



Energetics and the evolution of carnivorous plants - Darwin's "most wonderful plants in the world"

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1 Energetics and the evolution of carnivorous plants – Darwin’s “most
2 wonderful plants in the world”

3

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25 Abbreviations: A_{mass} , mass-based photosynthetic rate in $\text{nmol CO}_2 \text{ g}^{-1} \text{ s}^{-1}$; ANOVA,
26 analysis of variance; *atpB*, chloroplast gene encoding the β chain of membrane-bound
27 ATP synthase; C-value, amount of DNA in a haploid nucleus (in millions of base pairs
28 [Mbp]); *coxI*, mitochondrial gene encoding subunit 1 of cytochrome *c* oxidase ; ITS,
29 internal transcribed spacer; J_{Chao} , the Chao-Jaccard abundance-weighted index of
30 similarity; nrITS, nuclear ribosomal ITS; *matK*, chloroplast gene believed to encode a
31 maturase, it is located within the *trnK* intron; *PIE*, probability of interspecific encounter,
32 used here as a measure of specialization on prey by carnivorous plants; PRT1, nuclear
33 gene encoding peptide transferase 1; *rbcl*, chloroplast gene encoding ribulose-
34 bisphosphate carboxylase; *rps16*, a non-coding chloroplast intron; rRNA, ribosomal
35 ribonucleic acid; RRTree, software for comparing sequence divergence rates among
36 related lineages. By extension, it has also come to mean the statistical relative-rate test
37 between groups of sequences on a phylogenetic tree; *trnK*, a non-coding chloroplast
38 intron; it includes the *matK* exon; *trnF* and *trnL*, two other non-coding chloroplast
39 introns; *trnL-F*, intergenic spacer between the *trnL* and *trnF* introns.

40 **Abstract**

41 **Carnivory has evolved independently at least six times in five angiosperm**
42 **orders. In spite of these independent origins, there is a remarkable**
43 **morphological convergence of carnivorous plant traps and physiological**
44 **convergence of mechanisms for digesting and assimilating prey. These**
45 **convergent traits have made carnivorous plants model systems for addressing**
46 **questions in plant molecular genetics, physiology, and evolutionary ecology.**
47 **New data show that carnivorous plant genera with morphologically complex**
48 **traps have higher relative rates of gene substitutions than do those with simple**
49 **sticky traps. This observation suggests two alternative mechanisms for the**
50 **evolution and diversification of carnivorous plant lineages. The “energetics**
51 **hypothesis” posits rapid morphological evolution resulting from a few changes**
52 **in regulatory genes responsible for meeting the high energetic demands of**
53 **active traps. The “predictable prey capture hypothesis” further posits that**
54 **complex traps yield more predictable and frequent prey captures. To evaluate**
55 **these hypotheses, available data on the tempo and mode of carnivorous plant**
56 **evolution were reviewed; patterns of prey capture by carnivorous plants were**
57 **analyzed; and the energetic costs and benefits of botanical carnivory were re-**
58 **evaluated. Collectively, the data are more supportive of the energetics**
59 **hypothesis than the predictable prey capture hypothesis. The energetics**
60 **hypothesis is consistent with a phenomenological cost-benefit model for the**
61 **evolution of botanical carnivory and also accounts for data suggesting that**
62 **carnivorous plants have leaf construction costs and scaling relationships among**
63 **leaf traits that are substantially different from non-carnivorous plants.**

64 Key words: carnivorous plants, competition, construction costs, cost-benefit model,
65 Darwin, energetics, niche overlap, phylogeny, prey capture, universal spectrum of leaf
66 traits.

67 **Introduction**

68

69 “This plant, commonly called Venus’ fly-trap, from the rapidity and force of its
70 movements, is one of the most wonderful in the world.”

71 (C. Darwin, *Insectivorous Plants*, p. 231)¹

72

73 Carnivorous plants have evolved multiple times among the angiosperms (Fig. 1), and
74 the degree of morphological and physiological convergence across carnivorous taxa is
75 remarkable. Molecular sequence data have revealed the phylogenetic history of the
76 angiosperms (Stevens, 2007) and have yielded a better understanding of the patterns of
77 evolution of carnivorous plants. The availability of reliable phylogenies, new
78 observations and experiments, cost-benefit models (Givnish *et al.*, 1984; Laakkonen *et*
79 *al.*, 2006), and contemporary statistical methods have allowed carnivorous plants to
80 emerge as model systems that can be used to address a wide range of questions arising
81 from plant molecular genetics to physiology and evolutionary ecology (Ellison and
82 Gotelli, 2001; Ellison *et al.*, 2003).

83 Charles Darwin laid the foundation for modern research on carnivorous plants.
84 In *Insectivorous Plants*, Darwin (1875) applied his then relatively new conception of
85 homology to illustrate evolutionary and functional convergence across seemingly
86 unrelated taxa. He provided the first detailed descriptions of the structures by which
87 eight genera of plants could entrap insects. With careful observations and clever
88 experiments, Darwin determined for the first time that these plants directly dissolved

1 All quotations from Darwin’s *Insectivorous Plants* are from the second (1898) edition.

89 animal protein using enzymes whose action was similar to pepsin and other proteases
90 (see also Hepburn *et al.*, 1919, 1927). He further showed that dissolved nutrients were
91 directly absorbed by carnivorous plants and that captured prey contributes significantly
92 to plant growth (Darwin, 1875).

93 Drawing on more than 125 years of subsequent research, this review surveys
94 recent progress in three areas of inquiry that Darwin initiated in *Insectivorous Plants*:
95 (1) the tempo and mode of carnivorous plant evolution; (2) patterns and processes of
96 prey capture; and (3) the energetic costs and benefits of botanical carnivory. These three
97 research fronts are unified by stable phylogenetic placement of carnivorous taxa, new
98 data on gene evolution in carnivorous plants (Jobson and Albert, 2002; Müller *et al.*,
99 2004), and Laakkonen *et al.*'s (2006) refinement of the cost-benefit model for the
100 evolution of botanical carnivory originally formulated by Givnish *et al.* (1984).

101 Current understanding of the phylogenetic placement of carnivorous plants re-
102 affirms the occurrence of convergence in trapping mechanisms. Genomic data suggest
103 biochemical, physiological, and ecological mechanisms that could have led to the rapid
104 diversification of at least some carnivorous plant lineages. New analyses of published
105 data on prey capture permit the evaluation of the degree of specialization among
106 carnivorous plant genera and link evolutionarily convergent traits with the ecologically
107 important process of predation. The use of carbon to measure both costs and benefits of
108 carnivory allows carnivorous plants to be placed into the “universal spectrum of leaf
109 traits” (Wright *et al.*, 2004, 2005) that reflects fundamental trade-offs associated with
110 the allocation of carbon to structural tissues and photosynthesis (Shipley *et al.*, 2006).

111

112 **The tempo and mode of carnivorous plant evolution**

113

114 *“By comparing the structure of the leaves, their degree of complication, and*
115 *their rudimentary parts in the six genera [Drosophyllum, Roridula, Byblis,*
116 *Drosera, Dionaea, and Aldrovanda] , we are led to infer that their common*
117 *parent form partook of the characters of Drosophyllum, Roridula, and Byblis.”*

118 *(Insectivorous Plants, p. 289)*

119

120 *“It stands accordingly to reason that the carnivorous plants are quite as old as*
121 *angiospermy, as an independent angiospermous group bound with still older*
122 *groups eventually beyond the limits of angiospermy.”*

123 *(Croizat, 1960: 129)*

124

125 In *The Origin of Species*, Darwin (1859) asserted the importance of homology – the
126 similarity of traits resulting from shared ancestry – for understanding evolutionary
127 relationships. Although the importance of homologous traits (including sequences of
128 DNA, genes, and proteins) in reconstructing phylogenies is widely recognized, actually
129 identifying them remains a challenge. Nowhere is this challenge more evident than in
130 the history of the placement of carnivorous plants in angiosperm phylogenies (Juniper *et*
131 *al.*, 1989). A proper interpretation of patterns of prey capture, gene sequence data, and
132 the evolution of carnivory all rely on firm knowledge of the phylogenetic placement of
133 carnivorous plants and on stable nomenclature. Therefore, this review begins with a
134 survey of current knowledge of carnivorous plant systematics, focused on how recent
135 syntheses of molecular and morphological data illuminate the two most disparate

136 hypotheses for the evolution and diversification of carnivorous plants: Darwin's (1875)
137 hypothesis that the specialization and evolutionary novelty of carnivorous plants
138 indicated convergence in independent lineages, and Croizat's (1960) hypothesis that
139 carnivory evolved once near the base of the angiosperm lineage.

140 Darwin asserted that all of the species with sticky-leaf (or "flypaper") traps in
141 the genera *Drosera*, *Byblis*, *Roridula*, and *Drosophyllum*, along with the snap-trapping
142 Venus' fly-trap (*Dionaea muscipula* Ellis) and the water-wheel plant (*Aldrovanda*
143 *vesiculosa* L.) were closely related (19th century botanists placed all six genera in the
144 Droseraceae, the sundew family). In *Insectivorous Plants*, he discussed in detail the
145 apparent homology of the sessile glands that they use to digest prey. He also asserted
146 that neither the butterworts (*Pinguicula*) (or the other Lentibulariaceae: *Genlisea* and
147 *Utricularia*), nor the Asian pitcher plants (*Nepenthes*) were "at all related to the
148 Droseraceae" (*Insectivorous Plants*, p. 292). Darwin appears to have had little
149 familiarity with the American pitcher plants (*Sarracenia*, *Darlingtonia*, and
150 *Heliamphora*), nor did he discuss the Australian pitcher plant *Cephalotus follicularis*
151 Labill. (Cephalotaceae),² but it is safe to say that he recognized, at least three lineages of
152 carnivorous plants: his "Droseraceae", the Lentibulariaceae, and the (Asian) pitcher
153 plants (Nepenthaceae).

2 *Sarracenia* is mentioned in passing only on the penultimate page of *Insectivorous Plants*. In a letter to W. Thiselton-Dyer (letter 724 in F. Darwin, 1903), he refers to Asa Gray's examination of *Sarracenia*. In a letter to J.D. Hooker (letter 726 in F. Darwin, 1903), he writes of hoping that Hooker will resume work on *Cephalotus* and *Sarracenia* and provide comparative data for Darwin's ongoing studies of *Utricularia*.

154 In contrast to Darwin, Croizat (1960) asserted a common origin for all
155 carnivorous plants and placed them close to the base of the entire angiosperm lineage.³
156 Croizat (1960) asserted that the Lentibulariaceae, and in particular *Utricularia*, was the
157 basal angiosperm group, with morphological evolution proceeding from the relatively
158 amorphous *Utricularia* with its vestigial leaves, stems, and roots that are barely
159 distinguishable from one another, to plants with more differentiated characters including
160 cladodes, shoots, and leaves. In Croizat's view, *Nepenthes* was derived directly from
161 *Utricularia*.⁴ Although the scant fossil record of carnivorous plants does suggest a long
162 evolutionary history for at least some taxa (Thanikaimoni and Vasanthi, 1974; Li, 2005;
163 Heubl *et al.*, 2006), modern phylogenetic analyses of molecular markers and DNA
164 sequences suggest that carnivorous plants are highly derived, polyphyletic taxa. And
165 contrary to Croizat's (1960) assertions, carnivorous plants do not represent a
166 monophyletic ancestral Ur-angiosperm, nor are the vestigial structures of *Utricularia*
167 evolutionary precursors to the more familiar morphological characters of higher plants.
168
169 *Progress in resolving familial relationships*
170

3 "The 'carnivorous ancestor' can of course be figured, as I have, in function of a morphogenetic and phylogenetic average quantified to fit everything – by tendency – between the Podostemonaceae / Lentibulariaceae and the Sarraceniaceae / Dioncophyllaceae." (Croizat, 1960: 256)

4 "The difference in all these regards between *Nepenthes*, and *Utricularia* and other lentibulariaceous genera is in every respect one of degree, not at all one of kind. The "runner" which in the latter aggregate becomes by easy steps under our own eyes "cladode" and "leaf" (cf., e.g., *U. alpina* / *Pinguicula vulgaris*) is by now fully fixed as "foliage" in *Nepenthes*. ...the interrelations between "foliage" and "stem" turn out to be far more complicated in *Nepenthes* than they are in the simplest forms of the Lentibulariaceae [i.e., *Utricularia*]." (Croizat, 1960: 181-182).

171 “[C]onstructive discussion is out of the question, and attempts made at
172 demonstrating, e.g., that *Utricularia* is “derivative” forthwith disqualify their
173 proponents as essentially ill informed.”

174 (Croizat, 1960: 120)

175

176 Carnivorous plants can be found in four of the major angiosperm lineages (the
177 Monocots, Core Eudicots, Rosids, and Asterids), and in five orders: Poales,
178 Caryophyllales, Oxalidales, Ericales, and Lamiales (Fig. 1). Convergence of
179 carnivorous plants and their traps is most apparent at the ordinal level, whereas gene
180 sequences have distinguished between convergence and homology within orders,
181 families, and genera.

182 Over 95% of the more than 600 species of carnivorous plants are currently
183 placed within the Caryophyllales and Lamiales (Fig. 1). New combined analyses based
184 on sequences of the *trnK* intron and its associated *matK* gene, additional chloroplast
185 genes (*atpB*, *rbcl*), and nuclear 18S rDNA have clarified relationships among
186 carnivorous families within the Caryophyllales (Heubl *et al.*, 2006). These analyses
187 simultaneously confirm one of Darwin’s notions of homology,⁵ but dispel another:⁶
188 *Aldrovanda vesiculosa* and *Dionaea muscipula* are sister taxa, and this clade of snap-
189 trappers is a sister group to the sundews (*Drosera*) with their sticky leaves (Cameron *et*
190 *al.*, 2002, Rivadavia *et al.*, 2003).

5 “these octofid projections [of the footstalk, backs of leaves, and spikes of *Dionaea*] are no doubt homologous with the papillae on the leaves of *Drosera rotundifolia*” (*Insectivorous Plants*, p. 233)

6 “The circumferential part of the leaf of *Aldrovanda* thus differs greatly from that of *Dionaea*; nor can the points on the rim be considered as homologous with the spikes round the leaves of *Dionaea*, as these latter are prolongations of the blade, and not mere epidermic productions. They appear also to serve for a widely different purpose.” (*Insectivorous Plants*, p. 263)

191 Three other carnivorous families – Nepenthaceae, Drosophyllaceae, and
192 Dioncophyllaceae – also are clearly rooted within the Caryophyllales (Fig. 1). All three
193 of these families are in a large clade linked to the Droseraceae by a common ancestor,
194 presumably one with flypaper traps. Contrary to Darwin’s hypothesis that *Nepenthes*
195 was “not at all related to the Droseraceae” (*Insectivorous Plants*, p. 292), this genus
196 (*i.e.*, its monogeneric family, the Nepenthaceae) is the sister group of the Droseraceae
197 (Fig. 1). The dewy pine *Drosophyllum lusitanicum* Link is now firmly established in its
198 own family (Drosophyllaceae), and carnivory appears to have been re-derived in the
199 Dioncophyllaceae by the flypaper-trapping *Triphyophyllum peltatum* (Hutch. & Dalz.)
200 Airy Shaw (Cuenoud *et al.*, 2002; Heubl *et al.*, 2006).

201 Carnivory also had more than one independent origin in the Lamiales (Müller *et*
202 *al.*, 2004, 2006; Fig. 1). As in the Caryophyllales, evolution of trap structure in
203 carnivorous Lamiales has proceeded from flypaper traps in *Pinguicula* to the more
204 complex, unidirectionally twisted “eel” traps in *Genlisea* and the bladder traps of
205 *Utricularia* with their unique suction mechanism (Lloyd, 1942; Guisande *et al.*, 2007).
206 At least half of all described carnivorous species are in these three genera, which
207 historically were linked based on shared floral characters (Taylor, 1989). Contemporary
208 molecular analysis unites them based on shared sequences in the *trnL* and *rps16* introns,
209 *rbcL*, the functional *coxI* and *matK* genes, and 5.8S rDNA (Jobson and Albert, 2002;
210 Jobson *et al.*, 2003; Cieslak *et al.*, 2005; Müller *et al.*, 2004, 2006). Despite Croizat’s
211 posthumous protestations to the contrary, both genetic and morphological data support
212 the monophyly of the Lentibulariaceae, with *Pinguicula* sister to a *Genlisea-Utricularia*
213 clade. However, contrary to Albert *et al.* (1992), it is clear that the other carnivorous

214 family in this order, the Byblidaceae (*fide* Płachno *et al.*, 2006), is neither directly
215 ancestral to the Lentibulariaceae nor even closely related to it (Fig. 1).

216 The three remaining carnivorous dicot families – Roridulaceae, Sarraceniaceae,
217 and Cephalotaceae – illustrate variations on the convergent theme of trap evolution.
218 Based on *rbcL* and 18S rDNA analyses, the African endemic Roridulaceae (two species)
219 was considered to be the sister to the American Sarraceniaceae (three genera, 27
220 species) in the Ericales (Albert *et al.*, 1992; Conran and Dowd, 1993). But the current
221 placement of these two families in the overall angiosperm phylogeny (Stevens, 2007)
222 reverses this, and has the Sarraceniaceae with its pitcher traps sister to a clade
223 containing the sticky leaved Roridulaceae and the non-carnivorous Actinidaceae. If
224 this placement is confirmed, it would represent one instance among carnivorous plant
225 lineages of morphologically more complex traps (here, pitchers) being ancestral to
226 simpler sticky traps. Similarly, the Australian endemic *Cephalotus follicularis*
227 (Cephalotaceae) has no apparent sticky-leaved ancestor (Fig. 1).

228 Within the monocots, carnivory also has evolved at least twice in the
229 Bromeliaceae genera *Brocchinia* (*B. hectioides* Mez, *B. reducta* Baker, and possibly *B.*
230 *tatei* L.B. Smith) (Givnish, *et al.*, 1984; Benzing *et al.*, 1985) and *Catopsis berteroniana*
231 (Schultes & Schultes) Mez (Frank and O’Meara, 1984). As with *Cephalotus*, there is no
232 apparent sticky-leaved sister group to these bromeliads with pitcher traps.

233

234 *Progress in resolving generic and subgeneric relationships*

235

236 “...at the present moment, I care more about *Drosera* than the origin of all the
237 species in the world.”

238 (Darwin 1860, in a letter to Charles Lyell⁷)

239

240 As the ordinal placement and systematics of carnivorous plant families have stabilized,
241 attention has turned to resolving relationships among the genera and to resolving
242 subgeneric relationships in the most speciose carnivorous genera – *Drosera*, *Nepenthes*,
243 *Pinguicula*, *Genlisea*, *Utricularia*, and *Sarracenia*. In most cases, phylogenetic patterns
244 based only on inferred homologous morphological traits have been misleading. But
245 when morphological data have been combined with molecular analyses, novel insights
246 into the evolution and biogeography of these carnivorous plant genera have emerged.

247

248 *Drosera*

249 As mentioned above, *Drosera*, *Dionaea*, and *Aldrovanda* form a well-supported clade,
250 with snap-trapping having evolved only once in the clade consisting of *Dionaea* and
251 *Aldrovanda* (Cameron *et al.*, 2002; Rivadavia *et al.*, 2003). The infrageneric
252 classification of *Drosera*, on the other hand, has gone through many revisions. All data
253 point to the basal position of *D. regia* Stephens, a South African narrow endemic, in the
254 monophyletic *Drosera* clade. Beyond that conclusion, however, there is little
255 concordance among different proposed phylogenies and subgeneric classifications.

7 Page 492 of the 1911 edition of *The Life and Letters of Charles Darwin*, edited by F. Darwin.

256 Seine and Barthlott (1994) proposed a morphology-based classification of
257 *Drosera* consisting of three subgenera and 11 sections, but this classification is not
258 congruent with phylogenies based on molecular data alone (Rivadavia *et al.*, 2003,
259 Williams *et al.*, 2004) or on combining molecular and morphological data (Rivadavia *et*
260 *al.*, 2003). Further, different statistical analyses of *rbcL* data (e.g., using MacClade in
261 Rivadavia *et al.*, 2003 and PAUP in Williams *et al.*, 1994) do not concur. For example,
262 Williams *et al.* (1994) identified a “capensis” clade consisting of South African and
263 non-Australian temperate species, but this clade was not clearly identified by Rivadavia
264 *et al.* (2003), who sequenced many more species than did Williams *et al.* (1994).
265 Rivadavia *et al.* (2003) hypothesized that *Drosera* originated in southern Africa or in
266 Australia; that South American species arose by dispersal from Australia; and that
267 African species other than *D. regia* and *D. indica* L. were subsequently derived from
268 South American ancestors. While shades of Croizat and Gondwanan vicariance could be
269 inferred from this analysis, a Gondwanan origin of *Drosera* is not supported by the
270 recent evolution of the Droseraceae (Rivadavia *et al.*, 2003). Clearly much more work
271 remains to be done in this genus.

272

273 *Nepenthes*

274 About 90 species of *Nepenthes*, the sister group to the Droseraceae, occur throughout
275 southeast Asia, with many endemics on Borneo and Sumatra. Biogeographic outliers
276 (disjuncts) occur in India (*N. khasiana* Hook. f.), Sri Lanka (*N. distillatoria* L.), the
277 Seychelles (*N. pervillei* Blume), and Madagascar (*N. madagascarensis* Poir. and *N.*
278 *masoalensis* Schmid-Hollinger) (Dittrich *et al.*, 2001; Meimberg and Heubl, 2006).

279 Morphology has been of limited use in resolving systematic relationships in this genus
280 (Jebb and Cheek, 1997), but phylogenetic analysis of *Nepenthes* has improved
281 dramatically as molecular data have accrued (Meimberg *et al.*, 2001; Meimberg and
282 Heubl, 2006). Both chloroplast (*trnK* intron and *matK* gene) and nuclear (PRT1 along
283 with a non-plastid, translocated copy of *trnK*) genes have been used in phylogenetic
284 reconstruction (Meimberg *et al.*, 2001; Meimberg and Heubl 2006). These results
285 suggest that the five western, biogeographically disjunct species listed above are
286 ancestral to three clades consisting of the Indo-Malayan species. The relatedness and
287 more importantly the biogeographic origins of these latter species suggest repeated
288 colonizations and radiations by *Nepenthes* within the Indonesian islands throughout the
289 Tertiary (Meimberg and Heubl, 2006).

290

291 *Pinguicula*

292 As with studies of *Drosera* and *Nepenthes*, the new cladistic analyses of *Pinguicula* do
293 not agree with historical subgeneric classifications (Casper, 1966; Legendre, 2000).
294 Based on sequencing of *trnK/matK* and morphological analysis of 46 of the ~80 species
295 of *Pinguicula*, Cieslak *et al.* (2005) found high levels of support for five discrete,
296 geographically bounded lineages. This fundamental result supplanted and simplified
297 earlier subgeneric and sectional classifications (three subgenera and 12 sections; Casper,
298 1966; Legendre, 2000). In Cieslak *et al.*'s (2005) new classification, the basal lineage
299 appears to be tropical, with successive branchings of clades consisting of Eurasian
300 species, East Asian species, the Eurasian *P. alpina* L.; and a Central American /
301 Mexican / Caribbean group (Cieslak *et al.*, 2005; Müller *et al.*, 2006). However,

302 phylogenetic reconstruction based on sequencing nrITS1 and nrITS2 of 29 species of
303 *Pinguicula* offered a different picture (Degtjareva *et al.*, 2006). Although both
304 phylogenies found some support for a derived Central American / Mexican / Caribbean
305 clade, and the nrITS-based phylogeny was reasonably congruent with Casper's (1966)
306 morphological classification, the remaining clades identified by the nrITS-based
307 phylogeny were polyphyletic in the *trnK*-based phylogeny (Cieslak *et al.*, 2005).
308 Resolving the infrageneric phylogeny of *Pinguicula* requires clearer definition of
309 informative morphological and molecular characters as well as sequence data from a
310 wider range of species.

311

312 *Genlisea* and *Utricularia*

313 In contrast with the ongoing systematic confusion in *Pinguicula*, sequence data from
314 *matK*, *trnK*, *rbcL*, *rps16* and *trnL-F* (Jobson *et al.*, 2003; Müller *et al.*, 2004, 2006)
315 generally have supported the infrageneric grouping of the 21 species of *Genlisea* based
316 on differences in the way capsules dehisce (Fischer *et al.*, 2000). The South American
317 subgenus *Tayloria* is sister to a clade consisting of three African species and five
318 additional South American species. The African species do not form a natural clade, as
319 the East African / Madagascan species *G. margaretae* Hutchinson is more closely
320 related to the South American species than it is to the remaining African species
321 (Fischer *et al.*, 2000; Müller *et al.*, 2006).

322 The ~220 species of *Utricularia* have been organized into three subgenera and
323 ~21 sections. Analysis of *trnL-F*, *rps16*, and *trnK* sequence data (Jobson *et al.* 2003;
324 Müller and Borsch, 2005) suggested a refinement of the three subgenera

325 *Polypompholyx*, *Bivalvia*, and *Utricularia*. Taylor's (1989) 34 sections based on
326 morphology were, with three exceptions (sections *Iperua*, *Setiscapella* and
327 *Psyllosperma*), upheld as monophyletic. Current analysis suggests a single terrestrial
328 origin for bladderworts in South America; the aquatic and epiphytic habits of
329 *Utricularia* species appear to have been re-derived multiple times within the genus
330 (Jobson *et al.*, 2003; Müller and Borsch, 2005; Müller *et al.*, 2006).

331 Greilhuber *et al.* (2006) reported the remarkable result that many species of
332 *Genlisea* and *Utricularia* have very small nuclear genome sizes. In fact, they found that
333 *Genlisea margaretae* (C-value = 63 Mbp), *G. aurea* St.Hil. (64 Mbp), *Utricularia gibba*
334 L. (88 Mbp), *U. blanchetii* A.DC. (135 Mbp), and *U. parthenopipes* P. Taylor (140
335 Mbp) have smaller C-values than that found for the previous record-holder for the
336 smallest angiosperm genome, *Arabidopsis thaliana* (L.) Heynh. (157 Mbp). Neither the
337 functional significance nor the potential role in evolutionary diversification of this
338 apparent genome simplification in *Genlisea* and *Utricularia* is known.

339

340 *Sarracenia*

341 Recent genetic analyses have revealed perhaps the most taxonomic surprises in the
342 American pitcher plants (Sarraceniaceae). Three sets of phylogenetic reconstructions,
343 one based only on the chloroplast *rbcL* gene (Albert *et al.*, 1992), another that used
344 *rbcL* along with two nuclear ITS regions of rDNA (Bayer *et al.*, 1996), and a third that
345 used ITS-2 along with the 26S rRNA gene (Neyland and Merchant, 2006), all have
346 supported the monophyly of the Sarraceniaceae. Older analyses of biogeographical
347 (Croizat, 1960; McDaniel, 1971; Maguire, 1978), palynological (Thanikaimoni and

348 Vasanthy, 1972), and morphological (Macfarlane, 1893; deBuhr, 1977; Maguire, 1978;
349 Juniper *et al.*, 1989) data have traditionally grouped the North American genera
350 *Sarracenia* and *Darlingtonia* together and posited that the South American genus
351 *Heliamphora* was either sister to, or derived from, a *Sarracenia-Darlingtonia* clade. In
352 contrast, all of the molecular data suggest that *Darlingtonia* is sister to a derived
353 *Sarracenia-Heliamphora* clade. This result is concordant with Renner's (1989)
354 hypothesis that modern-day Sarraceniaceae are derived from a widespread common
355 ancestor (or ancestral stock).

356 These results do not settle the long-standing debate about whether the common
357 ancestor of modern Sarraceniaceae was Neotropical (South America) or subtropical
358 (southeast North America) (Bayer *et al.*, 1996; Neyland and Merchant 2006). However,
359 these results do help resolving species-level relationships within the genus *Sarracenia*.
360 Three distinct clades now seem plausible in this genus: one consisting of *S. psittacina*
361 Michx., *S. minor* Walt., and *S. flava* L.; another consisting of *S. rubra* Walt. (*sensu lato*),
362 *S. alata* Wood, *S. oreophila* (Kearney) Wherry, and *S. leucophylla* Raf.; and a third
363 consisting of *S. purpurea* L. (*sensu lato*).

364 Neither Bayer *et al.* (1996) nor Neyland and Merchant (2006) provide support
365 for separation of the *S. rubra* complex into the separate species and subspecies *S. jonesii*
366 Wherry, *S. alabamensis* Case & Case, *S. rubra* ssp. *gulfensis* Schnell, *S. rubra* ssp.
367 *wherryi* (Case & Case) Schnell, and *S. rubra* ssp. *rubra* Walt. (Case and Case, 1974,
368 1976; Schnell, 1977, 1979b; Godt and Hamrick, 1998). Although the *S. rubra* complex
369 is clearly derived within the genus (Romeo *et al.*, 1977), the molecular data provide no
370 apparent discrimination among them. The repeated failure to distinguish them as

371 distinct taxa raises questions about the separate listing of *S. jonesii* and *S. alabamensis*
372 as endangered species in the United States.

373 In contrast to the lack of taxonomic differentiation within *S. rubra*, there do
374 appear to be significant differences among named taxa within *S. purpurea*. This species
375 was divided by Gleason and Cronquist (1991) into two varieties (considered to be
376 subspecies by Schnell, 2002), *S. purpurea purpurea* (Raf.) Wherry and *S. purpurea*
377 *venosa* (Raf.) Wherry; the latter has been further subdivided into three varieties: *venosa*
378 (Raf.) Fernald; *montana* Schnell & Determann; and *burkii* Schnell (Schnell, 1979a,
379 1993; Schnell and Determann 1997) or two varieties (*venosa*, *montana*) and the separate
380 species *S. rosea* Naczi, Case & Case (Naczi *et al.*, 1999). The ITS-2 and 26S rRNA
381 analyses confirmed an earlier study based on allozymes (Godt and Hamrick, 1999); all
382 data clearly separate *S. purpurea venosa* var. *burkii* from the other named varieties of *S.*
383 *purpurea venosa* and *S. purpurea purpurea* and support its elevation to *S. rosea*
384 (Neyland and Merchant, 2006). Because *S. rosea* is endemic to the Florida panhandle,
385 additional data on its distribution, demography, and threats to its persistence are
386 immediately needed to determine if it should be a candidate for listing as threatened or
387 endangered at either the state or federal level.

388 Furthermore, both the allozyme work (Godt and Hamrick, 1999) and the
389 molecular analysis (Neyland and Merchant, 2006) linked the two varieties of *S.*
390 *purpurea venosa* more closely to each other than to *S. purpurea purpurea*; and the three
391 taxa diverge from each other by about as much as *S. rosea* diverges from the *S.*
392 *purpurea* clade (Neyland and Merchant, 2006). Thus, either the three other subspecies /
393 varieties of *S. purpurea* each should be raised to species status (as tentatively suggested

394 by Neyland and Merchant, 2006), or they should be considered as a single species with
395 broad geographic variability (as suggested by Gleason and Cronquist, 1991; and Ellison
396 *et al.*, 2004).

397

398 *Rates of genetic change and new hypotheses arising from carnivorous plant genomics*

399 As phylogenetic hypotheses have stabilized and as more gene sequence data have
400 accrued for carnivorous plant species, comparative analyses of evolutionary rates of the
401 different taxa have become possible. Initial attention has focused on the
402 Lentibulariaceae because of the extreme specialization in trap morphology within the
403 derived genera *Utricularia* and *Genlisea*. Jobson and Albert (2002) found that relative
404 rates of nucleotide substitutions (based on RRTree computations: Robinson-Rachavi
405 and Huchon, 2000) in seven loci (*trnL/matK* intron, *trnL* second exon, *trnL-F* spacer,
406 *rps16* intron, *cox1*, and 5.8S RNA) occurred 4 to 14 times faster in *Utricularia* than in
407 *Pinguicula*. Similarly, Müller *et al.* (2004) reported that *Genlisea* and *Utricularia* have
408 relative rates of nucleotide substitutions (relative to an *Amborella* + Nymphaeales out-
409 group) in *matK* that are 63% higher than they are in *Pinguicula*.⁸ Müller *et al.* (2004)
410 also found that substitution rates of *Genlisea* and *Utricularia* were higher than those of
411 292 other angiosperm taxa, and that four other carnivorous plant genera – *Pinguicula*,
412 *Drosera*, *Nepenthes*, and *Sarracenia* – had substitution rates more in line with those of
413 other angiosperms (Fig. 2).

8 This percentage comparison assumes similar molecular clocks and may be biased by using the basal angiosperm (*Amborella* + Nymphaeales) as the outgroup in the analysis (Kai Müller, *personal communication* to A. Ellison, 5 March 2008).

414 Two hypotheses have been suggested to account for the high rates of molecular
415 evolution observed in *Utricularia* and *Genlisea*. First, Jobson and Albert (2002)
416 hypothesized that a single or small number of changes in regulatory genes could have
417 led to rapid morphological evolution in *Utricularia*. In particular, Jobson *et al.* (2004)
418 focused on the *coxI* subunit of cytochrome *c* oxidase. They showed that a unique motif
419 of two contiguous cysteine residues in *coxI* has been subject to strong selection, and this
420 novel structure of *coxI* in *Utricularia* could help to provide the additional metabolic
421 energy required to reset *Utricularia* traps.

422 As Darwin and Croizat both noted, *Utricularia* shows little differentiation
423 between stems, shoots, and leaves. Such “relaxed” morphology is often observed in
424 aquatic and epiphytic habitats, where neutral buoyancy (in the water) or other
425 supporting structures (for epiphytes) obviate the need for structural tissues (such as
426 large stems or wood). Thus, the combination of a unique molecular mutation in a key
427 metabolic pathway and the relaxed morphological requirements of aquatic and epiphytic
428 habitats has been hypothesized to be the driver of morphological diversity in this genus
429 (Jobson *et al.*, 2004; Laakkonen *et al.*, 2006). We refer to this hypothesis as the
430 “energetics hypothesis”.

431 Alternatively, Müller *et al.* (2004) pointed to the extreme specialization of the
432 traps in *Genlisea* and *Utricularia* relative to the sticky leaves of *Pinguicula* and *Drosera*
433 and the pitfalls of *Nepenthes* and *Sarracenia* as paralleling the differences in genetic
434 substitution rates (Fig. 2). Like Jobson *et al.* (2004), Müller *et al.* (2004) suggested that
435 high mutation rates in *Utricularia* and *Genlisea* are related to relaxed morphological
436 constraints. However, Müller *et al.* (2004) further argued that morphological evolution

437 in carnivorous plants was achievable because they can directly take up large
438 biosynthetic building blocks, such as amino acids, peptides, and nucleotides, that the
439 plants obtain from capturing and dissolving prey. Importantly, Müller *et al.* (2004)
440 suggested that *Utricularia* and *Genlisea* have more predictable and frequent captures of
441 prey in their habitats relative to the other carnivorous genera, and that there is a positive
442 feedback between this reliable supply of prey and further morphological evolution. We
443 refer to this hypothesis as the “predictable prey capture hypothesis”.

444 These two hypotheses were formulated for carnivorous Lentibulariaceae
445 (*Genlisea* and *Utricularia* relative to *Pinguicula*), but the general pattern of complex
446 traps being derived relative to simple (sticky-leaf) traps (Fig. 1) suggests that these
447 hypotheses could apply across carnivorous plant lineages. Although the broader
448 application of these hypotheses to other carnivorous plant lineages is necessarily
449 speculative, testing between the energetics and predictable prey capture hypotheses
450 nonetheless could provide further insights into factors driving the evolution of
451 carnivorous plants. These analyses are the focus of the subsequent sections of this
452 paper.

453

454 **Pattern and process in prey capture by carnivorous plants**

455

456 “Now it would manifestly be a great disadvantage to the plant [*Dionaea*
457 *muscipula*] to waste many days in remaining clasped over a minute insect, and
458 several additional days or weeks in afterwards recovering its sensibility;
459 inasmuch as a minute insect would afford but little nutriment. It would be far

481 The accumulated contents of carnivorous plant traps can provide an aggregate
482 record of the prey that have been successfully “sampled” by the plant. Over the past 80
483 years, many naturalists, botanists, and ecologists have gathered data on prey contents of
484 carnivorous plants from around the world. Such samples can be used to begin to test the
485 hypothesis that carnivorous plant genera differ in prey composition and to look for
486 evidence of specialization in prey capture. Here we summarize and synthesize these
487 data in a meta-analysis to test for differences in prey composition among carnivorous
488 plant genera, and to look for evidence of specialization in prey capture.

489

490 *The data*

491 Prey capture data were gathered from 30 studies that were published (*in litt.* or in
492 otherwise unpublished M.Sc. and Ph.D. theses) between 1923 and 2007. These studies
493 encompass 87 records of prey capture for 46 species of carnivorous plants in 8 genera:
494 *Drosera* (13 species), *Dionaea* (1 species), *Triphyophyllum* (1 species), *Nepenthes* (11
495 species), *Pinguicula* (7 species), *Utricularia* (5 species), *Sarracenia* (7 species), and
496 *Brocchinia* (1 species). The geographic scope of these data is similarly broad,
497 encompassing all continents on which carnivorous plants occur. We treated each record
498 (prey composition of a single plant taxon at a single locality) as an independent
499 observation, and we did not distinguish within- and between-species variability within
500 each plant genus. Most studies contained from dozens to thousands of individual prey
501 items; the one record of *Drosera rotundifolia* measured by Judd (1959) in southwestern
502 Ontario, Canada that contained only 6 individual prey items was excluded from the
503 analysis. Using designations in the original publications, prey were classified into 43

504 taxonomic groups. For insects, these taxonomic groups were usually orders, although
505 virtually all authors distinguished ants from other Hymenoptera and this distinction was
506 retained in the analysis. There were a few coarser classifications (*e.g.*, “Other insects”,
507 “Mollusca”), but prey in these categories were very rare.

508 In the majority of the studies, the original data consisted of counts of individual
509 prey, usually pooled from traps of several plants. Some studies of *Pinguicula* and other
510 sticky-leaved plants recorded the number of prey per leaf area, whereas others
511 summarized data as percentages of captures per trap or as numbers of individuals per
512 trap. For the purposes of our analyses, all of the observations were converted to the
513 proportion of prey collected for each species within a study. Most carnivorous plants
514 consume a wide range of prey; a notable documented exception is *Nepenthes*
515 *albomarginata* Lobb ex Lindl., which, based on field observations (Kato *et al.*, 1993,
516 Merbach *et al.*, 2002) and stable isotope analysis (Moran *et al.*, 2001), appears to prey
517 almost exclusively on termites. Among other terrestrial carnivorous plants, captured
518 prey is dominated by ants and flies (Fig. 3), whereas captured prey of aquatic
519 *Utricularia* spp. is dominated by Cladocera (mean = 37% of prey) and cyclopoid
520 copepods (mean = 36% of prey).¹⁰

521

522 *Do different carnivorous plant genera specialize on particular prey?*

523 Methods of data analysis

10 The raw data and complete list of studies from which the data were drawn is available as dataset HF-111 from the Harvard Forest data archive:
<http://harvardforest.fas.harvard.edu/data/p11/hf111/hf111.html>.

524 The first question considered was whether there was any indication of specialization by
525 different carnivorous plant genera. A specialist would be one whose prey consisted of
526 many individuals of only a few prey taxon, whereas a generalist predator would have
527 prey consisting of relatively few individuals spread among many different prey taxon. A
528 useful index of specialization is Hurlbert's (1971) probability of an interspecific
529 encounter (*PIE*):

530
$$PIE = \frac{N}{N-1} \times 1.0 - \sum_{i=1}^S (p_i)^2$$

531 in which *S* is the number of prey taxa, *p_i* is the proportion of prey taxon *i* in the sample,
532 and *N* is the total number of individual prey items in the sample. *PIE* ranges from 0 to 1,
533 and can be calculated for data measured in disparate units such as counts, percentages,
534 or densities (Gotelli, 2008).

535 In this analysis, *PIE* has a simple and direct statistical interpretation: if an
536 investigator randomly sampled two individual prey items from the same trap (or set of
537 traps that are pooled for a species in a site), what are the chances that they represented
538 two different prey taxa? A value of *PIE* close to 1 implies that the carnivorous plant
539 genus was not a prey specialist because any two randomly sampled prey items would
540 likely be from different prey taxa. In contrast, a value of *PIE* close to 0 implies
541 specialization on a single prey taxon because any two randomly sampled prey items
542 would likely be the same. Note that the value of *PIE* contains no information about the
543 *identity* of the prey taxa, only the numbers of prey taxa and the relative distribution of
544 individuals among them. Thus, two carnivorous plant genera might have identical
545 values of *PIE*, but share no prey taxa in common.

546 In addition to *PIE*, the proportion of prey items represented by ants (Formicidae)
547 and the proportion represented by flies and mosquitoes (Diptera), two of the most
548 important prey taxa for most carnivorous plants, were also analyzed. *PIE* and the
549 proportion of ants and flies were arcsine-square root transformed prior to analysis
550 (Gotelli and Ellison 2004). A one-way ANOVA was used to compare the response
551 variables among the different genera of carnivorous plants, without distinguishing
552 among within- and between-species variation within a genus. Statistical analyses were
553 conducted using R version 2.6.1.¹¹

554

555 Results

556 The analysis of prey capture spectra using *PIE* suggests that different carnivorous plant
557 genera differ significantly in their relative degree of taxonomic specialization, at least at
558 the ordinal level of prey diversity ($F_{7,79} = 2.03$, $P = 0.009$). The analysis included a low
559 outlier for *Drosera erythrorhiza* Lindl. (Watson *et al.*, 1982) in which 10826 of 10911
560 prey items counted (99.2%) were Collembola ($PIE = 0.015$), and only one sample for
561 the genus *Triphyophyllum* (Green *et al.*, 1979), the most generalist taxa measured (PIE
562 $= 0.802$). However, removal of these two taxa from the analysis did not alter the
563 qualitative conclusion; *PIE* still differed among genera ($F_{6,78} = 3.84$, $P = 0.002$). The
564 most specialized carnivorous plant genera in the analysis were the pitcher plants
565 *Brocchinia* ($PIE = 0.189$), *Nepenthes* ($PIE = 0.452$), and *Sarracenia* ($PIE = 0.491$), and
566 the most generalized genera were *Triphyophyllum* ($PIE = 0.802$) and *Utricularia* ($PIE =$
567 0.713 ; Fig. 4A).

11 <http://www.r-project.org/>

568 Differences among genera in the capture of particular prey taxa also were very
569 strong. Genera differed dramatically in the proportion of ants and flies captured (ants:
570 $F_{7,79} = 36.01, P < 10^{-15}$; flies $F_{7,79} = 8.29, P = 1.5 \times 10^{-7}$). The pitcher plants *Brocchinia*,
571 *Nepenthes* and *Sarracenia* had the highest proportions of ants in their diets (90%, 73%
572 and 55% respectively), reflecting their higher specialization values (low *PIE*). Captures
573 of ants were much less frequent for the sticky traps of *Drosera* (3.4%) and *Pinguicula*
574 (0.5%), and for the aquatic, bladder-trapping *Utricularia* (0%). Flies predominated in
575 the diets of *Drosera* (44%) and *Pinguicula* (52%) (Fig. 4C), but were uncommon prey
576 for *Utricularia* (3%) and *Sarracenia* (14%). A notable outlier was a single study of
577 *Sarracenia purpurea* by Judd (1959), in which 690 of 1095 prey (63%) were Diptera
578 (not identified to suborders or families by Judd, 1959).

579 Collectively, these results illustrate that different genera of carnivorous plants do
580 indeed selectively capture different prey taxa. In some cases, the differences simply
581 reflect habitat differences: ants and adult flies are unavailable to aquatic *Utricularia* or
582 terrestrial *Utricularia* with subterranean traps. However, the statistical significance of
583 differences in captures of flies and ants by pitchers (*Sarracenia* and *Nepenthes*) and
584 sticky traps (*Drosera* and *Pinguicula*) is not dependent on the inclusion of *Utricularia*
585 in the analysis, but rather do appear to reflect the different morphological
586 specializations in these genera.

587

588 *Are they really specialists? Comparisons of captured prey and available prey*

589 Although the frequencies of prey collected in carnivorous plant traps are rarely

590 equiprobable, a predominance of a single prey taxon, such as ants, need not indicate

591 specialization because some taxa simply may be more abundant than others. In five
592 published studies (Watson *et al.*, 1982; Zamora 1990, 1995; Antor and García, 1994;
593 Harms 1999), the investigators not only collected prey from carnivorous plants but also
594 used passive traps in the habitat to sample available prey. Watson *et al.* (1982) used life-
595 sized and -shaped cardboard models of *Drosera erythrorhiza* coated with Hyvis 10 (a
596 tacky inert compound based on polymerized butane) to assess prey available to *Drosera*
597 *erythrorhiza* in the field. Zamora (1990) used life-sized and -shaped paper or wooden
598 models to assess prey available to *Pinguicula nevadense* (Lindbg.) and *P.*
599 *vallisneriifolia* Webb., respectively. Antor and García (1994) used sticky cards in one
600 year (1990) and sticky, life-sized, leaf-shaped models in another year (1991) to assess
601 prey available to *Pinguicula longifolia* Ram. ex. DC ssp. *longifolia*. Harms (1999) used
602 grab samples to determine prey available to *Utricularia intermedia* Hayne, *U. minor* L.
603 and *U. vulgaris* L.

604 The appropriate null hypothesis is that the carnivorous plant is a passive trap:
605 the relative abundance of the different prey categories does not differ from the relative
606 abundance of prey in the environment. The alternative hypothesis is that some prey taxa
607 are selectively attracted or captured by the plant. Under the alternative hypothesis, there
608 should be a significant difference in the relative proportions of prey caught and the
609 relative proportions of prey available.

610

611 Methods of data analysis

612 To quantify the similarity of the prey captured by plants with the prey collected in
613 passive traps, we used the Jaccard Index, *J* (Jaccard, 1901):

614

$$J = \frac{a}{a + b + c}$$

615 in which a is the number of shared species between two samples (plant traps and
616 passive traps), and b and c are the number of unique species in each of the two samples.
617 The Jaccard index was modified recently by Chao *et al.* (2005) to incorporate relative
618 abundance and to account statistically for undetected shared species that might be
619 present, but that did not occur in the samples. Like J , the Chao-Jaccard (or J_{Chao}) index
620 ranges from 0.0 (no shared to species) to 1.0 (all species shared). J_{Chao} was calculated
621 using the EstimateS software package (Colwell 2005); 1000 bootstrap replications were
622 used to estimate parametric 95% confidence intervals for the point-estimates of J_{Chao} .

623

624 Results

625 In all cases, J_{Chao} was close to 1.0, indicating a very high similarity between prey
626 captured by the plants and prey captured by inert traps or taken in a grab sample (Fig.
627 5). For each pairwise comparison (captures by plants *versus* prey available), the
628 confidence interval bracketed 1.0 (Fig. 5), so the null hypothesis that these carnivorous
629 plants were behaving as passive sampling traps could not be rejected. The occasional
630 observations of mass captures of locally abundant insects (Oliver, 1944; Evans *et al.*,
631 2002) are in line with this conclusion, as is Folkerts's (1992) observation that the
632 majority of ants captured by *Sarracenia minor*, *S. flava*, and *S. purpurea* in the southeast
633 United States are the very abundant, non-native fire ant *Solenopsis invicta* Buren. These
634 results do not necessarily imply that carnivorous plants are not "specialized" in their
635 diets. Rather, the observed degree of specialization is similar to that of a simple passive

636 trap of similar size and shape. Unique coloration (*e.g.*, Schaefer and Ruxton, 2008) or
637 chemical attractants (*e.g.*, Jaffe *et al.*, 1995; Moran, 1996) of some carnivorous plant
638 genera do not appear to contribute much to the composition of captured prey. Rather,
639 selectivity of a trap can be understood largely based on the simple geometry of its size,
640 shape, and orientation. As a caveat, note that the majority of these results are for genera
641 (*Pinguicula*, *Sarracenia*) that have traps that have relatively passive mechanisms for
642 attracting prey.

643

644 *Niche overlap among co-occurring carnivorous plants*

645 Darwin (1859) speculated that competition between species is more severe within a
646 genus. If this is true, co-occurring congeners should partition important ecological
647 resources, such as space, food, or time (Schoener 1974). Such partitioning should be
648 reflected in relatively low niche overlap between pairs of species. For carnivorous
649 plants, this question can be phrased as whether co-occurring congeners show any
650 evidence of partitioning or specialization on different categories of prey. Folkerts (1992)
651 provided prey utilization data on five *Sarracenia* species that co-occur in the
652 southeastern United States. Porch (1989), Thum (1986), van Achterberg (1973), and
653 Verbeek and Boasson (1993) provided data on co-occurring species of *Drosera* in,
654 respectively, the southeastern United States, Germany, the Netherlands, and
655 southwestern Australia. These same data were part of the prey utilization analyses
656 described above, but here these data are isolated for more detailed analysis of niche
657 overlap.

658

659 Methods of data analysis

660 How much niche overlap would be expected by chance, in the absence of any
661 competition? The EcoSim software (Gotelli and Entsminger 2007) was used to quantify
662 niche overlap using Pianka's (1973) index of overlap in resource use:

663
$$O_{12} = \frac{\sum_{i=1}^n p_{1i} p_{2i}}{\sqrt{\sum_{i=1}^n (p_{1i}^2)(p_{2i}^2)}}$$

664 where p_{1i} and p_{2i} are the proportion of prey used by species 1 and species 2,
665 respectively. O_{12} ranges from 0.0 (no shared prey) to 1.0 (identical prey utilization), and
666 is calculated for each pair of species in an assemblage. For assemblages with more than
667 two species, we calculated the average of all pairwise values of O_{ij} , where i and j index
668 each species. Null model analysis (Gotelli and Graves 1996) is a statistical method for
669 randomizing ecological data to see whether patterns are more extreme than expected by
670 chance. Thus, to determine whether our average value of O_{ij} differed from that expected
671 under the null hypothesis that the niche overlap reflected only random interactions, the
672 software "reshuffled" the observed utilization values to generate expected overlap in a
673 null community that was unstructured by competition. We used the "RA-3" algorithm in
674 EcoSim; it retains observed niche breadths within a species, but randomizes the
675 particular prey categories that were used. This algorithm has good statistical properties
676 (Winemiller and Pianka 1990) and has been used in many other studies of niche overlap
677 (reviewed in Gotelli and Graves 1996).

678

679 Results

680 For the most species-rich assemblages (5 species of *Sarracenia* [Folkerts, 1992] and 5
681 species of *Drosera* [Verbeek and Boasson, 1993]), niche segregation was not observed
682 (Table 1). In the *Sarracenia* assemblage, the highest observed niche overlap was
683 between *Sarracenia flava* and *Sarracenia purpurea* (overlap = 0.99) and the lowest
684 overlap was between *Sarracenia leucophylla* and *Sarracenia psittacina* (overlap =
685 0.26). The average overlap for all 10 unique pairs was 0.637 (Table 1), which is about
686 midway between complete segregation (0.0) and complete overlap (1.0). However, in
687 the simulated “null assemblages”, the average niche overlap was only 0.197, and the
688 observed overlap in the real *Sarracenia* community was larger than that found in 998
689 out of 1000 simulation trials. Thus, the real five-species *Sarracenia* assemblage (and all
690 pairwise comparisons) showed significantly *more* niche overlap than expected by
691 chance ($P = 0.002$), directly contradicting the hypothesis of niche segregation in
692 sympatry.

693 Similar results were found for five species of co-occurring *Drosera* at the
694 Fitzgerald River site in southwestern Australia (Verbeek and Boasson, 1993). Observed
695 pairwise niche overlaps ranged from 0.65 (*D. menziesii* versus *D. paleacea*) to 0.92 (*D.*
696 *glanduligera* versus *D. paleacea*). The average overlap for the pooled assemblage was
697 0.534, larger than 96% of the 1000 simulations (Table 1). This result again suggested
698 significantly more niche overlap than expected by chance ($P = 0.04$).

699 The high overlap in both cases was clear from an inspection of the raw data.
700 Except for *S. leucophylla*, which favored Diptera, all co-occurring *Sarracenia* primarily
701 captured ants (Folkerts 1992). The relatively modest morphological differences between
702 coexisting species of *Sarracenia* did not translate into appreciable differences in

703 composition of prey captured, suggesting that competition for limiting resources was
704 not regulating species coexistence. Similarly, among co-occurring *Drosera* at Fitzgerald
705 River, prey composition was dominated by Collembola, Homoptera, and Diptera
706 (Verbeek and Boasson 1993).

707 We also found no evidence of interspecific competition among the *Sarracenia*
708 assemblages composed of two or three species (Folkerts, 1992), or among the two- or
709 three-species assemblages of *Drosera* in the southeastern United States, Germany, the
710 Netherlands, and at Murdoch University (Porch, 1989; van Achterberg, 1973; Thum,
711 1986; Verbeek and Boasson, 1993) (Table 1). In all cases, the observed niche overlap
712 was significantly greater than expected (Table 1), which was opposite the pattern that
713 would be predicted by competitive segregation of prey.

714 The two caveats to these results are that prey were identified only to orders and
715 that the analysis assumed that all prey categories were equally abundant. Finer
716 taxonomic resolution of prey could reveal less overlap among prey. If the assumption of
717 equal abundance of prey categories is violated, the analytic method used tends to over-
718 estimate the amount of niche overlap because the results are dominated by common
719 taxa. In contrast, when independent estimates of prey abundance are available, values of
720 prey actually used can be rescaled to downweight the importance of common prey (see
721 Gotelli and Graves, 1996 for further discussion of statistical issues associated with
722 measures of niche overlap). Unfortunately, the studies we used for assessing niche
723 overlap did not include independent estimates of prey availability.

724

725 *Rates and efficiency of prey capture by pitcher plants and bladderworts*

750 nectaries lining the peristome, it became, like that of Macbride's (1818) *Sarracenia*
751 *flava*, a nearly frictionless surface. Foraging ants that contacted the wetted peristome
752 "aquaplaned" and slipped into the pitcher in very large numbers (Bauer *et al.*, 2008);
753 capture rates by *N. rafflesiana* under humid or wet conditions often reached 100% of
754 foraging ants (Bauer *et al.*, 2008). As the other pitcher plants – *Cephalotus* and all the
755 Sarraceniaceae – also have extrafloral nectaries ringing the peristome (Vogel, 1998;
756 Płachno *et al.*, 2007), it is not unreasonable to hypothesize that these taxa also have
757 peristomes that could be wetted to increase prey capture rates. Hopefully, we will not
758 have to wait another 200 years for a good microscopist to test this hypothesis for the
759 other groups of pitcher plants!

760 Adaptations to enhance prey capture by bladderworts have also been postulated.
761 The suction trap (described in detail by Lloyd, 1942; Guisande *et al.*, 2007) of
762 *Utricularia* is a highly specialized structure that is activated when a passing animal
763 touches a trigger hair (Lloyd, 1942 illustrated it as a "better mousetrap"). When
764 triggered, the trap opens inward, the prey is sucked in to the water-filled trap, the door
765 closes, and the prey is digested and absorbed. Finally, the water is pumped out and the
766 trap is reset. This energy-intensive process appears to be facilitated by the evolutionary
767 change in *coxI* described above (Jobson *et al.*, 2004).

768 Beginning with Darwin (1875) investigators have hypothesized that periphyton
769 growing on the hairs and bristles surrounding the trap attract zooplankton that graze
770 their way down to the trigger hairs. This hypothesis was verified experimentally for *U.*
771 *vulgaris* by Meyers and Strickler (1979) and for *U. foliosa* L. (Díaz-Olarte *et al.*, 2007).
772 However, the presence and species composition of periphyton on hairs and bristles of

773 *Utricularia* appears to depend on local environmental conditions (Díaz-Olarte *et al.*,
774 2007), not on a direct facilitation of periphyton growth by *Utricularia* (*cf.* Ulanowicz,
775 1995). Determining causal relationships between environmental conditions,
776 morphological structures, and prey capture rates and efficiency by *Utricularia* remains
777 an active area of research.

778

779 *Do fly-traps really catch only large prey?*

780

781 [Of 14 *Dionaea* leaves sent to Darwin by William M. Canby], “[*four of these*
782 *had caught rather small insects, viz. three of them ants, and the fourth a rather*
783 *small fly, but the other ten had all caught large insects, namely five elaters, two*
784 *chrysomelas, a curculio, a thick and broad spider, and a scolopendra....But*
785 *what most concerns us is the size of the ten larger insects. Their average length*
786 *from head to tail was 0.256 of an inch, the lobes of the leaves being on average*
787 *0.53 of an inch in length, so that the insects were very nearly half as long as the*
788 *leaves within which they were enclosed. Only a few of these leaves, therefore,*
789 *had wasted their powers by capturing small prey, though it is probable that*
790 *many small insects had crawled over them and been caught, but had then*
791 *escaped through the bars.”*

792

(*Insectivorous Plants*, p. 252)

793

794 Our analyses suggest that carnivorous plants are not selective predators with respect to
795 prey composition. But is there any evidence that, as Darwin hypothesized, they capture
796 only relatively large prey? Here the data are limited to two small collections of prey

797 contents of the Venus' fly-trap, *Dionaea muscipula* (Darwin, 1875; Jones, 1923). In
798 both cases, we had to make some assumptions to reconstruct the data and test the
799 hypothesis that *Dionaea* prey are unusually large.

800 Darwin (1875) provided the average size of only the ten largest prey (0.256 inch
801 = 6.5 mm); the sizes of the four smaller prey items (three ants and a fly) were not
802 reported. Jones (1923) gave a bit more detail for 50 dissected *Dionaea* leaves, each with
803 one prey item: of the 50 prey items recovered, “only one was less than 5 mm in length,
804 and only seven, less than 6 mm; ten were 10mm or more in length, with a maximum of
805 30 mm” (Jones 1923: 593). Jones also reported that the average length of the prey was
806 8.6 mm, and the normal minimum observed was 6.4 mm (approximately the average
807 length of Darwin's sub-sample).

808 Based on Jones's (1923) reported size intervals, prey size distributions were
809 simulated using R version 2.6.1 as being drawn from a mixture of three normal
810 distributions ($\mathcal{N}(5.5, 0.25)$, $\mathcal{N}(20, 5)$, and $\mathcal{N}(8, 1)$)¹², with sample sizes respectively
811 equal to 7 (“less than 6 mm”, but more than 5 mm), 10 (“10mm or more in length, with
812 a maximum of 30 mm”), and 32 (the remainder, unenumerated by Jones, but by
813 inference being between 6 and 10 mm long), plus one outlier (4 mm), corresponding to
814 the one “less than 5 mm in length”). This mixture gave a skewed distribution of prey
815 sizes with mean = 9.3 mm, and a median = 7.6 mm. Darwin's distribution of prey was
816 similarly simulated as a mixture of two normals: $\mathcal{N}(6.5, 1)$ and $\mathcal{N}(5.5, 0.25)$ with
817 sample sizes of 10 and 4, respectively. Because Darwin gave no information on the size

12 The notation $\mathcal{N}(\mu, \sigma)$ means a normal distribution with mean = μ and standard deviation = σ . We used the R command `rnorm(. . .)` to generate our size distributions.

818 of the four small prey items, the sample of small prey sizes in this mixture was drawn
819 from the same distribution as Jones's small prey. This mixture gave a skewed
820 distribution of prey sizes with mean = 6.0 mm and a median = 5.8 mm. The two
821 distributions are shown in Fig. 6.

822 The relevant question is whether either of these data sets support the hypothesis
823 that the average size of prey that *Dionaea* captures is at least half the length of a 13.5
824 mm leaf (Darwin's "0.53 of an inch"). A plausible way to determine this is to create
825 replicate bootstrapped samples (i.e., with replacement) of the available data and use
826 these bootstrapped samples to estimate the population mean and confidence intervals
827 (Efron, 1982).

828 We used the `sample` function in R to create 10 000 bootstrapped samples of
829 both Darwin's and Jones's prey size data. The estimated mean of the small population
830 from which Darwin drew his sample was 6 mm (95% CI = [5.70, 6.38]), which fails to
831 support the hypothesis that *Dionaea* catches prey that is on average half as large as the
832 trap (6.75 mm). In contrast, the estimated population mean of Jones's larger sample was
833 9.3 mm (95% CI = [7.92, 10.86]), a result that is more in line with Darwin's expectation.
834

835 **What do they do with all that prey? The energetics of botanical carnivory**

836

837 *Ordinary plants...procure the requisite inorganic elements from the soil by*
838 *means of their roots....[T]here is a class of plants which digest and afterwards*
839 *absorb the animal matter, namely, all the Droseraceae, Pinguicula, and, as*
840 *discovered by Dr. Hooker, Nepenthes.*

841

(*Insectivorous Plants*, p. 365)

842

843 Based on his detailed observations of feeding behavior and nutrient absorption, Darwin
844 discussed *how* carnivorous structures might have evolved in plants. Later authors (*e.g.*,
845 Lloyd, 1942; Juniper *et al.*, 1989) generally followed his lead. Little attention was paid
846 to *why* botanical carnivory might evolve until Givnish *et al.* (1984) proposed a cost-
847 benefit model to explain why carnivorous plants are most common in habitats that are
848 bright and wet but very low in nutrients. Givnish *et al.*'s (1984) model postulated a
849 trade-off between the nutrients gained by capturing animals and the energy foregone by
850 constructing photosynthetically inefficient traps instead of leaves. Givnish *et al.* (1984)
851 asserted that carnivory would be expected to evolve if the increased nutrients provided
852 by carnivory gave plants possessing carnivorous structure an energetic advantage
853 relative to co-occurring non-carnivorous plants. This model was elaborated by Benzing
854 (2000), who additionally considered decaying litter as a nutrient source and a third axis
855 of selection. Both models were initially derived from studies of carnivorous bromeliads,
856 but the cost-benefit framework has been used to interpret results from a wide range of
857 observational and experimental studies on many carnivorous plant species (reviewed by
858 Ellison and Gotelli, 2001; Ellison, 2006).

859

860 *The benefits of carnivory*

861 Givnish *et al.* (1984) identified three ways in which nutrients acquired through
862 carnivory could result in energetic benefits to the plants. First, photosynthesis could
863 increase with increasing nutrient uptake (following prey capture and digestion). This

864 photosynthetic benefit could be realized either through an increase in the total mass of
865 leaves the plant can support or an increased A_{mass} . Second, the excess nutrients derived
866 from carnivory could be disproportionately allocated to reproduction. This allocation to
867 reproduction should be measurable either as a positive relationship between prey
868 captured and seeds produced or an increase in nutrient content within the seeds. Third,
869 if carnivorous plants could extract carbon from prey, they could bypass photosynthesis
870 as a means of producing sugars. This last benefit could be most important for aquatic
871 carnivorous plants, as CO_2 used for photosynthesis is often limiting because it must be
872 obtained by diffusion from the surrounding water (Adamec, 1997a, 1997b, 2006).

873 Most studies on the benefits of carnivory have found that plants significantly
874 increase growth (in terms of leaf mass or total biomass) in response to prey additions
875 (see Table 1 of Ellison, 2006). However, detailed measurements of photosynthesis of
876 carnivorous plants in response to prey or nutrient additions – the primary measure of the
877 first hypothesized benefit of carnivory – have generated more equivocal results. Méndez
878 and Karlsson (1999) reported no significant increase in photosynthetic rates of
879 *Pinguicula villosa* L., *P. vulgaris* L., or *Drosera rotundifolia* when they were provided
880 supplemental prey. Adamec (2008) found that photosynthetic rate of *Aldrovanda*
881 *vesiculosa* increased following prey additions, but that of *Utricularia australis*
882 decreased following prey additions. But for both species, supplemental prey caused an
883 increase in growth rates. (Adamec, 2008). Wakefield *et al.* (2005) also reported no
884 significant change in photosynthetic rates of *Sarracenia purpurea* pitchers fed additional
885 prey in a field study, although tissue N and P concentrations did increase with feeding
886 level. Nutrient storage in new *Sarracenia* pitchers (Butler and Ellison, 2007) or

887 reproductive structures (see below) are alternative sinks for excess nutrients derived
888 from prey captured by existing pitchers. For example, in a greenhouse study of prey
889 addition to ten species of *Sarracenia*, A_{mass} increased in new pitchers and photosystem
890 II stress (as measured by fluorescence) decreased with prey additions (Farnsworth and
891 Ellison 2008).

892 The second postulated benefit of carnivory also has been demonstrated.
893 Temperate-zone *Pinguicula* species, which exhibit reproductive preformation (buds set
894 in year y flower and produce seeds in year $y+1$; Worley and Harder, 1999) increased
895 vegetative reproduction in the year of prey additions and also increased sexual
896 reproduction in subsequent years (Thorén and Karlsson, 1998; Worley and Harder
897 1999). In *P. vallisneriifolia*, neither flower set nor fruit set changed with prey additions,
898 but seed set (measured as seed:ovule ratio) did increase (Zamora *et al.*, 1997). A similar
899 increase in seed:ovule ratio in response to prey availability and inorganic nutrient
900 addition was observed in *Sarracenia purpurea* (Ne'eman *et al.*, 2006), which also
901 makes preformed buds (Shreve, 1906). Three other *Pinguicula* species (*P. alpina*, *P.*
902 *villosa*, and *P. vulgaris*) all preferentially allocated nitrogen to reproductive structures
903 (Eckstein and Karlsson 2001). Both fruit set and seed set of *Drosera intermedia* and *D.*
904 *rotundifolia* were positively correlated with prey captured (Thum, 1989; Stewart and
905 Nilsen, 1992). Experimental prey additions subsequently confirmed these correlative
906 results (Thum, 1988).

907 In summary, increases in plant growth, nutrient storage, and reproduction in
908 response to increased prey have been documented in a number of carnivorous plant
909 species, although evidence for elevated photosynthetic rates is weak. To date, there is

910 only scant evidence for Givnish *et al.*'s (1984) third prediction, that of heterotrophic
911 uptake of C from prey. Fabian-Galan and Savageanu (1968) found that ^{14}C from labeled
912 *Daphnia* fed to both *Aldrovanda vesiculosa* and *Drosera capensis* L. was incorporated
913 into leaf and stem tissues and into new growing tips of these carnivorous plants.
914 Similarly, *Drosera erythrorhiza* stored ^{14}C from labeled flies in new growth (Dixon *et*
915 *al.*, 1980). Additional evidence for facultative heterotrophy in carnivorous plants is
916 most likely to be found in aquatic carnivorous plants (Adamec, 1997a, 1997b, 2006), as
917 dissolved CO_2 can limited photosynthetic rates in submerged plants.

918

919 *The costs of carnivory*

920 The costs of carnivory have been assessed much less frequently than the benefits,
921 perhaps because measuring energy foregone is more difficult than measuring increased
922 growth, photosynthetic rates, or seed set. But the existing measurements do suggest that
923 the costs can be substantial. Among carnivorous plants with flypaper traps, carbon and
924 nutrients (in proteins) must be allocated to construction of specialized leaf glands,
925 sticky mucilage, and digestive enzymes. Pate (*unpublished data*, as cited in Pate 1986,
926 p. 320) reported that Australian *Drosera* spp. allocated 3-6% of net photosynthate to the
927 production of mucilage for leaf glands. In shaded conditions when light levels fell well
928 below photosynthetic saturation, *Pinguicula vallisneriifolia* reduced its mucilage
929 production, presumably because it lacked sufficient carbon (Zamora *et al.* 1998). At the
930 opposite extreme, when nutrients were added to the soil, *Drosera rotundifolia* reduced
931 its mucus gland production (Thorén *et al.* 2003). This result was attributable to the
932 avoidance of the costs of carnivory when nutrients were obtained at a lower carbon cost.

933 Similar plasticity has been observed in *Utricularia* spp. and *Sarracenia* spp.
934 When prey or dissolved nutrients were plentiful, the number of carnivorous bladders
935 declined significantly in *U. macrorhiza* Le Conte (Knight and Frost, 1991), *U. vulgaris*
936 (Friday, 1992), and *U. foliosa* (Guisande *et al.*, 2000, 2004). Bladder traps are
937 photosynthetically inefficient, and Knight (1992) calculated that *U. macrorhiza* of a
938 given mass without bladders would grow $1.2 - 4.7 \times$ faster than *U. macrorhiza* of the
939 same mass with bladders. Likewise, *Sarracenia purpurea* produced non-carnivorous
940 leaves (phyllodia) when inorganic nutrients were added to levels comparable to
941 atmospheric inputs from anthropogenic sources, and these phyllodia photosynthesized
942 ~25% faster than did carnivorous pitchers (Ellison and Gotelli, 2002). Similar results
943 were obtained for *S. purpurea* and eight other species of *Sarracenia* fed supplemental
944 prey (Farnsworth and Ellison, 2008). The related *Darlingtonia californica* had absolute
945 levels of A_{mass} of carnivorous plants that were 30-50% lower than predicted from
946 scaling relationships between leaf nitrogen content and A_{mass} of non-carnivorous plants
947 (Ellison and Farnsworth, 2005), and similar departures from the universal spectrum of
948 leaf traits have been observed for other species of *Sarracenia* (Farnsworth and Ellison,
949 2008).

950 Photosystems of carnivorous plants do appear to be nutrient-limited.
951 Fluorescence measurements of greenhouse-grown *Sarracenia* species suggested
952 significant “stress” of photosystem II at low levels of prey capture, and this stress was
953 alleviated by prey additions (Farnsworth and Ellison, 2008). Observations of spectral
954 reflectance also implied low chlorophyll content and similar photosystem stress in
955 *Nepenthes rafflesiana* in the field (Moran and Moran, 1998). Overall photosynthetic

956 nitrogen use efficiency ($\mu\text{mol CO}_2 \cdot \text{mol N} \cdot \text{s}^{-1}$; Aerts and Chapin, 2000) is 50% lower
957 for carnivorous plants than for non-carnivorous plants ($P = 1.3 \times 10^{-14}$, *t*-test; Fig. 7);
958 and photosynthetic phosphorus use efficiency is 60% lower for carnivorous plants than
959 for non-carnivorous plants ($P = 5.5 \times 10^{-7}$, *t*-test; Fig. 7). These data on photosynthetic
960 nutrient use efficiency further support the hypothesis that carnivorous plants are outliers
961 with respect to scaling relationships between tissue nutrient content and A_{mass} that have
962 been compiled for thousands of non-carnivorous species (Wright *et al.*, 2004, 2005).
963 However, the data for non-carnivorous plants come from a wide range of habitats and
964 plant life-forms. It is not known whether carnivorous plants have higher photosynthetic
965 nutrient use efficiencies than *co-occurring* non-carnivorous plants. However, there is no
966 evidence to suggest that carnivorous plants and non-carnivorous plants are actually
967 competing for nutrients (Brewer, 1999a, 1999b, 2003).

968

969 *Can carnivorous plants escape Hobson's Choice?*

970

971 *Where to elect there is but one,*

972 *'Tis Hobson's choice—take that, or none.*

973 (from *England's Reformation*, by Thomas Ward; 1710)

974

975 The observations that carnivory appears to be energetically costly, that excess nutrients
976 do not lead directly to increasing photosynthetic rates in existing leaves or traps, and
977 that photosynthetic nutrient use efficiency of carnivorous plants is extremely low led
978 Ellison and Farnsworth (2005) to suggest that botanical carnivory is an evolutionary

979 Hobson's Choice – the last resort when nutrients are scarcely available from the soil.

980 Two new lines of evidence challenge this interpretation, however.

981 First, two recent studies have shown that the actual energetic costs of
982 constructing carnivorous traps are significantly lower than the energetic costs of
983 constructing phyllodia of carnivorous plants (Osunkoya *et al.*, 2007; Karagatzides and
984 Ellison, 2008) or leaves of non-carnivorous plants (Fig. 8). These data include not only
985 “passive” traps (flypaper traps of *Drosera*, pitfall traps of *Nepenthes* and *Sarracenia*)
986 but also the “active” snap-traps of *Dionaea*. Thus, carnivorous traps are relatively
987 inexpensive structures that provide substantial nutrient gain for little energetic cost;
988 thus, it would take very little photosynthetic gain to yield a substantial *marginal*
989 benefit¹³ from a small investment in carnivory.

990 Not all active traps are equally active, however. The snap-trap of the Venus' fly-
991 trap uses a mechanical trigger (the mechanism of which is still poorly understood) to
992 passively release elastic energy stored in the fully hydrated leaf (Forterre *et al.*, 2005).
993 This relatively cheap trap is rarely reset; rather after one (rarely 2 or 3) captures, the trap
994 senesces (Darwin, 1875). In contrast, *Utricularia*'s suction trap is used multiple times,
995 and must be reset after it captures prey (Lloyd, 1942). Pumping out water is an
996 energetically expensive process, and how *Utricularia* bears this cost has come to light
997 only recently.

998 Jobson *et al.* (2004) found that the *coxI* gene in *Utricularia* has a markedly
999 different structure – with two contiguous cysteines – from that seen in 99.9% of *coxI*

13 The marginal benefit is the difference between the total photosynthetic increase resulting from nutrients gained from producing a new trap and the total photosynthetic cost of producing a trap as opposed to a phyllode or other photosynthetically more efficient structure)

1000 sequences recorded from Archaea, bacteria, or eukaryotes. This dicysteine motif causes
1001 a conformational change that at least partly decouples this protein's electron transport
1002 function from its proton pumping function. Laakkonen *et al.* (2006) estimated that this
1003 conformational change optimizes power output when the bladder trap is reset. Although
1004 there is an associated respiratory cost to this change, this cost ought to be offset by gains
1005 due to carnivory. Laakkonen *et al.* (2006) modified Givnish *et al.*'s (1984) original cost-
1006 benefit model to replace photosynthetic costs with respiratory costs. The rapid rate of
1007 gene substitution rates in *Utricularia* (Müller *et al.*, 2004; see Fig. 2) further suggests
1008 that once this mutation arose in *coxI*, selective pressures on *Utricularia* were relaxed
1009 and “runaway” morphological evolution occurred in this genus. Whereas this mutation
1010 in *coxI* has been completely or partially lost in *Genlisea*, its rapid rate of evolution has
1011 been attributed to the smaller energetic costs of the passive, albeit morphology complex,
1012 eel traps in that genus (Jobson *et al.*, 2004). Measurements of construction costs of traps
1013 in *Pinguicula*, *Genlisea*, and *Utricularia* would shed additional light on the generality
1014 of this hypothesis.

1015

1016 **Conclusions and directions for future research**

1017

1018 The integration of three research areas – the tempo and mode of carnivorous plant
1019 evolution as revealed through molecular analysis; the dynamics of prey capture
1020 illuminated with rigorous statistical analysis; and the physiological energetics of
1021 botanical carnivory in the context of cost-benefit models – has dramatically improved
1022 our understanding of many of the questions that Darwin first raised in *Insectivorous*

1023 *Plants*. This integration also permits the evaluation of existing hypotheses that may
1024 explain the evolution of carnivorous plants and the convergence of trap structures in a
1025 wide range of angiosperm lineages. The well-documented restriction of carnivorous
1026 plants to low-nutrient, high-light, and wet environments was explained
1027 phenomenologically by a cost-benefit model (Givnish *et al.*, 1984). Molecular data have
1028 revealed novel mutations and accelerated mutation rates in carnivorous plants,
1029 suggesting plausible alternative mechanisms underlying this phenomenological model
1030 (Jobson *et al.*, 2004; Müller *et al.*, 2004; Laakkonen *et al.*, 2006). Analysis of
1031 carnivorous plant nutrient physiology, trap and leaf construction costs, and overall
1032 physiological energetics support the hypothesis that mutations in *coxI* provide an
1033 energetic boost in the *Genlisea-Utricularia* clade. Statistical analyses support the
1034 hypotheses that carnivorous plants have evolved varying degrees of prey specialization
1035 (Figure 4), although there is no evidence for niche partitioning among co-existing
1036 congeners (Table 1).

1037 This review also raises unanswered questions and highlights research needs in
1038 the areas of carnivorous plant systematics and taxonomy, dynamics of prey capture, and
1039 physiological energetics. Priority areas include:

1040

1041 *Systematics and taxonomy*

- 1042 1. By identifying a key configurational change in *coxI*, Jobson *et al.* (2004) found a
1043 plausible molecular and physiological pathway to botanical carnivory. Are there
1044 alternative pathways that overcome the energetic costs of carnivory in other
1045 carnivorous plant lineages, including others within unrelated carnivorous groups

1046 within the Lamiales?

1047 2. Molecular data have strongly supported infrageneric morphology-based
1048 classification systems for the speciose carnivorous genera of *Utricularia* and
1049 *Genlisea*, but do not agree with morphological-based classifications of *Drosera*,
1050 *Pinguicula*, or *Sarracenia*. Better integration of morphological and molecular
1051 data (*cf.*, Williams et al., 1994), along with full genomic sequences of
1052 representative carnivorous plant species could help to resolve phylogenies of
1053 many groups of carnivorous plants

1054 3. Complete genomic data also would allow for less biased estimates of mutation
1055 rates in carnivorous plants relative to non-carnivorous plants, and could provide
1056 an explanation for the remarkably low C-values found in *Utricularia* and
1057 *Genlisea* (Greilhuber et al., 2006). C-values are well-known to be correlated
1058 with cell size (Gregory, 2001), which in turn may be correlated with bladder
1059 size. Further analysis of the relationship between trap size (and prey capture
1060 rates; see *e.g.*, Sanabria-Aranda *et al.*, 2006), cell size, and C-values of
1061 *Utricularia* would be illuminating.

1062 4. The genetic analyses to date have suggested some biogeographical anomalies.
1063 Examples include repeated transoceanic dispersal events in *Drosera*; repeated
1064 colonizations of the Indonesian islands by *Nepenthes*; and evidence that
1065 *Darlingtonia* is sister to a *Sarracenia-Heliamphora* clade. As better
1066 distributional data and genetic data become available, these should be explicitly
1067 linked (using tools such as GeoPhyloBuilder¹⁴) to create formal

14 https://www.nescent.org/wg_EvoViz/GeoPhyloBuilder

1068 phylogeographic hypotheses regarding the origin and diversification of
1069 carnivorous plants.

1070

1071 *Dynamics of prey capture*

1072 1. Prey capture data should be better resolved taxonomically; existing, order-level
1073 data clearly are quite coarse but family (and lower) level data are harder to come
1074 by. Specialization and niche segregation may become more apparent if prey are
1075 sorted to finer taxonomic levels.

1076 2. Measures of specialization, niche overlap, capture rate, and capture efficiency all
1077 are potentially biased without parallel measurements of available prey (*cf.*
1078 Gotelli and Graves, 1996) and prey size. Future studies of prey capture by
1079 carnivorous plants should also measure the relative abundance of potential prey
1080 in the surrounding habitat.

1081 3. The dichotomy between “passive” and “active” traps needs to be rethought.
1082 Darwin observed movement by the tentacular glands in *Drosera* and
1083 hypothesized selectivity in size of prey captured by *Dionaea*. Macbride (1818)
1084 proposed the existence of a frictionless peristome in *Sarracenia*, and Federle and
1085 his colleagues (Bohn and Federle, 2004; Bauer et al., 2008) found such
1086 frictionless surfaces in *Nepenthes*. The amount of friction, however, can be
1087 controlled either by environmental conditions (rain, fog) or by the plant itself
1088 (nectar secretion). Because hypotheses regarding the evolution and
1089 diversification of carnivorous plants depend, at least in part, on mechanisms and
1090 rates of prey capture, renewed attention should be focused on the activity of

1091 “passive” traps, especially in the pitcher plants and in *Genlisea*.
1092 4. Similarly, better assessment of the relative importance of environmental control
1093 and direct control by the plant itself of periphyton abundance on *Utricularia*
1094 traps and its role in prey capture will help to clarify exactly how active these
1095 traps are (Lloyd, 1942, Meyers 1982). Such studies also will expand the focus of
1096 research on prey capture by carnivorous plants beyond simple predator-prey
1097 models (*cf.* Ulanowicz, 1995; Díaz-Olarte *et al.*, 2007).

1098

1099 *Carnivorous plant energetics*

- 1100 1. The benefits of botanical carnivory are well-established (Ellison, 2006). More
1101 importantly, an assessment of the relationship (or lack thereof) between changes
1102 in growth rate and underlying ecophysiological processes such as photosynthesis
1103 and respiration or tissue nutrient content and stoichiometry (see Shipley, 2006)
1104 would unify the currently discordant data on responses of carnivorous plants to
1105 experimental prey and nutrient additions.
- 1106 2. Available data indicate that most responses to prey addition do not occur in the
1107 fed traps, but in traps and leaves that are subsequently produced (Butler and
1108 Ellison, 2007; Farnsworth and Ellison, 2008). Therefore, not only should future
1109 studies assess changes in A_{mass} in leaves produced subsequently to feeding, but
1110 they should also better delineate where nutrients are stored and how they are
1111 subsequently remobilized in current and future growing seasons. Stable isotopes
1112 can be used effectively for such studies (Butler and Ellison, 2007; Butler *et al.*,
1113 2008).

1114 3. Measurements of the costs of carnivorous structures have lagged well behind
1115 measurements of the benefits. Estimates of trap construction costs in the
1116 Lentibulariaceae and other carnivorous Lamiales are needed to complement
1117 existing data on Sarraceniaceae and carnivorous Caryophyllales.

1118 4. Many derived lineages of carnivorous plants have separated traps from
1119 photosynthetic structures: phyllodia of *Nepenthes*, *Cephalotus*, and *Sarracenia*;
1120 leaves of *Utricularia* and *Genlisea*; and loss of carnivory in *Triphyophyllum* as
1121 the plant matures (Green *et al.*, 1979). Detailed analysis of construction costs of
1122 traps and photosynthetic structures in these genera will provide additional
1123 insights into the true costs of botanical carnivory.

1124 5. How is the carbon derived from prey used by carnivorous plants? This last
1125 question is perhaps the most vexing and hearkens back to Darwin:

1126

1127 *“Most, however, of the plants belonging to these four classes*

1128 *[carnivorous plants that directly and indirectly digest prey, those that*

1129 *derive nutrients only from decaying litter, and parasitic plants] obtain*

1130 ***part of their carbon** [emphasis added] like ordinary species, from the*

1131 *atmosphere. Such are the diversified means, **as far as at present known***

1132 *[emphasis added], by which higher plants gain their subsistence.”*

1133 *(Insectivorous Plants, p. 367)*

1134

1135 Since Darwin's seminal publication, carnivorous plants have continued to

1136 provide general insights into the evolution and biogeography of plant lineages,

1137 the physiological ecology of nutrient uptake and use, and the evolution of leaf
1138 form. There is much yet to learn about these most wonderful plants in the world.

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1573 **Table 1.** Summary of null model analysis of niche overlap in prey utilization by
1574 congeneric carnivorous plants. Each row gives a different study and the number of
1575 coexisting congeneric species. **Observed** is the observed average pairwise niche
1576 overlap. **Expected** is the mean value of average pairwise niche overlap in 1000
1577 randomizations of the resource utilization data. The *P*-value is the upper tail probability
1578 of finding the observed pattern if the data were drawn from the null distribution.
1579

Genus	Site	Species	Niche overlap		<i>P</i>
			Observed	Expected	
<i>Sarracenia</i> ¹	Okaloosa County, Florida, USA	5	0.637	0.197	0.002
<i>Sarracenia</i> ²	Santa Rosa County, Florida, USA	2	0.996	0.128	0.038
<i>Sarracenia</i> ³	Turner County, Georgia, USA	3	0.634	0.235	0.013
<i>Sarracenia</i> ⁴	Brunswick County, N. Carolina, USA	3	0.975	0.128	0.001
<i>Drosera</i> ⁵	Baldwin County, Alabama, USA	3	0.880	0.241	0.001
<i>Drosera</i> ⁶	Santa Rosa County, Florida, USA	2	0.868	0.256	0.001
<i>Drosera</i> ⁷	Walton County, Florida, USA	2	0.738	0.205	0.031
<i>Drosera</i> ⁸	Chiemsee, S. Bavaria, Germany	2	0.708	0.226	0.045
<i>Drosera</i> ⁹	Eastern Netherlands	3	0.796	0.168	0.001
<i>Drosera</i> ¹⁰	Fitzgerald River, SW Australia	5	0.534	0.486	0.043
<i>Drosera</i> ¹¹	Murdoch University, SW Australia	3	0.801	0.614	0.001

- 1580 ¹*S. flava*, *S. leucophylla*, *S. rubra*, *S. purpurea*, *S. psittacina*; ²*S. flava*, *S. psittacina*; ³*S.*
- 1581 *flava*, *S. minor*, *S. psittacina*; ⁴*S. flava*, *S. purpurea*, *S. rubra*; ⁵*D. filiformis* Raf. var.
- 1582 *tracyi* (Macf. ex Diels) Diels, *D. intermedia* Hayne, *D. capillaris* Poir.; ⁶*D. intermedia*,
- 1583 *D. capillaris*; ⁷*D. filiformis* var. *tracyi*, *D. capillaris*; ⁸*D. rotundifolia* L., *D. intermedia*;
- 1584 ⁹*D. rotundifolia*, *D. intermedia*, *D. anglica* Huds.); ¹⁰*D. menziesii* R.Br. ex. DC, *D.*
- 1585 *drummondii* Lehm. [= *D. barbiger* Planch.], *D. glanduligera* Lehm., *D. paleacea* DC,
- 1586 *D. erythrorhiza* Lindl.; ¹¹*D. pallida* Lindl., *D. stolonifera* Endl., *D. menziesii*.

Figure Legends

1587

1588

1589 **Fig. 1.** Positions of carnivorous plant families in the current overall angiosperm
1590 phylogeny (Stevens 2007; relationships within the Lamiales from Müller *et al.*, 2006).
1591 Families that are exclusively carnivorous are set in bold-face type and highlighted in
1592 green; families with only one (Dioncophyllaceae) or two (Bromeliaceae) carnivorous
1593 genera are set in italic type and highlighted in yellow; and the family (Martyniaceae)
1594 with the possibly carnivorous *Ibicella lutea* v. Eselt. is set in italic type and highlighted
1595 in blue. Representative traps of each genus are illustrated (drawings by Elizabeth
1596 Farnsworth), and the number of species in each genus is given in parentheses. The
1597 phylogenetic tree was drawn using the MrEnt software package (Zuccon and Zuccon,
1598 2006); branch lengths are drawn only to emphasize the location of carnivorous families
1599 and otherwise are not meaningful (*i.e.*, do not signify time since divergence or any other
1600 metric of relatedness).

1601

1602 **Fig. 2.** Relative rates of gene substitution in carnivorous plant genera relative to the
1603 basal angiosperm (*Amborella* + Nymphaeales). Angiosperm taxa are arrayed on the *x*-
1604 axis from smallest to largest rates of *matK* substitution rates. The relative substitution
1605 rate on the *y*-axis is calculated as the difference between $K(\textit{Genlisea}, \textit{outgroup}) -$
1606 $K(\textit{other taxon}, \textit{outgroup})$, where $K(\textit{taxon}, \textit{outgroup}) =$ the maximum likelihood estimate
1607 of substitutions per site between the taxon and the outgroup (Müller, 2005). A rough
1608 estimate of the percentage difference in substitution rates between two carnivorous plant

1609 taxa can be found as $100 \times 1 - \frac{CP_1 - CP_2}{CP_1}$, where CP_i is the relative substitution rate of

1610 carnivorous plant species i (see text footnote 8 for caveats in using this estimator).

1611 Figure reprinted from Müller (2004) with permission of the author and the publisher,

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1613

1614 **Fig. 3.** Prey spectra of terrestrial carnivorous plant genera. The slices of each “star” plot

1615 are scaled to the average proportion of each prey taxon (order except for ants – family

1616 Formicidae). Only the 12 most common prey orders are shown. Key to the colors is

1617 given in the lower right of the figure.

1618

1619 **Fig. 4.** Results of the analysis of prey capture by seven carnivorous plant genera. **A** –

1620 Probability of interspecific encounter (*PIE*), or the probability that two prey items

1621 drawn at random from a trap are from different taxa. High values of *PIE* indicate less

1622 specialization on particular prey orders than do low values of *PIE*. **B** – proportion of

1623 ants in the prey captured by each genus. **C** – proportion of flies in the prey captured by

1624 each genus. For each variable, boxes illustrate the median (horizontal line), upper and

1625 lower quartiles (limits of the box), upper and lower deciles (limits of the vertical lines),

1626 and extreme values (individual points). The width of the box is proportional to the

1627 square-root of the sample size. Note that for *Brocchinia* and *Triphyophyllum* the sample

1628 size is only equal to 1 each, so there is no distribution from which to draw a box. The

1629 values for those two species are indicated by a single horizontal line.

1630

1631 **Fig. 5.** Results of the similarity analysis for four studies in which prey abundances were
1632 measured in carnivorous plants and in artificial traps in, or grab samples from, the same
1633 habitat. Prey taxon categories used were the same as in the original study, and
1634 microhabitat differences were retained in separate analyses. The value plotted is the
1635 Chao-Jaccard abundance-based similarity index J_{Chao} adjusted for unobserved taxa
1636 (Chao *et al.*, 2005); 95% parametric confidence intervals are derived from 1000
1637 bootstrap samples. If the interval includes 1.0 (gray vertical dotted line), then the J_{Chao}
1638 value does not differ from that expected given the null hypothesis that the distribution
1639 of prey captures by the plants is not different from that in the traps.

1640

1641 **Fig. 6.** Simulated frequency distributions of sizes of prey captured by the Venus' fly-
1642 trap, *Dionaea muscipula*, described by Darwin (1875; black bars) and Jones (1923; gray
1643 bars). The arrow indicates the average size of the *Dionaea* traps studied by Darwin
1644 (Jones did not report trap size).

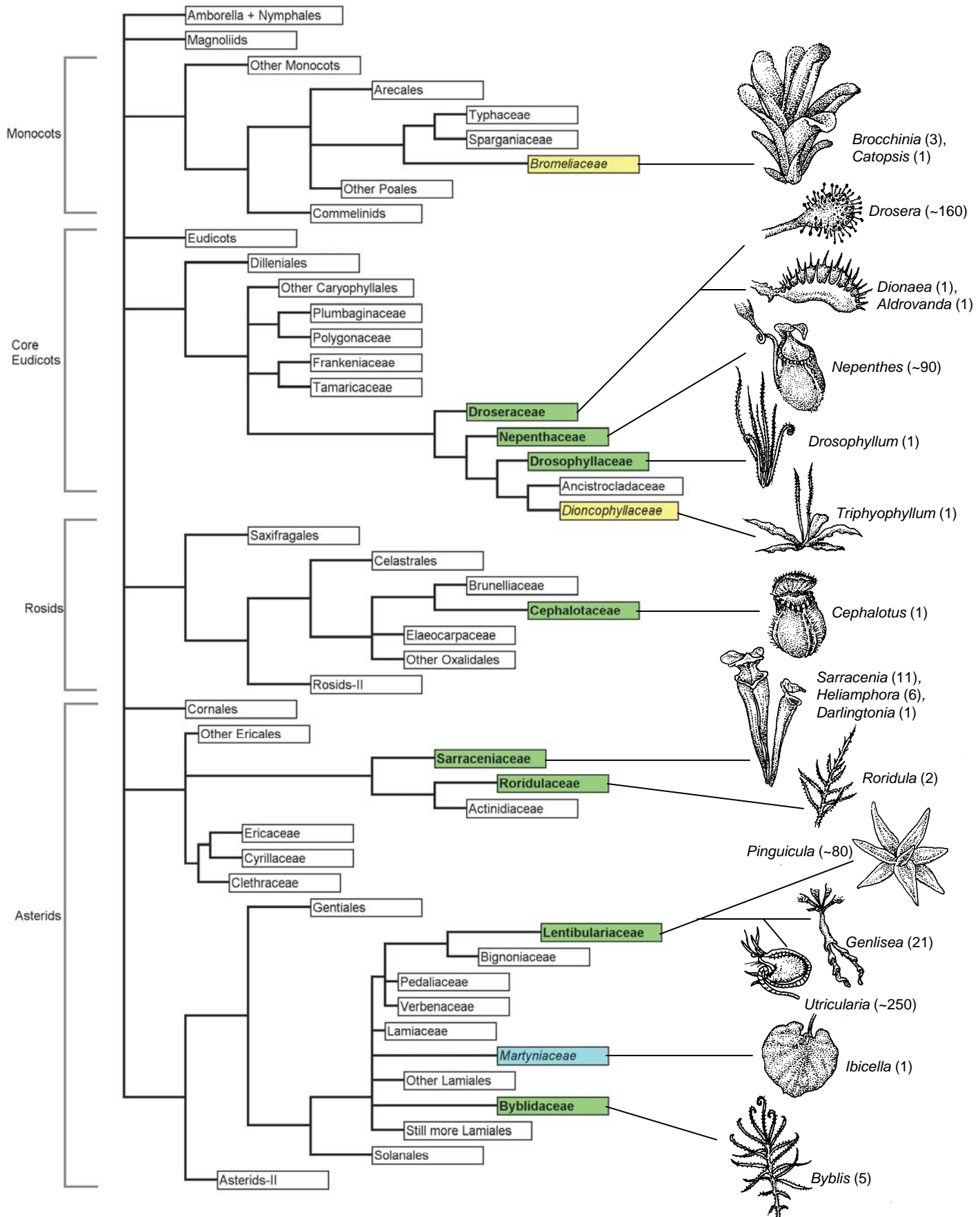
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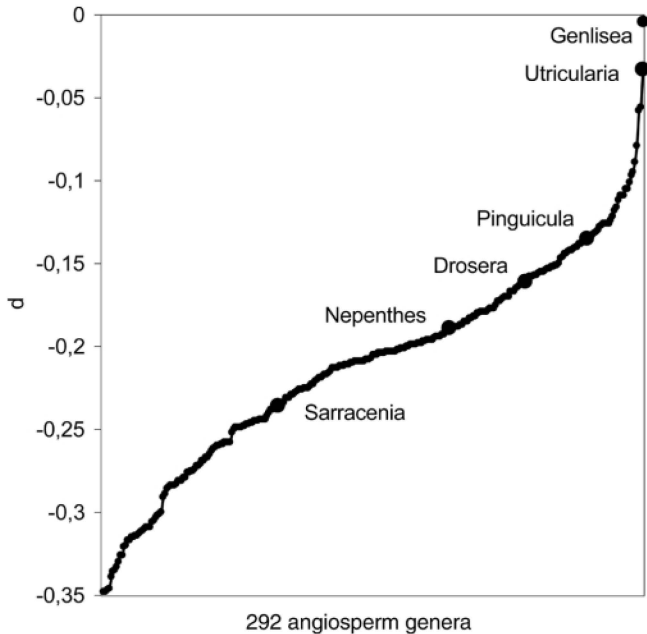
1646 **Fig. 7.** Photosynthetic nitrogen and phosphorus use efficiency by carnivorous plants and
1647 non-carnivorous plants. Data for carnivorous plants from Weiss (1980), Knight (1992),
1648 Adamec (1997), Méndez and Karlsson (1999), Wakefield *et al.* (2005), Ellison and
1649 Farnsworth (2005), Farnsworth and Ellison (2008), and Karagtzides and Ellison (2008).
1650 Data for non-carnivorous plants from Wright *et al.* (2004) and Santiago and Wright
1651 (2007).

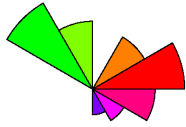
1652

1653 **Fig. 8.** Box-plots illustrating leaf construction costs for traps of 23 carnivorous plants
1654 (data from Osunkoya *et al.*, 2007; Karagatzides and Ellison, 2008) and 269 non-
1655 carnivorous plants (data summarized in Karagatzides and Ellison, 2008)¹⁵. The scatter-
1656 plot illustrates the difference between construction costs of traps and laminae of
1657 *Nepenthes* (solid symbols); or phyllodia and pitchers of three species of *Sarracenia*
1658 (open symbols) (data from Osunkoya *et al.*, 2007; Karagatzides and Ellison, 2008); the
1659 dotted line indicates the location where the construction costs of traps and laminae
1660 would be equal.

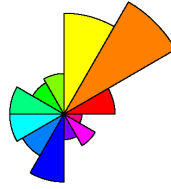
15 Data available from the Harvard Forest Data Archive, dataset HF-112:
<http://harvardforest.fas.harvard.edu/data/p11/hfX112/hf112.html>



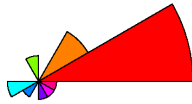




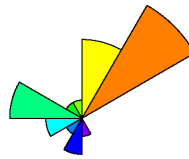
Dionaea



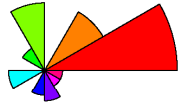
Drosera



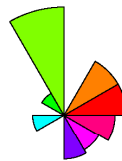
Nepenthes



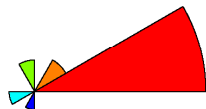
Pinguicula



Sarracenia



Triphyophyllum



Brocchinia

