwestern and southeastern Australia and can thus tolerate a much wider climate. These models predict suitable climates in most of southern Australia, as well as globally, including the South African Cape and parts of the Mediterranean basin. These two are similar to the model for *D. binata* (the sister species to subgenus *Ergaleium*), which also shows a discontinuous E/SW Australian distribution, and both occur in New Zealand.

Average similarity between models within subgenus *Ergaleium* is significantly higher than within *Drosera* as a whole (Table 4), it is also significantly higher than selecting random groups within *Drosera* of a similar size. This pattern is repeated for all of the clades of interest with one exception. Table 5 shows the complete similarity matrix for all *Drosera*, the African clade, the group *D. graminifolia*–*D. montana* and section *Thelocalyx*

are clearly delimited as groups with high model similarity. Subgenus *Ergaleium* has the highest internal similarity of any clade, but this pattern is obscured in Table 5 by the similarity with models from section *Bryastrum*, which is also predominantly southwest Australian. However, these together with their sister taxa form a monophyletic Australian clade. There is also a similarity of models with many of the South African Cape species.

Wide-ranging species such as *D. rotundifolia* L., *D. indica* L., and *Aldrovanda vesiculosa* L. are revealed in Table 5 by a horizontal line of high overlap with other species, their climatic preferences are broad enough to encompass that of most *Drosera* species. Examining the same species on the vertical axis shows very low similarity as few other species have this broad climate tolerance.

The ancestral model for subgenus *Ergaleium*, when projected into the present (Fig. 5), selects a suitable range most like the more wide-ranging taxa within subgenus *Ergaleium* and its sister species *D. binata*. The ancestral model for node 9 was projected into the relevant time frame indicated by the chronogram. This ancestral bioclimatic model projected into a palaeo-climate scenario for 8 Mya predicts a similar range to that of the present-day projection, most of the south coast of Australia appears suitable, as does Tasmania. The predicted range does not include the extreme southwestern corner, where most of the group currently occur.

This palaeo-projection is also possible for the ancestral node for section *Psycophila* (node 82). This was dated to the late Miocene and has a bioclimatic model suited to the climate of New Zealand during this period (Fig. 6). New Zealand is the only place shown as suitable in the southern hemisphere. Both extant members of section *Psycophila* show present day New Zealand as having a suitable climate, although *D. uniflora* Willd. occurs only in southern South America, whilst *D. stenopetala* Hook.f. is a New Zealand endemic. New Zealand origin is plausible for this section.

DISCUSSION

The use of phylograms from a Bayesian analysis as replicates for constructing dating confidence intervals is an underused approach. It assesses age estimates based on both topological uncertainty and model variation (Sanderson and Doyle, 2001). We agree with Sanderson et al. (2004) who suggest that the impact of incorrect tree topology on dating lineages is a source of error which has received too little attention. An examination of 20 recent (2005) publications employing temporal calibration found that all report ages based on a single fixed topology, without reference to variation caused by topological variation and phylogenetic uncertainty. By using all trees from a Bayesian analysis, this approach produces age estimates that include variation due to topological differences. The number of times each topology occurs within the replicates is directly proportional to the probability of that topology (Huelsenbeck et al., 2002); thus the variation in ages based on topological uncertainty is weighted by the probability of that topology. The inclusion of this topological uncertainty did

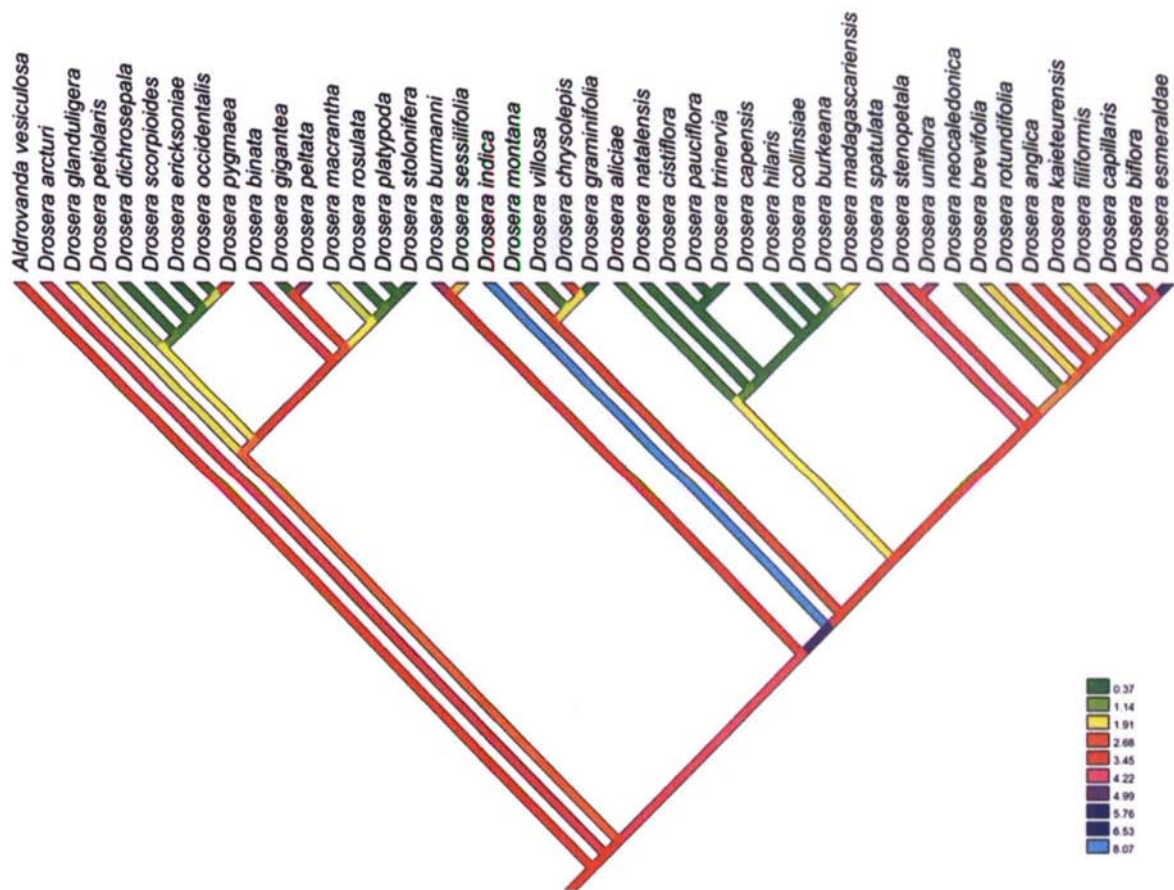


FIGURE 3. Continuous square change parsimony optimization of the maximum range of mean daily precipitation in the driest month. Optimization in Mesquite. QVI = 0.36.

produce age estimates significantly different from the traditional bootstrapping method built from a fixed tree topology. It is noted that selecting a different tree from among the maximum parsimony trees before bootstrapping would also result in different node ages. However, the two age estimates (based on Bayesian replicates and bootstrap replicates) were within one standard deviation for those nodes with consistent topology, suggesting a closer agreement between the methods when topology is more certain. Finally, this method has the practical advantage of not requiring the time-consuming process of constructing bootstrap replicates.

The phylogenetic heritability of environmental characteristics and bioclimatic models found by Davies et al. (2004b), Martinez-Meyer et al. (2004), and Peterson et al. (1999) is supported by this study. There are phylogenetic patterns displayed for single climate variables such as annual mean temperature and precipitation. The tuberous (Subgenus *Ergaleium*) and pygmy (section *Bryastrum*) sundews demonstrate conserved environmental preferences with seasonal characteristics associated with the Mediterranean climate type. These groups, along with other recognized clades, arose during the development of this winter-wet climate zone thought to be between 15 and 10 million years ago (Willis and McElwain, 2002).

This supports the hypothesis that the key innovation of tubers in the tuberous sundews is an adaptation to the formation of the seasonal winter-wet, summer-dry cli-

mate. All species in subgenus *Ergaleium* share the characteristic tuber, which is a water-storage device advantageous in this kind of seasonal climate. The subgenus arose during the formation of this climate type, and diversified within it.

The summer resting bud for pygmy sundews can also be viewed as an adaptation to seasonal climate. This is shared by the majority of section *Bryastrum*, with the exception of the wider ranging species such as *D. pygmaea* (Lowrie, 1987, 1989, 1998). This section also began its diversification at about this 13- to 12-Mya period.

The bioclimatic models also demonstrate phylogenetic patterns. The models are significantly more similar amongst members of monophyletic groups than within *Drosera* as a whole (Table 4). In such cases the climate could be viewed as a limiting factor for the group, suggesting specialized adaptation to the relevant environmental conditions. Conversely, the development of the Mediterranean-type climate can be seen as the opening of a new and novel climatic niche, to which lineages have adapted and speciated, by accumulating morphological change unknown in other climate zones.

The clade above node 65 (*D. capillaris*–*D. neocaledonica*), comprising predominantly American species, demonstrates high climate heterogeneity. Within this clade are some of the most widely distributed species (e.g., *D. anglica*) as well as more geographically restricted species that still span temperate through to tropical climates

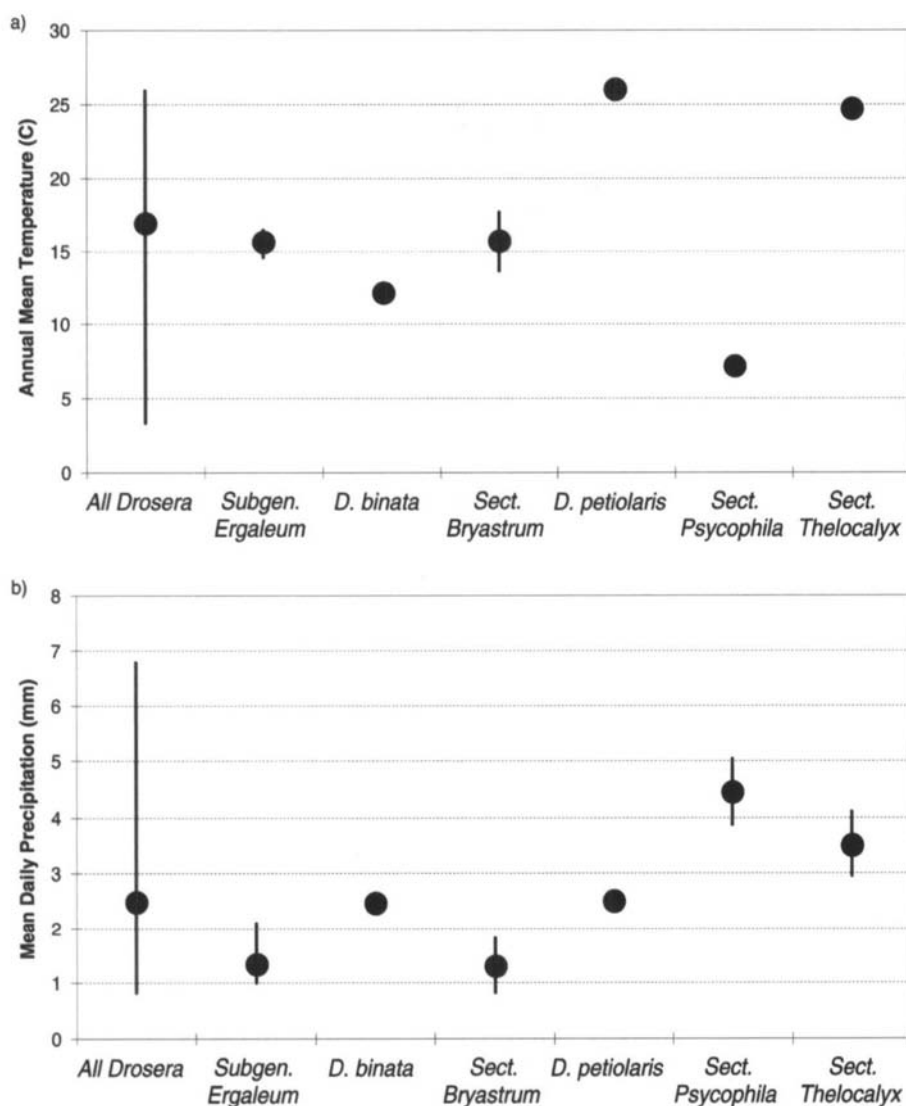


FIGURE 4. Mean annual temperature (a) and daily precipitation (b) for selected groups of extant taxa. Lines show range of values within the groups, dots show mean of group.

(e.g., *D. capillaris*). It is evident that this lineage, although it shows no morphological evidence of superior dispersal ability (e.g., seed size and number; Culham, 1993), has spread more successfully than other lineages of comparable age. This would support a hypothesis of relaxed climate constraint in this lineage that would be worthy of further investigation.

The use of bioclimatic models to estimate palaeo-distributions produces consistent and intuitive results. The prediction of New Zealand as the ancestral area for section *Psycophila* is intuitive, as the extant *D. stenopetala* occurs only here, and the bioclimatic model for *D. uniflora* suggests that South Island falls within its bioclimatic range. The biogeographic affinity of New Zealand with southern South America is well studied (McDowall, 2005; Sanmartin and Ronquist, 2004), and dispersal from New Zealand to Patagonia has been suggested for lots of groups including many plants (McDowall, 2005) and lichens (Bjerke and Elvebakk,

2004). These palaeo-projections are the first attempted on evolutionary timescales and give support to Hugall et al. (2002), who suggested the utility of bioclimatic models in providing hypotheses for historical distributions. We have demonstrated that climate characteristics show clear phylogenetic patterns that are repeated in several groups and that these patterns are correlated with the formation of the Mediterranean climate zones. We further demonstrate that the phylogenetically optimized climate parameters generate plausible palaeo-distributions under the models we have available, which are spatially consistent with current distributions.

There is, of course, a level of uncertainty with these predictions (Davies et al., 2004a; Hugall et al., 2002; Peterson et al., 2004). They are built on four uncertain processes, phylogenetic reconstruction, time calibration, environmental niche (bioclimatic) modeling, and palaeo-climate modeling. Each process, although widely accepted, has its own potential errors, which have been well

TABLE 3. Optimization of climatic variables at internal nodes of chronogram of Figure 2. Node numbers as Figure 2. Nodes mentioned in the text are in bold.

Node	Mean temp. (°C)	Mean temp. in warmest month (°C)	Mean daily precip. (mm)	Mean daily precip. in warmest month (mm)	Mean temp. in coolest month (°C)	Mean daily precip. in driest month (mm)	SD of mean precip. (mm)	Mean daily precip. in wettest month (mm)	Mean daily precip. in coolest month (mm)	SD of mean temp. (°C)
0	12.17	19.85	2.14	2.01	3.88	1.07	1.02	3.98	1.94	5.71
3	13.71	19.76	2.13	2.02	7.75	1.04	0.95	3.75	2.04	4.31
4	16.55	22.30	2.21	2.16	11.04	0.82	1.35	4.63	1.91	4.02
5	16.21	22.73	1.77	1.71	10.31	0.68	1.08	3.72	1.64	4.42
6	17.10	22.85	1.94	1.94	11.84	0.69	1.39	4.55	1.58	3.92
7	14.88	20.96	2.02	2.07	9.34	0.98	0.94	3.64	1.88	4.16
8	15.21	21.99	1.64	1.58	9.20	0.75	0.77	2.95	1.79	4.57
9	15.5	22.79	1.30	1.10	9.19	0.51	0.66	2.40	1.66	4.85
10	15.71	22.67	1.21	0.87	9.75	0.42	0.68	2.34	1.78	4.62
12	16.15	22.04	1.35	0.93	11.14	0.45	0.81	2.71	2.12	3.94
16	15.25	22.22	1.60	1.57	9.07	0.74	0.72	2.80	1.81	4.71
20	20.22	24.86	2.05	2.05	15.88	0.42	2.14	6.30	1.21	3.18
21	17.65	22.30	1.68	1.37	13.52	0.48	1.35	4.19	1.90	3.17
22	16.61	21.93	1.42	1.09	11.94	0.46	0.95	3.12	1.89	3.61
24	16.45	23.14	1.21	0.92	10.65	0.40	0.71	2.43	1.71	4.48
26	15.12	22.05	1.28	1.03	9.15	0.55	0.57	2.21	1.66	4.62
32	19.74	24.42	2.75	2.76	15.07	0.76	2.04	6.42	2.04	3.32
33	19.60	24.26	2.77	3.18	14.77	0.82	2.11	6.71	1.69	3.37
34	15.13	19.65	3.31	3.67	10.47	1.51	1.64	6.11	2.55	3.29
35	15.93	20.36	3.09	3.69	11.18	1.38	1.47	5.57	2.34	3.32
36	14.82	18.96	3.04	3.75	10.26	1.40	1.37	5.21	2.06	3.16
37	16.00	19.58	2.05	2.53	12.17	0.86	1.09	3.83	1.54	2.73
38	16.70	20.52	1.88	2.76	12.32	0.54	1.36	4.23	1.01	3.02
39	16.29	20.01	1.45	1.84	12.31	0.49	0.96	3.08	1.08	2.86
45	16.21	19.71	1.33	1.51	12.53	0.48	0.86	2.76	1.13	2.67
46	16.19	19.58	1.47	1.80	12.43	0.45	1.04	3.22	1.06	2.67
47	15.93	20.03	2.02	3.09	10.83	0.30	1.74	5.01	0.65	3.44
56	12.54	16.93	3.99	5.03	7.44	1.96	1.55	6.24	2.28	3.43
57	16.60	19.99	3.62	5.27	12.39	1.08	2.21	6.92	1.35	2.78
58	18.95	22.05	3.34	5.28	15.16	0.84	2.23	6.76	1.00	2.53
60	19.56	22.13	3.71	5.96	15.86	0.71	2.82	8.14	0.80	2.33
65	17.82	22.48	2.91	3.66	12.81	1.24	1.41	5.38	2.43	3.50
67	13.99	20.97	2.86	3.19	6.15	1.34	1.22	4.99	2.47	5.31
68	12.12	20.91	2.55	2.93	2.36	1.30	0.94	4.14	2.12	6.64
71	12.01	19.51	3.13	2.97	3.27	1.47	1.31	5.44	2.85	5.79
72	18.37	23.04	3.76	3.10	12.88	1.43	1.85	7.12	3.21	3.58
74	19.82	25.10	4.08	4.23	13.30	1.53	1.69	6.77	4.09	4.21
75	22.93	25.73	5.28	4.75	19.66	1.78	2.09	8.27	5.92	2.12
77	24.25	26.36	4.97	4.27	21.87	1.57	2.09	7.92	5.12	1.55
82	9.87	14.32	4.07	4.13	5.47	2.31	1.35	6.05	3.61	3.19
86	23.06	26.69	3.26	2.93	19.40	0.63	2.65	7.92	2.52	2.56

TABLE 4. Mean similarity amongst bioclimatic models within selected clades.

Node	Clade name/taxa	Mean similarity*	N**	95% CI	SD
8	Subgen. <i>Ergaleium</i>	0.64	30	0.52–0.77	0.34
20	Sect. <i>Bryastrum</i>	0.43	20	0.29–0.57	0.33
37	African group	0.55	90	0.48–0.62	0.32
56	<i>D. graminifolia</i> – <i>D. spatulata</i>	0.46	12	0.27–0.65	0.34
65	<i>D. capillaris</i> – <i>D. neocaledonica</i>	0.19	72	0.09–0.28	0.41
82	Sect. <i>Psycophila</i>	0.23	2	—	—
86	Sect. <i>Thelocalyx</i>	0.45	2	—	0.22
3	All <i>Drosera</i>	0.17	1980	0.16–0.19	0.31
	Random groups of 10 spp.	0.17	100	0.16–0.18	0.07
	Random groups of 5 spp.	0.16	100	0.14–0.18	0.10
	Random groups of 2 spp.	0.16	100	0.11–0.20	0.25

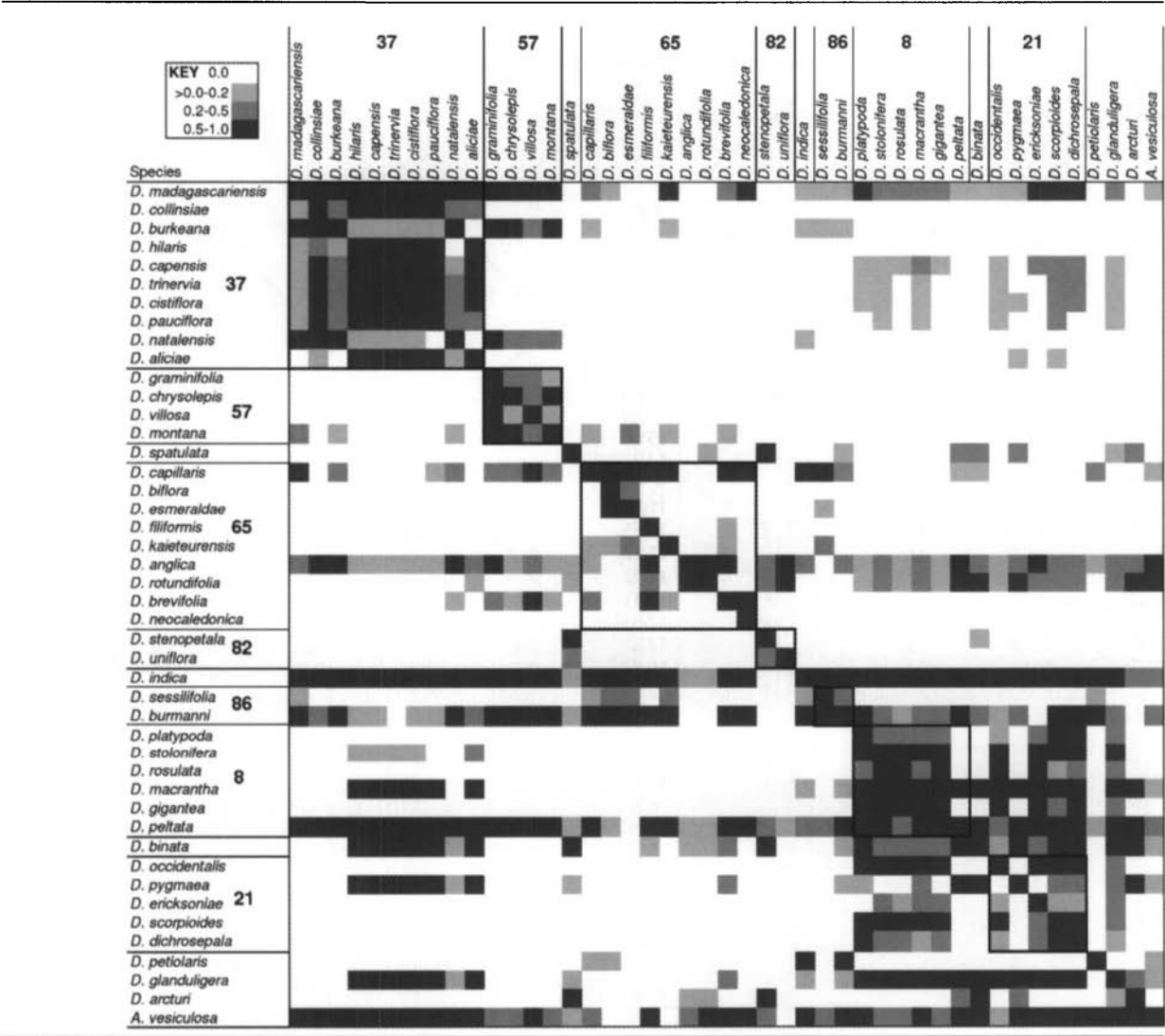
*Similarity denotes the proportion of occurrence points predicted by the bioclimatic model of another species, where unity denotes prediction of all occurrence points by the model of another species. After Martinez-Meyer et al. (2004).

**N is number of model comparisons $N = n(n-1)$ where n = number of taxa within the clade. One hundred replicates for random groups of 10, 5, and 2 species were also tested for similarity to check the dependence of similarity on overall group size. Node numbers refer to Figure 2.

documented elsewhere. These potential errors could be compounded by this process of building one on top of another. The generic concerns with phylogenetic reconstruction of ecological parameters are not specific to this study and are discussed at length in Hardy and Linder (2005).

The issue of the correlation of climate preference with geographic range is also a cause for concern. The phylogenetic patterns found for climatic characters could be the direct consequence of closely related species being more likely to have range overlaps and therefore climatic overlap. It is certainly the case that species pairs with a range overlap have significantly higher mean similarity of bioclimatic models than those without (0.39 versus 0.10). This is hardly surprising, but more critical is whether range overlap is the driving force for bioclimatic model similarity. There are many cases of species pairs with shared climate preferences that have no range overlap (e.g., *D. sessilifolia*+*D. burmanni*,

TABLE 5. Visual representation of similarity of bioclimatic models. Darker boxes represent higher similarity (values as Table 4). Clades of interest are boxed. Clade numbers refer to node numbers of Figure 2. Note this is not symmetric (for example, a model for one species may entirely encompass the range of another but may also occupy areas outside this range). Names across the top row indicate point localities, names in the left-hand column indicate climate envelopes.



D. stenopetala+*D. uniflora*). Furthermore, if there is a strong link between range overlap and climatic preference, then we should expect those species with a higher geographic overlap to exhibit higher model similarity. However, our measure of geographic overlap shows no correlation with range overlap (*r*-squared value 0.12), which suggests that range overlap is not driving model similarity.

Another concern is the temporal alignment of ancestral nodes into the correct time period. The date of any node on a phylogeny and the date of palaeo-climate models both have temporal errors associated with them. However, in this example the confidence intervals for the ancestral nodes are much narrower than those associated with the palaeo-climate models. The ancestral nodes in this example had a maximum confidence interval of 1.23 million years compared with the ± 2 million years confidence interval for the palaeo-climate model used

here (Paul Valdes, personal communication); thus all the nodes ages can be placed wholly within an appropriate time frame.

The use of specific palaeo-climate scenarios does not preclude the projection of our phylogenetically optimized parameters into any other such scenarios; indeed, further such projections would help demonstrate the sensitivity of these predictions to different scenarios. For the purposes of illustration we have chosen a likely scenario for the period of Mediterranean climate development that provides a biologically and historically plausible distribution for our study group. Further exploration of alternative palaeo-climate scenarios will provide a more complete understanding of possible palaeo-distributions and patterns of migration that might be needed to explain current observed data. It is possible that a bioclimatic model will select no area as having a suitable climate.

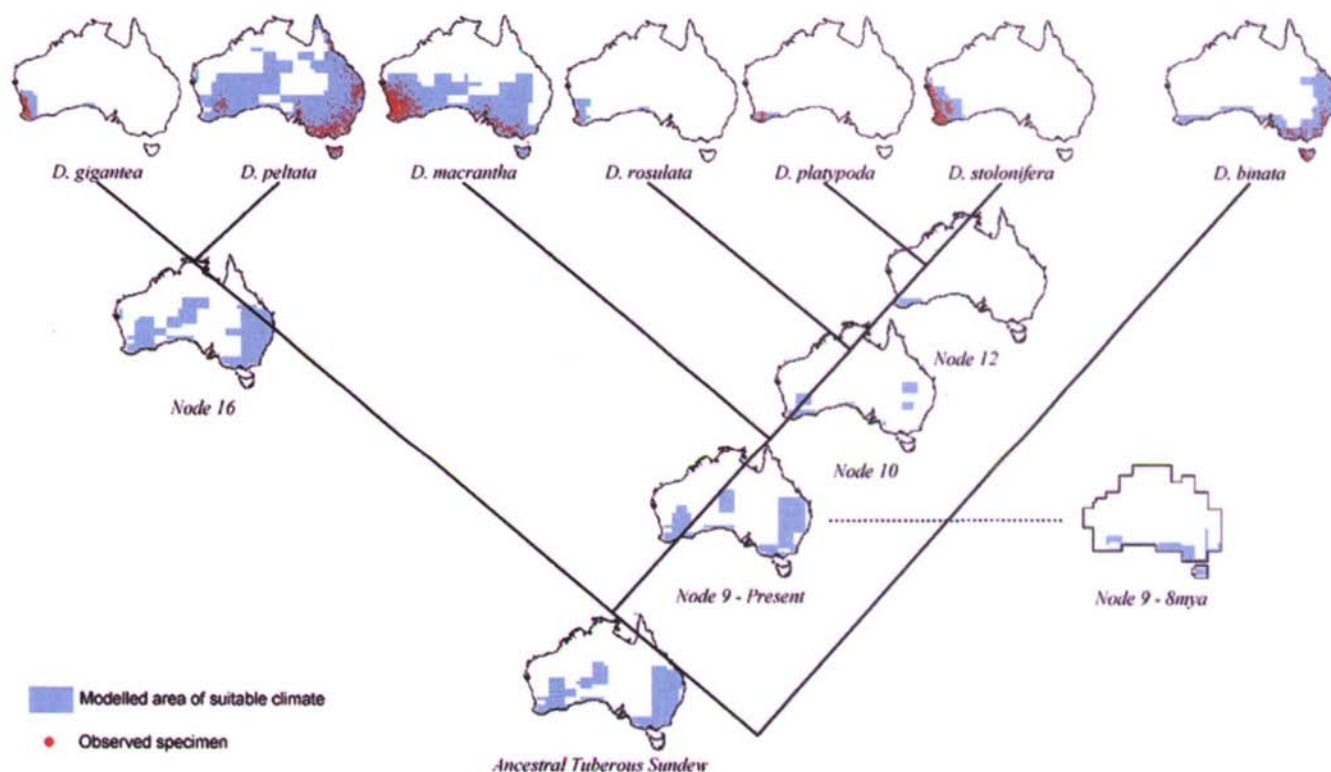


FIGURE 5. Bioclimatic models projected into modeled present-day climate of Australia. Full extent of bioclimatic range marked blue. Red dots show locality data used to construct models. Internal nodes projected into the same present climate to demonstrate model similarity. (Node 9 also projected into model of 8 Mya.)

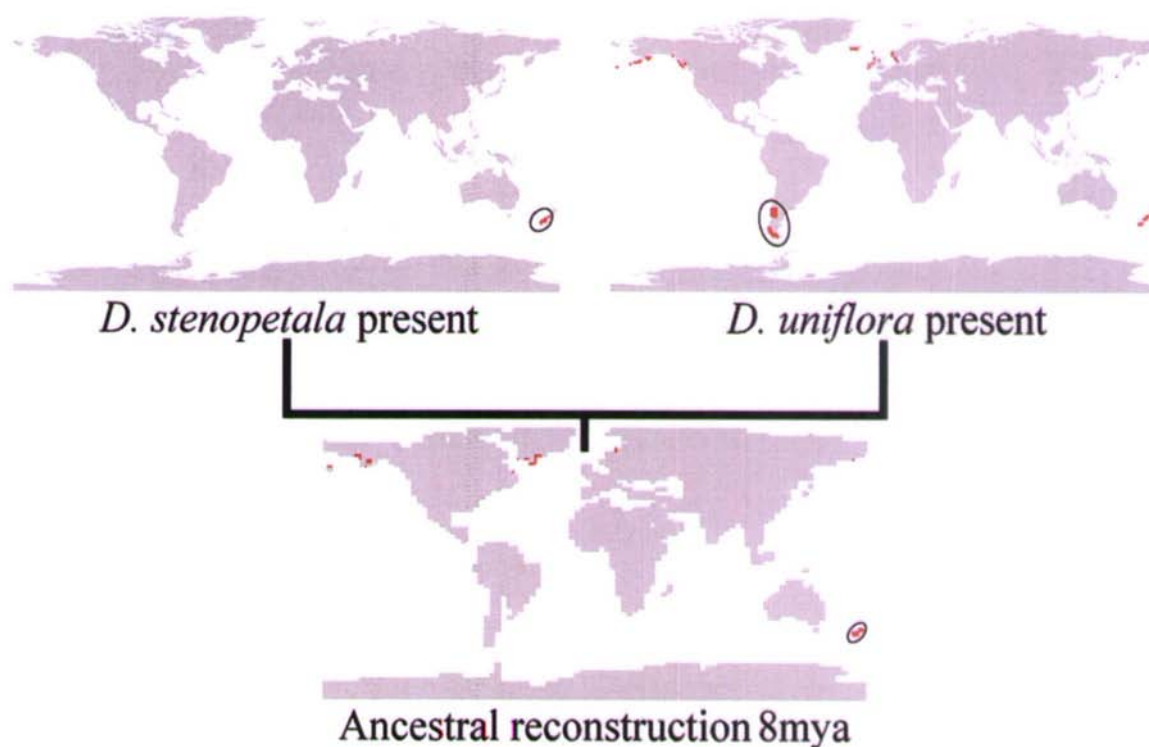


FIGURE 6. Bioclim models for sister taxa *D. stenopetala* and *D. uniflora*, projected into present-day modeled climate. Current distribution circled. Reconstruction of ancestral bioclimatic model (dated at 8.4 to 7.95 Mya) projected into modeled climate for 8 Mya. Late Miocene New Zealand (circled) is the only suitable climate projected in the southern hemisphere. Northern areas with similar climate have also been identified by the models. There is no evidence of long-distance dispersal to these regions.

The value of projecting bioclimatic envelopes into the appropriate palaeo-climatic models is evidenced by the current distribution patterns of several species of tuberous sundews. Current bioclimatic envelopes indicate that for instance *D. macrantha* could occupy central regions of Australia. However, study of the ancestral bioclimatic envelope for this clade shows that the region of palaeoclimatic suitability was restricted to southern and eastern coastal regions of the continent, very similar to the areas now occupied by this species. This addresses one aspect of the thorny issue of bioclimatic modeling: why do species not fill their potential bioclimatic envelope?

The fossil record for almost all plant groups is not sufficient to map true ancestral distribution areas. This method is a viable alternative option for most plant groups. This is a testable method, which Hugall et al. (2002) suggested would be "most informative at broad spatial scales and systems where simple parameters such as annual mean rainfall and temperature are highly informative." The *Drosera* example is just such a case, which demonstrates the efficacy of this method.

Future work will see these methods tested on larger groups, projecting into more palaeo-climates, ideally verified with fossil distributions.

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APPENDIX 1. Genbank accession numbers and taxa, ordered as chronogram in Figure 2.

Accession no.	Species	Subgenus	Section
AB072533.1	<i>Drosera madagascariensis</i> DC.	<i>Drosera</i>	<i>Drosera</i>
AB072524.1	<i>Drosera collinsiae</i> Brown ex Burtt Davy	<i>Drosera</i>	<i>Drosera</i>
AB072520.1	<i>Drosera burkeana</i> Planch.	<i>Drosera</i>	<i>Drosera</i>
AB072530.1	<i>Drosera hiliaris</i> Cham. & Schlecht.	<i>Drosera</i>	<i>Drosera</i>
L01909.2	<i>Drosera capensis</i> L.	<i>Drosera</i>	<i>Drosera</i>
AB072553.1	<i>Drosera trinervia</i> Spreng.	<i>Drosera</i>	<i>Ptycnostigma</i>
AB072523.1	<i>Drosera cistiflora</i> L.	<i>Drosera</i>	<i>Ptycnostigma</i>
AB072552.1	<i>Drosera pauciflora</i> Banks ex DC.	<i>Drosera</i>	<i>Drosera</i>
AB072537.1	<i>Drosera natalensis</i> Diels	<i>Drosera</i>	<i>Drosera</i>
AB072516.1	<i>Drosera aliciae</i> Raym.-Hamet	<i>Drosera</i>	<i>Drosera</i>
AB072528.1	<i>Drosera graminifolia</i> St. Hil.	<i>Drosera</i>	<i>Drosera</i>
AB072522.1	<i>Drosera chrysoplepis</i> Taub.	<i>Drosera</i>	<i>Drosera</i>
AB072541.1	<i>Drosera villosa</i> St. Hil.	<i>Drosera</i>	<i>Drosera</i>
AB072534.1	<i>Drosera montana</i> St. Hil.	<i>Drosera</i>	<i>Drosera</i>
L19530.2	<i>Drosera spatulata</i> Labill.	<i>Drosera</i>	<i>Drosera</i>
AB072521.1	<i>Drosera capillaris</i> Poir.	<i>Drosera</i>	<i>Drosera</i>
AB072518.1	<i>Drosera biflora</i> Willd. ex Roem. & Schult.	<i>Drosera</i>	<i>Drosera</i>
AB072526.1	<i>Drosera esmeraldae</i> (Steyerm.) Maguire & Wurdack	<i>Drosera</i>	<i>Drosera</i>
L01911.2	<i>Drosera filiformis</i> Raf.	<i>Drosera</i>	<i>Drosera</i>
AB072532.1	<i>Drosera kaieteurensis</i> Brumm.-Ding.	<i>Drosera</i>	<i>Drosera</i>
AB072517.1	<i>Drosera anglica</i> Huds.	<i>Drosera</i>	<i>Drosera</i>
AB072538.1	<i>Drosera rotundifolia</i> L.	<i>Drosera</i>	<i>Drosera</i>
AB072519.1	<i>Drosera brevifolia</i> Pursh	<i>Drosera</i>	<i>Drosera</i>
AB072544.1	<i>Drosera neocaledonica</i> R.Hamet	<i>Drosera</i>	<i>Drosera</i>
AB072539.1	<i>Drosera stenopetala</i> Hook. f.	<i>Drosera</i>	<i>Psycophila</i>
AB072540.1	<i>Drosera uniflora</i> Willd.	<i>Drosera</i>	<i>Psycophila</i>
L19529.2	<i>Drosera indica</i> L.	<i>Drosera</i>	<i>Drosera</i>
AB072551.1	<i>Drosera sessilifolia</i> St. Hil.	<i>Drosera</i>	<i>Thelocalyx</i>
L01908.2	<i>Drosera burmanni</i> Vahl	<i>Drosera</i>	<i>Thelocalyx</i>

APPENDIX 1. Genbank accession numbers and taxa, ordered as chronogram in Figure 2. (Continued)

Accession no.	Species	Subgenus	Section
AB072547.1	<i>Drosera platypoda</i> Turcz.	<i>Ergaleium</i>	<i>Stoloniferae</i>
L19531.2	<i>Drosera stolonifera</i> Endl.	<i>Ergaleium</i>	<i>Stoloniferae</i>
AB072555.1	<i>Drosera rosulata</i> Lehm.	<i>Ergaleium</i>	<i>Erythrorhizae</i>
AB072549.1	<i>Drosera macrantha</i> Endl.	<i>Ergaleium</i>	<i>Ergaleium</i>
L19528.2	<i>Drosera gigantea</i> Lindl.	<i>Ergaleium</i>	<i>Ergaleium</i>
L01912.2	<i>Drosera peltata</i> Thunb.	<i>Ergaleium</i>	<i>Ergaleium</i>
L01906.2	<i>Drosera binata</i> Labill.	<i>Drosera</i>	<i>Phycopsis</i>
AB072506.1	<i>Drosera occidentalis</i> Morr.	<i>Drosera</i>	<i>Bryastrum</i>
AB072505.1	<i>Drosera pygmaea</i> DC.	<i>Drosera</i>	<i>Bryastrum</i>
AB072507.1	<i>Drosera ericksoniae</i> N. Marchant & Lowrie	<i>Drosera</i>	<i>Bryastrum</i>
AB072509.1	<i>Drosera scorpioides</i> Planch.	<i>Drosera</i>	<i>Bryastrum</i>
L01910.2	<i>Drosera dichrosepala</i> Turcz.	<i>Drosera</i>	<i>Bryastrum</i>
L01913.2	<i>Drosera petiolaris</i> Kondo	<i>Drosera</i>	<i>Lasiocephala</i>
AB072511.1	<i>Drosera glanduligera</i> Lehm.	<i>Drosera</i>	<i>Coelophylla</i>
AB072512.1	<i>Drosera arcturi</i> Hook	<i>Drosera</i>	<i>Arcturi</i>
AB072550.1	<i>Aldrovanda vesiculosa</i> L.	Outgroup	Outgroup
L01904.2	<i>Dionaea muscipula</i> Soland. ex Ellis	Outgroup	Outgroup

APPENDIX 2. List of climate profile parameters used in this analysis.

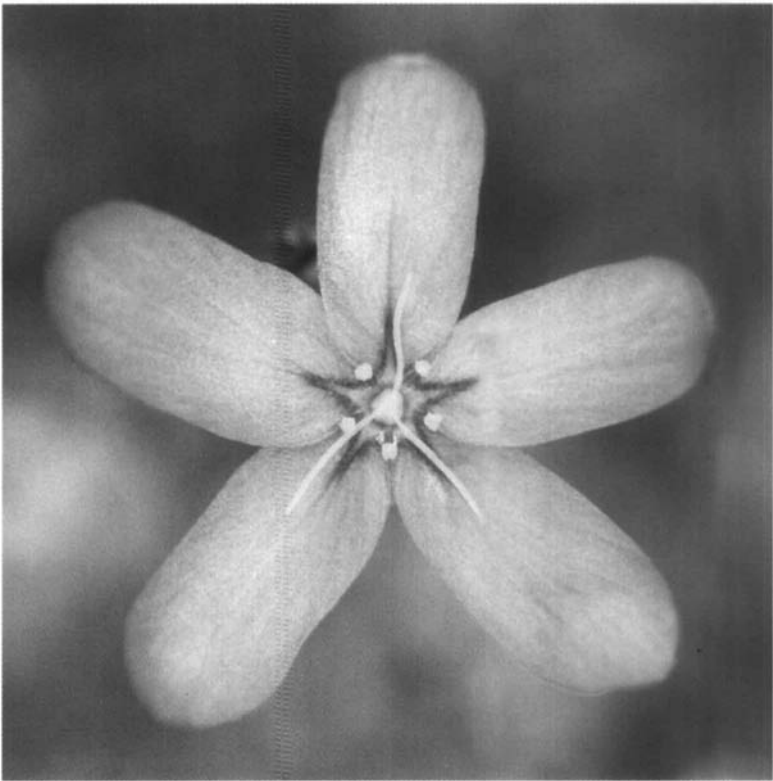
Annual mean surface air temperature
Mean surface air temperature in the warmest month
Mean surface air temperature in the coolest month
Standard deviation of mean temperature
Mean daily precipitation
Mean daily precipitation in wettest month
Mean daily precipitation in warmest month
Mean daily precipitation in driest month
Mean daily precipitation in coolest month
Standard deviation of mean precipitation

APPENDIX 3. Sources of distribution data used in this study. Herbarium codes in parentheses.

Source	Institution/publication	Total
Publication	Jalas, J., Suominen, J., Lampinen, R., and Kurtto, A. (eds.) 1999. Atlas Florae Europaeae. Distribution of Vascular Plants in Europe., Vol. 12. The Committee for Mapping the Flora of Europe and Societas Biologica Fennica Vanamo, Helsinki	1732
www.gbif.org	Department of Conservation and Land Management, Perth, Australia (PERTH)	1595
www.gbif.org	Royal Botanic Gardens, Melbourne, Australia (MEL)	1210
www.gbif.org	Bundesamt für Naturschutz/Zentralstelle für Phytodiversität Deutschland–Bundesamt für Naturschutz/Zentralstelle für Biodiversität Deutschland, Germany	1161
Herbarium specimens	Royal Botanic Gardens, Kew, UK (K)	469
Leased Herbarium Data	National Botanical Institute, Pretoria, South Africa (PRE)	432
Herbarium specimens	University of Reading, UK (RNG)	427
www.gbif.org	Plant Biodiversity Centre, Adelaide, Australia (AD)	417
www.gbif.org	Ratcliffe College, Leicester, UK (LCR)	369
www.gbif.org	Parks & Wildlife Commission of the Northern Territory, Australia (DNA)	360
www.gbif.org	Centre for Plant Biodiversity Research, Canberra, Australia (CANB)	305
www.gbif.org	Tasmanian Museum & Art Gallery, Australia (HO)	293
www.gbif.org	Brisbane Botanic Gardens, Australia (BRI)	216
Publication	Arkticheskaya Flora SSSR IX 1: Droseraceae–Rosaceae	146
www.gbif.org	Australian National Botanic Gardens, Canberra, Australia (CBG)	137
http://arctos.database.museum/	University of Alaska Museum, USA (ALA)	128
Herbarium specimens	Natural History Museum, UK (BM)	118
www.gbif.org	Missouri Botanical Garden, USA (MO)	115
Publication	Distribution of the Droseraceae in Japan, Bulletin of Nippon Dental University, General Education No. 7, March 1978, pp 165–205	112
www.gbif.org	University of British Columbia, Canada (UBC)	89
Publication	Hulten, E. (1968). Flora of Alaska and Neighbouring Territories, Stanford University Press	83
Publication	Wynne, F. E. (1944). <i>Drosera</i> in Eastern North America: Bulletin of the Torrey Botanical Club 71: 166–174	73
www.gbif.org	Regionherbariet i Oskarshamn, Sweden (OHN)	72
www.gbif.org	Royal Botanic Gardens, New South Wales, Australia (NSW)	68
Herbarium specimens	Field Museum, Chicago, USA (F)	47

APPENDIX 3. Sources of distribution data used in this study. Herbarium codes in parentheses. (Continued)

Source	Institution/publication	Total
Publication	Exell and Laundon (1956). New and noteworthy species of <i>Drosera</i> from Africa and Madagascar. Bol. Soc. Brot. 30:213–211	40
www.gbif.org	Icelandic Institute of Natural History, Iceland (ICEL)	32
www.gbif.org	University of Texas, USA (TEX)	29
www.gbif.org	New York Botanical Gardens, USA (NY)	15
www.gbif.org	University of Alabama, USA (UNA)	15
www.gbif.org	University of California, USA (JEPS)	13
www.gbif.org	Herbier de la Guyane-Herbier de la Guyane, French Guiana (CAY)	11
Publication	Burrows, C. J. (1965). Some discontinuous distributions of plants within New Zealand and their ecological significance, part II. Tuatara 13:9-29	10
Publication	Dawson, G. (1938). Las Especies genero <i>Drosera</i> de la flora Argentina. Revista Argentina de Agronomica 5:231–239	5
http://persoon.si.edu/	DC Herbarium, Smithsonian Institute, Washington, USA (US)	5
http://www.rbgkew.org.uk/	Royal Botanic Gardens, Kew, UK (K)	5
http://www.antarctica.ac.uk/	British Antarctic Survey, UK (AAS)	3
www.gbif.org	GBIF–Herbarium WU–Phanerogamen (WU)	3
http://splink.cria.org.br/	SinBiota, Sao Paulo, Brazil	3
www.gbif.org	University of Reading, UK (RNG)	3
http://www.botany.wisc.edu/	University of Wisconsin, USA (WIS)	3
http://www.flmnh.ufl.edu/	Florida Museum of Natural History, USA (FLAS)	2
www.gbif.org	University of Colorado Museum, USA (COLO)	1
www.gbif.org	University of Kansas, USA (KANU)	1
http://herbarium.botany.washington.edu/	University of Washington, USA (WTU)	1
http://www.xtbg.org.cn/	Xishuangbanna Tropical Botanical Garden, China (HITBC)	1



A single flower of *Drosera leucoblata* (section *Bryastrum*), from south-west Australia. Photo by A. Culham.