Carnivorous Plants: Phylogeny and Structural Evolution

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The carnivorous habit in flowering plants represents a grade of structural organization. Different morphological features associated with the attraction, trapping, and digestion of prey characterize a diversity of specialized forms, including the familiar pitcher and flypaper traps. Phylogenetic analysis of nucleotide sequence data from the plastid *rbc*L gene indicates that both carnivory and stereotyped trap forms have arisen independently in different lineages of angiosperms. Furthermore, these results demonstrate that flypaper traps share close common ancestry with all other trap forms. Recognition of these patterns of diversification may provide ideal, naturally occurring systems for studies of developmental processes underlying macromorphological evolution in angiosperms.

The carnivorous syndrome in flowering plants represents a highly integrated interaction of form and function. Carnivory involves morphological features associated with the attraction, retention, trapping, killing, and digestion of animals and absorption of their nutrients (*1*). Variation in these parameters characterizes a diversity of specialized forms, including the familiar flypaper and pitcher traps as well as the snap-traps of *Dionaea* and the suctioning bladders of *Utricularia*. The literature of carnivorous plants is replete with ontogenetic hypotheses of structural evolution, from the mechanism of epiascidiation (inrolling of the adaxial leaf surface followed by marginal fusion) in pitcher traps (*1*) to the derivation of *Dionaea* trigger hairs (*1, 2*) and shoot-leaf indistinctness in *Utricularia* (*3*). Accordingly, carnivorous plants provide an opportunity to uncover macroevolutionary patterns and processes that may be generalized to other structural phenomena in angiosperms. Here, we describe carnivore diversity from its own historical (namely, phylogenetic) perspective.

Carnivorous angiosperms have been used as model systems for anatomical and physiological studies of responsive movement and glandular secretion since the pioneering and exhaustive experiments of Charles Darwin (*1, 2, 4, 5*). Much like his other works after *Origin of the Species*, Darwin's primary message in *Insectivorous Plants* (*5*) was the importance of these specialized organisms to the emerging field of evolutionary biology (*6*). Accordingly, carnivores have often been subjects of adaptationist arguments. Darwin himself hypothesized that carnivory resulted from natural selection operating on preexisting variation. Specifically, he implicated sticky, insect-catching glands with digestive properties, a feature that many carnivorous plants share (*5*). A more recent hypothesis concerns the evolution of pitcher-bearing carnivores; epiascidiation of nectary-bearing leaves might have conferred an immediate advantage through novel capacities of water storage and nutrient absorption (*1*). Both of these scenarios invoke natural selection and suggest orthogenetic (directional) tendencies (*7*) in different phylogenetic groups (if carnivorous plants do not have a unique origin).

Léon Croizat devoted 232 pages of his monumental *Principia Botanica* to the dispersal and morphogeny of carnivorous plants in an explicit attempt to provide orthogenetic links among all carnivores (*8*). He even provided a carnivorous ancestor, defined as "a morphogenetic and phylogenetic average qualified to fit everything—by tendency . . . along a broad trajectory of evolution . . ." (*8*). According to Croizat, evolution equals time plus space plus form. Nevertheless, evolutionary explanations that invoke underlying tendencies, potentials, or constraints (*7*) add an unnecessary layer of presumption to empirically observed patterns. We therefore argue that mechanistic speculations cannot be evaluated in the absence of an explicit phylogenetic framework. Strong inferences about both phylogeny and character evolution can be made objectively using minimal ad hoc assumptions (*9*).

Prospectus

From the taxonomy of his day, Darwin imagined several independent origins of carnivory among flowering plants (*5*). Indeed, this conjecture has been widely accepted by 20th-century systematists but not without substantial disagreement as to carnivore interrelationships and their placement among other angiosperms (*10–13*).

For a phylogenetic perspective on carnivorous plants, we limited ourselves to data with substantial independence from trap form. Here, we discuss aspects of carnivore structural evolution with respect to a cladistic analysis of nucleotide sequence variation. In agreement with Darwin, our results indicate that carnivorous plants and their associated syndrome of features have multiple origins among angiosperms. At variance with Darwin's ideas are (i) the phylogenetic dispersion (polyphyly) of structurally similar flypaper traps and (ii) their repetitive patterns of common ancestry with other trap forms. For example, the three pitcher-plant groups appear to be only distantly related, yet two are closely associated with independent, flypaper-trap groups. Among the carnivores, structural homologies do not necessarily correlate with trap form, and similar trap forms may not be structurally homologous. The carnivorous habit is thus a grade of organization that exhibits themes of both convergent and divergent evolution.

Phylogenetic Relationships

Hypotheses of carnivorous plant phylogeny involve hypotheses about structural relationships. To remain as free as possible from ad hoc assertions about structural homologies, we have used genotypic rather than morphological characters for phylogenetic reconstruction. The plastid gene *rbc*L encodes the large subunit of ribulose-1,5-bisphosphate carboxylase/oxygenase (RuBisCO), a primary enzyme in the Calvin-Benson cycle (*14*). Rates of nucleotide substitution in *rbc*L are amenable to parsimony analyses at many levels within seed plants (*15*). Nevertheless, phylogenetic hypotheses from *rbc*L sequence variation represent gene trees, which may or may not depict the true organismal tree with relative accuracy (*16*). For the present purpose, our assumption is that the proportion of reliable historical evidence in *rbc*L sequences is sufficient to address gross phylogenetic relationships among angiosperms and patterns of structural evolution in carnivorous plants (*17*).

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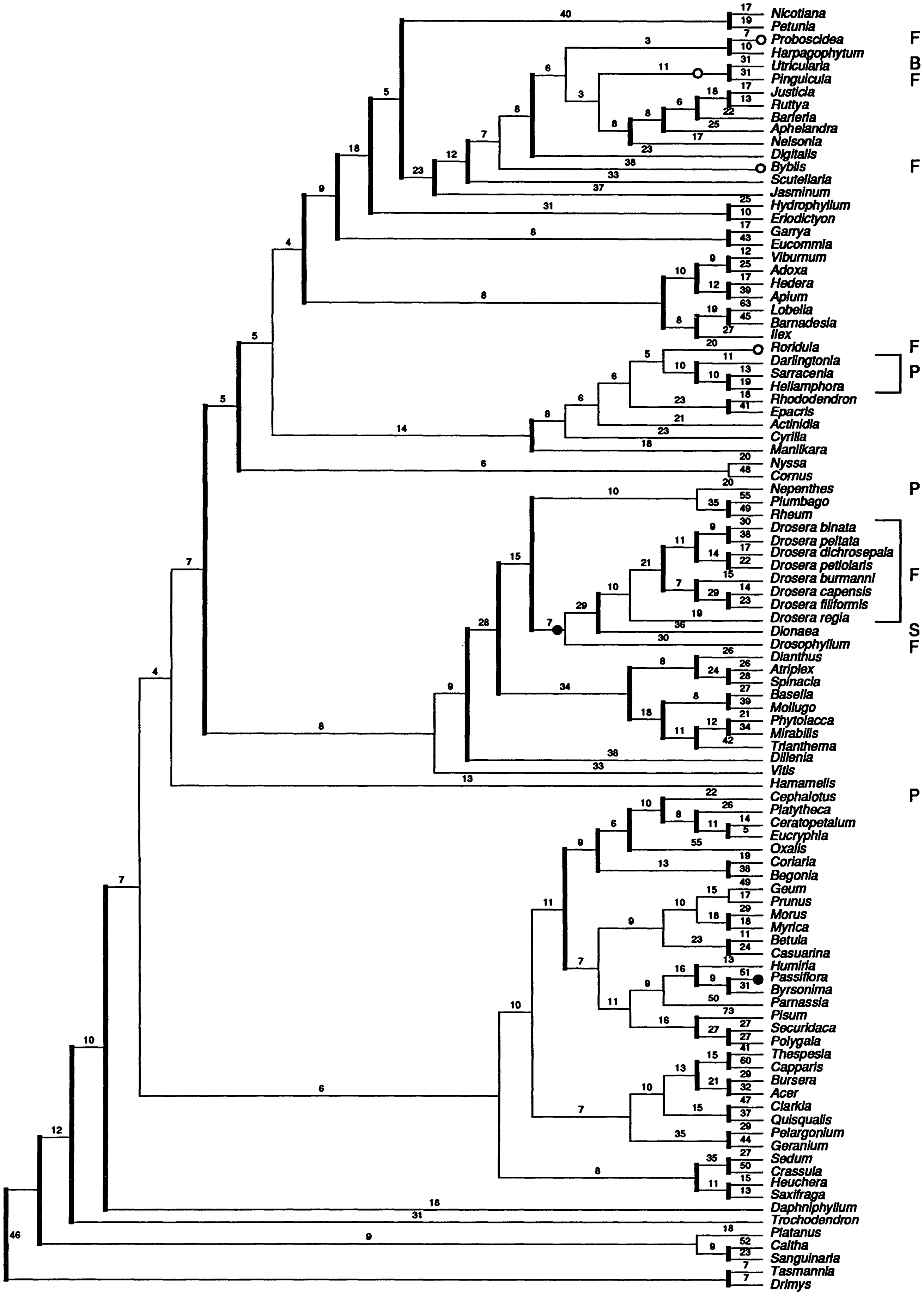
Nicotiana
Petunia
Proboscidea
F
Harpagophytum
Utricularia
B
Pinguicula
F
Justicia
Ruttya
Barleria
Aphelandra
Nelsonia
Digitalis
Byblis
F
Scutellaria
Jasminum
Hydrophyllum
Eriodictyon
Garrya
Eucommia
Viburnum
Adoxa
Hedera
Apium
Lobelia
Barnadesia
Ilex
Roridula
F
Darlingtonia
Sarracenia
P
Heliamphora
Rhododendron
Epacris
Actinidia
Cyrilla
Manilkara
Nyssa
Cornus
Nepenthes
P
Plumbago
Rheum
Drosera binata
Drosera peltata
Drosera dichrosepala
Drosera petiolaris
Drosera burmanni
F
Drosera capensis
Drosera filiformis
Drosera regia
Dionaea
S
Drosophyllum
F
Dianthus
Atriplex
Spinacia
Basella
Mollugo
Phytolacca
Mirabilis
Trianthema
Dillenia
Vitis
Hamamelis
Cephalotus
P
Platytheca
Ceratopetalum
Eucryphia
Oxalis
Coriaria
Begonia
Geum
Prunus
Morus
Myrica
Betula
Casuarina
Humiria
Passiflora
Byrsonima
Parnassia
Pisum
Securidaca
Polygala
Thespesia
Capparis
Bursera
Acer
Clarkia
Quisqualis
Pelargonium
Geranium
Sedum
Crassula
Heuchera
Saxifraga
Daphniphyllum
Trochodendron
Platanus
Caltha
Sanguinaria
Tasmannia
Drimys

An exploratory parsimony analysis of *rbc*L nucleotide sequences from 475 seed plants included information for several carnivores (*18*). The results suggested that there were at least six origins of carnivory among different groups of angiosperms. Using this heuristic study as a guide, we selected 100 dicotyledonous taxa [including additional carnivores (*19*)] for more rigorous treatment [carnivorous bromeliads (*20*), the only monocotyledonous carnivores, were not considered further]. Parsimony analysis of this smaller data set (*21*) replicates most of the taxonomic patterns found in the larger study and suggests similar relationships among the carnivorous taxa (Fig. 1).

Fig. 1 (**facing page**). Phylogenetic hypothesis of carnivorous plant relationships based upon cladistic analysis of sequence variation in the plastid *rbc*L gene. An even taxonomic sampling including taxa from 72 families [sensu Thorne (*13*)] was guided by the results of a larger, exploratory parsimony analysis (*18*); all major eudicot groups are represented (*38*), with *Tasmannia* and *Drimys* (Winteraceae) included to provide outgroup orientation [see (*36*)]. The topology shown is one of 396 maximum parsimony trees found (*21*); it was selected for display because of its substantial congruence with earlier results (*18*). Branch lengths in terms of inferred nucleotide changes under the accelerated transformation optimization (*26*) are indicated. The strict consensus (*39*) of all equally parsimonious trees is shown on the topology by bold vertical lines connecting branches compatible among all trees. The overall relationships are sufficiently preserved in consensus to address the questions at hand. Carnivorous dicotyledons are unambiguously polyphyletic. As many as seven independent origins of the syndrome can be hypothesized. Flypaper (**F**) and pitcher (**P**) traps appear independently five and three times, respectively. These trap forms co-occur in the same lineages twice [*Roridula* sister to Sarraceniaceae; *Nepenthes* proximal to Droseraceae (*40*)]. Flypaper traps are associated with divergent trap forms in two lineages: *Utricularia* (bladder: **B**) in Lentibulariaceae, and *Dionaea* (snap: **S**) in Droseraceae. Character evolution in flypaper traps was studied by optimization of specific character states. If the flypaper trapping mechanism is considered structurally homologous (that is, the apomorphic or derived state) across all relevant taxa, then moderate homoplastic tendencies of both clustering and localization are apparent [filled and open circles; see (*27*)]; a prominent cluster is found in the Bignoniales, and localization is restricted to the upper half of the tree. However, the nonhomologous glandular anatomy of flypaper traps suggests two characters to be optimized: elaboration of epidermal tissues [open circles; see (*1*)] versus altered differentiation of parenchyma, vascular strands, and epidermal tissues [filled circles; see (*1, 28*)] in the formation of stalked, secretory glands. The apomorphic state of the former is strongly clustered among bignonialean carnivores, but its presence in *Roridula* and numerous other noncarnivorous taxa represented here [see (*11*)] render this characteristic more likely plesiomorphous (ancestral) than apomorphous for the eudicots. Vascularized glands as described above are present only in Droseraceae, Passifloraceae, *Triphyophyllum*, and Turneraceae (*28*). The apomorphic state is once homoplastic on this tree (*Triphyophyllum* and Turneraceae were unavailable for study), showing neither clustering nor localization.

In parallel with the carnivorous syndrome, stereotyped trapping mechanisms show a disjunct (polyphyletic) distribution. Flypaper traps have five separate origins among dicotyledons, whereas pitcher traps have three (Fig. 1). Unexpectedly, these trap types co-occur in two lineages: the Sarraceniaceae (American pitcher plants) are sister to *Roridula* [the South African fly bush; a trapper but unconfirmed carnivore (*22*)], and *Nepenthes* (Old World pitcher plants) and Droseraceae (sundews plus *Dionaea*, the Venus flytrap) are members of the same clade. *Cephalotus* (the Australian pitcher plant) is phylogenetically distant from other known carnivores. The remaining flypaper traps are separated into three distinct lineages of Bignoniales sensu Thorne (*13*): *Proboscidea* [the unicorn plant, representing Martyniaceae (*23*)], Lentibulariaceae, and *Byblis* (the rainbow plant). The Lentibulariaceae include flypaper-trapping *Pinguicula* (butterworts) as well as *Utricularia* (bladderworts) with unique, aquatic suction traps. Although *Byblis* is resolved as sister to the Lentibulariaceae in analyses focusing on bignonialean relationships (*24*), the sparser sampling of appropriate taxa in our analysis does not show this relationship at maximum parsimony.

We addressed the internal (that is, data-dependent) robustness of these phylogenetic statements using forced-topology experiments (*25*). The surprising results [such as the placement of *Byblis* within Bignoniales rather than Saxifragales sensu Takhtajan (*12*); Fig. 1] hold up strongly under the parsimony criterion. The particular flypaper–pitcher-trap relationships outlined above are similarly well supported (*25*).

Another line of inference that may be drawn from our phylogenetic results is with regard to the evolution of morphological and anatomical characters pertinent to carnivory. Patterns of character evolution were studied a posteriori by optimization of character states onto the *rbc*L-based cladogram (Fig. 1) (*26*). It is from this approach that tendencies may be addressed within a phylogenetic framework (*27*). For example, Darwin (*5*) envisioned that the flypaper mechanisms of Droseraceae, *Roridula*, and *Byblis* were homologous (that is, derived from a common ancestor). Under this assumption, homoplastic (parallel) tendencies in glandular evolution may be invoked, as flypaper-trap lineages are moderately clustered and localized on the cladogram (*27*). However, if the glandular apparati of flypaper traps are considered to be separate (that is, nonhomologous) characters on the basis of their different anatomies, the homoplastic tendency disappears (see Fig. 1).

Patterns in Structural Evolution

The phylogenetic relationships of carnivorous plants (Fig. 1) suggest that there is a hierarchy of convergent evolution from the level of the syndrome itself to the distribution of trap forms, their phyletic co-occurrence, and details of their functional morphology. This hierarchy is well illustrated by comparison of the bignonialean carnivores with those of the Droseraceae. For example, *Byblis* and *Drosophyllum* both have flypaper traps. *Byblis* is a topological neighbor of *Utricularia*, which has bladder-like suction traps. *Drosophyllum* is closely related to *Nepenthes*, a pitcher plant (Fig. 1). *Byblis* and *Drosophyllum* share such characteristics as woodiness, filiform leaves with reverse circination (that is, with croziers curling over abaxial surfaces), and dimorphic stalked and sessile glands (*1*). In both taxa, the stalked glands secrete mucilage that entangles and encoats prey, and the sessile glands secrete hydrolytic digestive fluids. However, the mucilage-secreting glands of *Byblis* have unicellular stalks protruding from epidermal reservoir cells, whereas those of *Drosophyllum* are multicellular and vascularized by five to ten tracheids and associated phloem. The sessile digestive glands of *Byblis* are relatively simple with four to eight head cells, whereas those of *Drosophyllum* are multicellular and layered. These distinct patterns of gland anatomy are recapitulated, albeit with modification, in (i) *Pinguicula*, *Utricularia*, and Martyniaceae (Bignoniales) and (ii) *Drosera* and *Dionaea* (Droseraceae) (*1*). Although members of each group have homologous glandular anatomy, the trapping mechanism is grossly divergent in taxa such as *Utricularia* and *Dionaea*. Conversely, the flypaper anatomy of *Byblis* and *Drosophyllum* is nonhomologous despite the remarkable extent of structural and functional similarity. Therefore, form is not a reliable indicator of phylogenetic relationships among carnivorous plants at highly inclusive levels (such as trapping mechanism), whereas it appears to be at less inclusive ones (such as glandular anatomy).

The Droseraceae-*Nepenthes* cluster is exemplary of structural evolution in a monophyletic lineage. A key taxon for integrating the group is the rare African carnivore *Triphyophyllum* (*28*). Although unavailable for our molecular-phylogenetic study, *Triphyophyllum* can be placed with this clade a posteriori: its vexing combination of Droseraceae-specific and *Nepenthes*-specific character states (*28*) becomes simplified when these two groups are brought into phylogenetic proximity (Fig. 1). *Triphyophyllum* is heterophyllous, producing three distinct leaf types that correlate with phases of maturation. Juvenile leaves with a condensed spiral phyllotaxy are borne on short shoots approximately 50 cm in height. They are of two types: (i) laminate and eglandular, or (ii) filiform with stalked and sessile glands. Transitional forms sometimes occur in which the basal lamina abruptly shifts to the filiform, glandular state. A phase shift of another kind occurs when juvenile shoots rapidly elongate to form a liana, which may be 50 m long at maturity. The lianas bear only leaves of the third type. These are eglandular but have terminal midrib extensions bearing paired, crozier-like hooks reminiscent of tendrils on *Nepenthes* (*28*). *Nepenthes* displays a similar phase shift from condensed short shoots to elongate growth; each phase bears morphologically distinct pitchers (*1*, *29*). Some *Drosera* species (for example, *D. peltata*) also show this pattern, beginning as juvenile rosettes and elongating upon maturity. Leaf form also shifts from spathulate to peltate in these taxa. Other Droseraceae mature in the rosette form (*30, 31*).

Despite its provisional systematic affinities, *Triphyophyllum* provides a morphogenetic link between all carnivores of the Droseraceae-*Nepenthes* group. Concerning phylogenetic relationships, the trapping mechanism of *Triphyophyllum* appears to be structurally homologous to that of *Drosophyllum* (*28*). The filiform leaves of *Triphyophyllum* are reversely circinate and its stalked and sessile glands are anatomically comparable to those of *Drosophyllum*, albeit more elaborate. Like *Drosophyllum* and *Drosera*, both gland types are fully vascularized in *Triphyophyllum*. Vascular organization in the glandular appendages of *Triphyophyllum* is typically leaf-like, although differentiation of other cells has been altered from leaf-blade production. With strong evidence of both morphogenetic and phylogenetic patterns in hand, integrating hypotheses about structural evolutionary processes can be evaluated.

Process Hypotheses

The switch from laminate to glandular states within single leaves of *Triphyophyllum* suggests that a transmissible stimulus may be responsible for altering the pattern of differentiation. Indeed, many aspects of plant morphogenesis are known to be controlled by transmissible phytohormones: apical dominance, vascular differentiation, heterophyllous determination of leaf form, phase-shifting from adult to juvenile plant morphology, and elongate growth before flowering (bolting) in rosette plants (*32*). In a possible response to release from apical dominance, axillary short shoots of *Triphyophyllum* will again produce juvenile, glandular leaves if the elongate stem of a mature liana is removed (*28*). *Triphyophyllum* is not readily available for study, but its putative relatives in the Droseraceae may provide model systems for developmental and physiological experiments that could address specific roles for phytohormones in macromorphological evolution.

Processes such as changes in the timing or placement of developmental events (*33*) may be implicated in the evolutionary history of the genus *Drosera*. If leaves without specialized trapping glands and stem elongation represent ancestral conditions in adult plants of the Droseraceae-*Nepenthes* group (compare *Triphyophyllum* with *Nepenthes* and related taxa such as *Plumbago*, *Rheum* and Chenopodianae sensu Thorne; Fig. 1), then leaves with stalked or sessile glands and maturation as a basal rosette may result from paedomorphic development (juvenilization) (*34*). In addition to typical laminate appendages, some Australian sundews (for example, *D. dichrosepala*) produce specialized leaves with terminal, abscising propagules. These gemmae consist of nutritive tissue and embryonic leaf and root structures (*31*); their appearance in place of the trapping lamina is clearly homeotic and more likely represents a shift in cell differentiation rather than development of a de novo structure (*35*).

Synthesis

Carnivorous plants present a mixture of homology and analogy in structural evolution. The phylogenetic perspective developed here has permitted the recognition of patterns of (i) structural convergence from separate ancestry, and (ii) structural divergence from common ancestry. Thus, form and function appear to be tightly coupled in the broad sense of the carnivorous syndrome itself (for example, in *Byblis* and *Drosophyllum*), but only loosely coupled in terms of trap-form diversity in monophyletic lineages (for example, the Lentibulariaceae). From a phylogenetic perspective, carnivory is polyphyletic (Fig. 1). Homology versus analogy in structural gestalts such as pitcher plant, which arose from the interaction between form and function, has become discernable. This distinction is of immediate importance in defining patterns in the evolutionary history of this unusual syndrome; structural homologies of pitcher traps (*1*), for example, may now be sought in phylogenetically related taxa. Carnivorous plants provide a conspicuous example of the need for phylogenetic information in all studies of angiosperm form and function.

Indeed, the complex, hierarchical nature of convergent evolution observed between distantly related carnivorous plants (such as *Byblis* and *Drosophyllum*) mirrors other highly integrated structure-function relationships that are similarly polyphyletic in angiosperms [for example, the water lily habit (*36*) as well as C_4 photosynthesis (*37*)]. The independent evolution of such inclusive suites of characteristics in carnivorous plants might reflect underlying morphogenetic phenomena [such as heterochrony and homeosis (*33*)], which are themselves patterns of less-inclusive processes [such as phytohormone regulation (*32*)]. In turn, such considerations may be generalized to other aspects of angiosperm structural evolution. Beyond the assumptions discussed here lies the unknown importance of forces such as natural selection and orthogenesis. Despite blindness to these issues, the understanding gained from phylogenetic hypotheses of structural evolutionary patterns in carnivorous plants suggests an area of research that could profoundly affect our understanding of angiosperm macroevolution.

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7. Orthogenetic tendencies are thought to be determined by some factors internal to organisms, rather than by natural selection. J. R. Grehan and R. Ainsworth [*Syst. Zool.* **34**, 174 (1985)] argue that Darwin's laws of growth were orthogenetic, as are all modern discussions of constraints, biases, and potentials. See, for example, the somewhat contradictory discussion by S. J. Gould and R. C. Lewontin [*Proc. R Soc. London Ser. B* **205**, 581 (1979)] of "unknown and perhaps 'internal' mechanisms . . . [being] close to an appeal to mysticism" (p. 593) versus their recognition of phyletic, developmental, and architectural constraints.
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15. Rates calculated for *rbc*L range between approximately 5×10^{-11} and 5×10^{-10} total substitu-

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17. In addition to the considerations addressed in (*15*), physiological correlates in *rbc*L sequence evolution should be minimal. Although specific differences in *rbc*L sequence among C_3 and C_4 species pairs within three separate angiosperm genera may parallel different RuBisCO kinetics [G. S. Hudson *et al.*, *J. Biol. Chem.* **265**, 808 (1990)], parsimony analysis readily discerns generic affinities [V. A. Albert and M. W. Chase, unpublished data]. Correspondingly, partial heterotrophy in carnivorous plants is not expected to confound phylogenetic analysis through correlated nucleotide substitutions.
18. M. W. Chase and V. A. Albert, unpublished data.
19. Previously unavailable *rbc*L sequences were determined for the following taxa: *Byblis liniflora, Darlingtonia californica, Heliamphora nutans, Dionaea muscipula, Drosera binata, Drosera burmanni, Drosera capensis, Drosera dichrosepala, Drosera peltata, Drosera petiolaris, Drosera regia,* and *Drosophyllum lusitanicum.* These were obtained by amplification [R. K. Saiki *et al.*, *Science* **239**, 487 (1988)] from whole-cell DNA preparations, cloning of the product into Bluescript + vector (Stratagene, Inc.), and dideoxy nucleotide sequencing [F. Sanger, S. Nicklein, A. R. Coulson, *Proc. Natl. Acad. Sci. U.S.A.* **74**, 5463 (1977); M. Hattori and Y. Sakaki, *Anal. Biochem.* **152**, 232 (1986)]. Amplification was accomplished using primers containing engineered restriction sites (underlined) [forward: 5′-TGTGTTGTCGAC**ATG**TCACCACAAACAGAAACTAAAGC-3′ (Sal I; methionine initiation codon in bold), reverse: 5′-GTCGACGCGGCCGCTTTTTGAGGAAAGATTGGGCCAAG-3′, or (from position 1352): 5′-TGTGTTGCGGCCGCCTTCACAAGCAGCAGCTAGTTCAGGACTCC-3′ (Not I)]. These permitted sequencing of the entire coding region (1428 base pairs or greater, excluding 26 nucleotides of the forward primer), except when the 1352 reverse primer was used (up to 1325 base pairs recovered). Internal sequencing primers were designed by G. Zurawski. The GenBank accession numbers for the 81 previously unpublished sequences are L01881 through L01961 and M95754.
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21. Parsimony analysis of *rbc*L sequence data for 100 taxa (*19*) was accomplished using PAUP 3.0s [D. L. Swofford, *PAUP: Phylogenetic Analysis Using Parsimony, Version 3.0s* (Illinois Natural History Survey, Champaign, IL, 1991)]. To exclude all primer sequences (which vary from 26 to 30 5′ base pairs), nucleotides before position 31 were ignored. Equal weighting of nucleotide transformations was performed under the Fitch criterion [W. M. Fitch, *Syst. Zool.* **20**, 406 (1971)] with ACCTRAN (accelerated transformation) optimization. Because of the software and hardware limitations put on a data matrix of this size, we used a successive and approximate search strategy (beginning with SIMPLE data addition sequence) to maximize both the parsimony and number of trees found. Aware of the possibility of islands of equally parsimonious trees [D. R. Maddison, *Syst. Zool.* **40**, 315 (1991)], we used the MULPARS, STEEPEST DESCENT, and KEEP options at appropriate points in the search. NNI (nearest neighbor interchange) and TBR (tree bisection-reconnection) branch-swapping routines were used successively on most-optimal trees found from earlier runs. At one stage, 132 trees of 4066 steps (which we infer to be the maximum-parsimony length including all of the data) were found with TBR branch swapping. Using the above options, we then performed NNI branch swapping on these trees to save the original 132 plus approximately 4500 trees one step longer; NNI swapping on all of these found another 264 trees of length 4066 (presumably representing additional islands of trees separated by suboptimal branch-swaps). The 396 trees found at this length form the basis of our study. The consistency and retention indices for these trees are 0.281 and 0.528, respectively [see A. G. Kluge and J. S. Farris, *Syst. Zool.* **18**, 1 (1969); J. S. Farris, *Cladistics* **5**, 417 (1989); P. A. Goloboff, *ibid.* **7**, 215 (1991)].
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25. Because the search for maximum parsimony trees was computer-intensive (*21*), separate analyses using prespecified topological constraints were not technically feasible. We therefore used a compromise, a posteriori procedure to examine the number of extra steps required for alternative taxon placements. The tree from Fig. 1 was manipulated (in its parenthetical notation format) to create several topologies with different assumptions about carnivorous plant relationships. Although Fig. 1 shows only one of the 396 maximum parsimony trees (*21*), relative uniformity among them is indicated by the large number of components retained by strict consensus (as shown in Fig. 1). Therefore, the extra steps calculated for these forced relationships would likely be similar for any of the 396 trees [4066 steps (*21*) *Roridula* placed sister to *Byblis* [see (*10, 11*)]—51 extra steps; *Byblis* placed sister to *Roridula*—44; *Byblis* placed sister to Droseraceae—56; *Byblis* plus *Roridula* placed sister to *Droseraceae* [see (*5*)]—76; *Byblis* plus *Roridula* placed sister to *Cephalotus* [see (*1, 12*)]—90; *Cephalotus* placed sister to Droseraceae [see (*13*)]—54; *Cephalotus* placed sister to *Nepenthes*—56; *Cephalotus* placed sister to Sarraceniaceae—45; *Nepenthes* placed sister to Sarraceniaceae [see (*1, 11*)]—52; Sarraceniaceae placed sister to *Nepenthes*—50; Sarraceniaceae and *Nepenthes* switched—96. The following relationships were substantially closer to maximum parsimony: *Byblis* placed sister to Lentibulariaceae (*18, 24*)—4 extra steps; *Proboscidea* placed sister to *Byblis* plus Lentibulariaceae—7; *Nepenthes* placed sister to Droseraceae—6.
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40. The sister-group relationship of Droseraceae to *Nepenthes* plus *Plumbago* and *Rheum* is not compatible with a single loss of the plastid *rpl2* intron in the common ancestor of this clade and the Chenopodianae sensu Thorne (*13*). However, this loss is clearly polyphyletic among angiosperms, so our results could indicate parallel losses in closely related lineages. See S. R. Downie *et al.* [*Evolution* **45**, 1245 (1991)] and S. R. Downie and J. D. Palmer [in *Molecular Systematics of Plants*, P. S. Soltis, D. E. Soltis, J. J. Doyle, Eds. (Chapman and Hall, New York, 1992), pp. 14–35].

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