CHAPTER
4

Saltational evolution of form in vascular plants: a neoGoldschmidtian synthesis

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CONTENTS

Abstract

Saltational evolution, a much abused term, is here narrowly defined as a genetic modification that is expressed as a profound phenotypic change across a single generation and results in a potentially independent evolutionary lineage (prospecies: 'hopeful monster' of Richard Goldschmidt). Dichotomous saltation is driven by mutation within a single ancestral lineage, and can result not only in instantaneous speciation but also in the simultaneous origin of a supraspecific taxon. Reticulate saltation is driven by allopolyploidy and thus incorporates genes of two ancestral lineages; it results in speciation only. Several exceptionally rapid but multigenerational evolutionary mechanisms are collectively termed parasaltational. Saltational evolutionary mechanisms probably generated many vascular plant species and most higher taxa. Hypotheses of saltation can be falsified using cladograms, which also provide an essential context for interpretations of evolutionary process as well as pattern – here illustrated using studies of evolutionary developmental change in architectures of fossil lycopsids and living angiosperms.

The neoGoldschmidtian synthesis advocated here accepts Goldschmidt's concept of speciation across a single generation but rejects his preferred causal mechanism of large-scale mutations and his requirement for competitively high levels of fitness in the monsters. Rather, we postulate that vast numbers of hopeful monsters are continuously generated by mutation of key homoeotic genes that control ontogeny via morphogens ('D-genes' of Wallace Arthur). The fitness of hopeful monsters is inevitably too low to survive competition-mediated selection – their establishment requires temporary release from selection in unoccupied niches. The prospecies can then be honed to competitive fitness by gradual reintroduction to neodarwinian selection.

When viewed backward through geological time, niches become less well-defined and more often vacant, causing a corresponding increase in the probability of successful establishment of hopeful monsters. Hence, saltation was most important among the earliest land plants, explaining the Siluro-Devonian origins of all class-level taxa. Although D-genes are similar at the molecular level across the biotic kingdoms, their phenotypic expression differs between higher plants and higher animals; this reflects highly contrasting modes of growth, notably the localization of plant growth in numerous meristems and consequent continuous, largely iterative development. More importantly, the sessile life-style of plants renders competition indirect and environmentally mediated; thus, vectorial selection is a far less profound cause of evolution in plants than in animals. Plants enjoy much greater latitude for non-lethal experimentation in form by saltation. Future advances in the study of evolutionary mechanisms will require cladograms that use phenotypically expressed genes as characters, rather than static morphology or cryptic base pairs, thereby allowing reciprocal illumination between phenotype and genotype.

INTRODUCTION

Despite continual undercurrents of dissent, the neodarwinian model of competitively driven selection has dominated evolutionary theory for several decades. Critics of neodarwinism have advocated a wide range of alternative or supplementary theories and thus have never coalesced into a coordinated opposition. Widespread discord continues among proponents of competing evolutionary theories, driven by two fallacious arguments. Firstly, contrasting hypotheses tend to be regarded as mutually exclusive; just as there is undoubtedly 'one true tree' of evolutionary relationships among all species, it is assumed that there must also be one true underlying mechanism that is transcendent over all others. Secondly, any one theory must be generally applicable to all taxa. Even when originally advanced as taxon-specific, an attractive theory is rapidly coopted by increasing numbers of sympathetic biologists studying other taxa. The generalization process usually requires progressive abandonment of facets of the original theory as additional organisms are shoe-horned into place; indeed, the relative resilience of Darwin's (1859) original formulation of adaptation by competitive selection can be attributed to the exceptional range of invertebrate, vertebrate and plant groups studied by this remarkable natural historian before finalizing his evolutionary hypothesis (e.g. Desmond & Moore, 1991).

However, the neodarwinian synthesis was fashioned largely by biologists and palaeobiologists studying only one of the five to seven widely recognized kingdoms (Whittaker, 1969; Field *et al.*, 1988; Margulis & Schwartz, 1988; Fernholm *et al.*, 1989; Gouy & Li, 1989; Woese *et al.*, 1990; Grant & Horn, 1992; Wainwright *et al.*, 1993), namely the Animalia (Haldane, 1932; Simpson, 1944; Dobzhansky, 1951; Mayr, 1963; Maynard Smith, 1972; Ayala & Valentine, 1979; Dawkins, 1986, 1989; Futuyma, 1986, 1987; Ridley, 1992). Emphasis on an even narrower and more highly derived clade, the Vertebrata, has further weakened the validity of generalizing the neodarwinian paradigm across the far more extensive tree of life (cf. Fernholm *et al.*, 1989; Woese *et al.*, 1990). Certainly, the remarkable repertoire of the most prominent living evolutionary essayist, S.J. Gould, is notable for a dearth of botanical examples. Reviews of evolutionary mechanisms in the kingdoms Plantae (e.g. Bell, 1992; Cronquist, 1968; Grant, 1971; Knoll, 1984; Knoll *et al.*, 1984; Knoll & Niklas, 1987; Raven *et al.*, 1986; Stace, 1989; Stebbins, 1950, 1971, 1974; Takhtajan, 1969, 1980, 1992) and Fungi (e.g. Rayner *et al.*, 1987) are far fewer and have coopted with minor modifications theories that are essentially zoocentric.

Occasional attempts to challenge (or at least supplement) neodarwinism have experienced similarly divergent fates according to the kingdom under scrutiny. Contributions by zoologists (e.g. Goldschmidt, 1940; Gould & Lewontin, 1979) have often prompted heated debate, whereas those from botanists (e.g. Croizat, 1962; Lewis, 1962; Sattler, 1986; Traverse, 1988; van Steenis, 1969, 1976) have received little attention.

Several Victorian naturalists (e.g. Bateson, 1894) advocated various saltational mechanisms; indeed, following his catalytic voyage on *HMS Beagle*, Darwin himself flirted with saltation (Desmond & Moore, 1991, p. 225). Perhaps the most notorious advocacy of saltation was *The Material Basis of Evolution*, an uncompromising anti-darwinian critique first published in 1940 by Berkeley developmental zoogeneticist Richard Goldschmidt. Most notably, Goldschmidt argued that 'systemic mutations'

(large-scale chromosomal rearrangements) altered early developmental trajectories to generate 'hopeful monsters' – teratological lineages of radically different phenotypes. By chance, some hopeful monsters possessed high levels of fitness that enabled their persistence as new lineages of great evolutionary significance. Burdened thus with an inviable underlying mechanism and an unreasonable assertion of competitively high fitness, aggressive proponents of the neodarwinian *New Synthesis* easily – but wrongly – discredited Goldschmidt's entire saltational paradigm (cf. Dawkins, 1986; Dietrich, 1992; Gould, 1977a, b). Occasional attempts to resurrect aspects of Goldschmidt's paradigm (Arthur, 1984, 1988; Bateman, in press; Dietrich, 1992; DiMichele *et al.*, 1989; Gould, 1982; Schindewolf, 1950; Stidd, 1987; Valentine, 1980; van Steenis, 1976; Waddington, 1957) had little impact on the scientific community.

   We believe that saltation is supradarwinian rather than antidarwinian. Here, we argue that saltation has been a stronger driving force of evolution among higher plants than higher animals, and among extinct rather than extant species. We also emphasize the importance of a phylogenetic context for the interpretation of evolutionary processes as well as patterns, focusing on developmental constraints to vascular plant architecture.

DEFINING SALTATIONAL EVOLUTION

Core mechanisms: saltation *sensu stricto*

Although few evolutionary biologists have provided explicit definitions of saltational (or 'saltatory') evolution, it is clear that overall the term has been used to encompass a wide range of often conflicting concepts (cf. Dawkins, 1986). Below we examine potential criteria for defining and recognizing saltation.

Cause of evolutionary change

By definition, any evolutionary event must involve changes in both genotype and phenotype *sensu lato* (i.e. *sensu* Dawkins, 1982). Hence, we immediately exclude from further consideration all non-genetic contributors to phenotype – ecophenotypy and ontogeny, significant causes of phenotypic variation within most plant species. This highlights a subtle difference between the concept of a teratos – an individual possessing a radically different morphology from its immediate ancestor(s) irrespective of the underlying causal mechanism – and Goldschmidt's concept of a 'hopeful monster', where a genetic cause of the morphological discontinuity is assumed and non-heritable causes (for example, an environmental perturbation of a plant meristem) are specifically excluded.

Discontinuity of evolutionary change

As noted by van Steenis (1976) and Dawkins (1986), almost any biological phenomenon is discontinuous if viewed in sufficient detail. Any point mutation (or, for that matter, any meiotic division with recombination) is a quantum change in genotype at the scale of base-pair sequences, and cannot in itself define saltation.

Magnitude of evolutionary change

If the mere presence of an evolutionary discontinuity is insufficient, an objective measure of the magnitude of the discontinuity is desirable in order to define a quantitative threshold that must be surpassed for a change to qualify as saltation. It also becomes important to specify whether the evolutionary change should be measured genotypically or phenotypically, as recent studies have conclusively refuted Goldschmidt's (1940) assertion that the magnitude of genetic change is reflected in the magnitude of its phenotypic expression. We would argue that hopeful monsters are best quantified phenotypically, provided that an underlying genetic cause of the phenotypic change has been documented.

Directionality of evolutionary change

There is no requirement that a saltational change should be progressive in the sense of increasing overall complexity or fitness. Indeed, current evidence suggests that saltational events which suppress developmental genes and consequently reduce morphological complexity are more common than saltational events which increase overall complexity. In either case, we believe that decreased initial fitness is inevitable, and that saltation therefore lacks vectorial properties (i.e. predictable directionality). Admittedly, not all current saltationists are willing to relinquish the concept of a spontaneously fit monster.

Rate of evolutionary change

Some authors (e.g. Ayala & Valentine, 1979) defined saltation as a period when the temporal rate of evolution (change/time) is substantially greater than the long-term average within the lineage; this criterion underlay the original concept of 'punctuated equilibria' (Eldredge & Gould, 1972). We concur with the assertion of Dawkins (1986), Lemen & Freeman (1989) and Gould & Eldridge (1993) that mere changes in evolutionary rate are not true saltation, and that punctuationist patterns are more remarkable for periods of apparent evolutionary stasis than for periods of rapid evolutionary change. We believe that saltation is better defined by generation time than absolute time: a saltational change must occur across a single generation. This crucial and controversial defining criterion excludes several contrasting mechanisms of rapid evolutionary change that we collectively term 'parasaltational' (see later).

Reproductive isolation caused by the evolutionary change

Hopeful monsters resulting from a high-magnitude phenotypic change will have a much greater likelihood of retaining their novel phenotype if they become isolated from introgression with the parental population, particularly if the isolation reflects intrinsic properties of the monsters rather than mere *ad hoc* spatial separation (i.e. sympatry rather than allopatry). However, new lineages can become established even in the absence of reproductive isolation (Arthur, 1984). This criterion is therefore ancillary to, rather than inherent in, saltation.

Demographic entity affected by the evolutionary change

Bateman & Denholm (1989) argued that there is a recognizable and definable demographic hierarchy: individual organisms > populations > infraspecific taxa > species. (Here, population describes a geographically and ecologically restricted aggregate of conspecific organisms: ecotopodemes *sensu* Gilmour & Heslop-Harrison, 1954; ava-

tars *sensu* Damuth, 1985; metapopulations *sensu* Levin, 1993.) Saltation can temporarily compress this hierarchy. A single hopeful monster is by definition highly geographically and ecologically restricted and can also be reproductively isolated, thereby meeting the criteria of a biological species *sensu* Mayr (1963). However, it is unlikely to be awarded specific rank by a practising taxonomist – indeed, it is unlikely to even be examined by a practising taxonomist, given the relative rarity of both hopeful monsters and taxonomists. In practice, a taxonomic species is obliged to prove its historical tenacity, by establishing a sizeable population that persists through many generations. Most lineages resulting from saltation fail to survive beyond a single generation, and few exceed 10^1–10^3 generations; these ephemeral entities are better described as prospecies. It should be emphasized that there is no intrinsic biological distinction between prospecies and taxonomic species; they can only be distinguished retrospectively, on the basis of the far greater temporal continuity and spatial extent of the latter.

Degree of genetic novelty generated during the evolutionary change
Mutation, the underlying cause of hopeful monsters, is by definition the generation of genetic novelty. However, other modes of genotypic change rely on the mixing of pre-existing genes from two species (hybridization) or on the duplication of pre-existing genes in one species (autopolyploidy). Mixing and duplication are combined and fixed in allopolyploidy (Stace, 1989, 1993; Stebbins, 1971; Thompson & Lumaret, 1992). Hybridization *per se* does not generate a new evolutionary lineage across a single generation and hence fails to qualify as saltation. In contrast, the genetic isolation that generally (though not inevitably) follows the doubled karyotype in allopolyploidy successfully generates a new saltational lineage.

Thus, two distinct modes of saltation are evident. In dichotomous saltation, hopeful monsters originate by mutation; one new daughter lineage diverges from the ancestral lineage, thereby forming a dichotomous pattern that can in theory be resolved cladistically (though note that this scenario requires persistence of the parental species beyond the speciation event, in contravention of cladistic principles). In reticulate saltation, allopolyploidy combines elements from two ancestral lineages; the resulting reticulate pattern cannot be adequately accommodated in a dichotomous cladogram. The general absence of mutation in reticulate saltation restricts the potential range of phenotypic innovation, so that speciation events are less likely to coincide with the origins of supraspecific taxa than is the case in dichotomous saltation (cf. Arthur, 1984; Stace, 1989, 1993; van Steenis, 1976). Reticulate saltation remains important, however, as it is more likely to lead to long-term lineage establishment.

Definitions
Taken together, the above arguments lead to the following formal definitions of key terms relating to instantaneous speciation:

Saltation: a genetic modification that is expressed as a profound phenotypic change across a single generation and results in a potentially independent evolutionary lineage (for the present, we prefer to evade our responsibility to quantify 'profound').

Dichotomous saltation: saltation driven by mutation within a single ancestral lineage.

Reticulate saltation: saltation driven by allopolyploidy and thus incorporating genes of two ancestral lineages.

Teratos (or *teras*): an individual showing a profound phenotypic change from its parent(s) irrespective of the underlying cause (plural *terata*).

Hopeful monster: an individual showing a profound phenotypical change from its parent(s) that demonstrably reflects a genetic modification.

Prospecies: a recently evolved lineage possessing the essential properties of a taxonomic (putatively biological) species but yet to achieve acceptable levels of abundance and historical continuity (longevity).

Ancillary mechanisms: parasaltation

The narrowness of the above definition of saltation excludes several under-explored evolutionary mechanisms capable of causing speciation events that are greatly accelerated but not instantaneous.

Firstly, the stringent requirement for both genotypic and phenotypic change across a single generation excludes most mutations of recessive alleles; here, the genotypic change can only be expressed in the F_1 generation in rare cases where a recessive mutation in a germ cell precursor is followed by self-fertilization involving two mutant gametes (Arthur, 1984). Hybridization *per se* is also excluded (cf. Abbott, 1992).

Specifying instantaneous speciation also rules out scenarios that focus on populations of small effective sizes, typically due to reduction induced by various forms of stress or by a vicariance event leading to allopatry (Levinton, 1988). The neutral theory (Kimura, 1983) states that random sampling effects alone can lead to allele fixation or extinction in small populations, largely independent of selective advantage. Various reformulations of Wright's (1932, 1968) shifting balance theory (Carson, 1985; Lande, 1986; Levin, 1970, 1993; Lewis, 1962, 1966, 1969; Templeton, 1982) predict that random genetic drift in small populations can temporarily override selective pressures on alleles, thereby allowing populations to cross valleys on the adaptive landscape to the slopes of another peak, which is then climbed by classic neodarwinian selection. Drift is expressed most profoundly when it disrupts and destabilizes developmental homoeostasis (Levin, 1970). Although most such populations fail, this process provides an opportunity to reorganize the developmental programming under conditions of low intraspecific competition and high physical stress ('catastrophic selection' *sensu* Lewis, 1962, 1966, 1969; see also Carson, 1985). An alternative formulation allows populations to rapidly cross adaptive valleys for some characters as a correlated response to selection imposed directly on other characters (Price *et al.*, 1993).

Shifting balance scenarios are consistent with evolutionary patterns that were termed punctuated equilibria by Eldredge & Gould (1972) – long periods of stasis followed by brief periods of rapid phenotypic change. Vermeij (1987) extended the ecological component of these scenarios, arguing that periods of stasis reflect neodarwinian processes and are punctuated by ecosystem disruptions that locally reduce selection pressure, species diversity and population sizes. Each such disruption allows escalation – a brief interval of intense competition to fill the vacated niches that increases the fitness of the competitors. Many of these observations apply equally well to populations that are very small not because they have declined but because they have just evolved by saltation – we will return to them later. In contrast, other explanations of punctuational patterns focus on selection among species (Gould, 1986; Gould & Eldredge, 1977, 1993; Levinton, 1988; Stanley, 1975) or even among clades (Williams, 1992). Requiring differential survival of lineages, these hypotheses lie well outside the bounds of saltation *sensu stricto*.

CLADISTIC TESTS OF SALTATIONAL HYPOTHESES

The dissemination of cladistic methods during the 1980s has elevated phylogeny reconstruction to a cornerstone of modern evolutionary biology. Although the methodology is becoming increasingly complex, the basic principles of cladistics remain simple (e.g. Doyle, 1993; Farris, 1983; Forey *et al.*, 1992; Patterson, 1982; Wiley, 1981; Wiley *et al.*, 1991). Each species selected for comparison is coded for a predetermined range of characters, each potentially informative character possessing two or more states among the chosen range of species. In the most common protocol, alternative states for each character are designated primitive and derived (polarized) by selecting one or more of the species as outgroup(s) (e.g. Maddison *et al.*, 1984). Parsimony is then used to filter, from among the many possible repeatedly dichotomous arrangements (topologies) of the species, one or more topologies that require the smallest number of state transitions (steps) among the characters coded in the primary matrix. The resulting distribution of character-state transitions across the chosen most-parsimonious topology can (and in our opinion should) be interpreted as an explicit statement of evolutionary pattern. However, if a bistate character changes more than once on the topology (Fig. 1A), cannot be scored for at least one species (Fig. 1B), or must be scored as two or more states for at least one species (Fig. 1C), the precise position of the state transition can be ambiguous. A particular optimization algorithm is then selected to yield an arbitrary solution to each ambiguity (e.g. Swofford, 1993).

The resulting preferred most-parsimonious cladogram, replete with optimized character-state transitions, is open to interpretation in terms of evolutionary process. However, many cladists deliberately ignore this opportunity. The few mechanistic interpretations attempted to date have focused on adaptation (Coddington, 1988; Donoghue, 1989; Greene, 1986; Harvey & Pagel, 1991; Maddison, 1990), and require three important codicils. (1) Many traits are adaptive (contribute to the fitness of the organism) but far fewer are adaptations that evolved via natural selection to fulfil a specific function. This key distinction is often overlooked. (2) Morphological cladistic analyses by definition employ 'form' as characters, but rarely include explicit functions
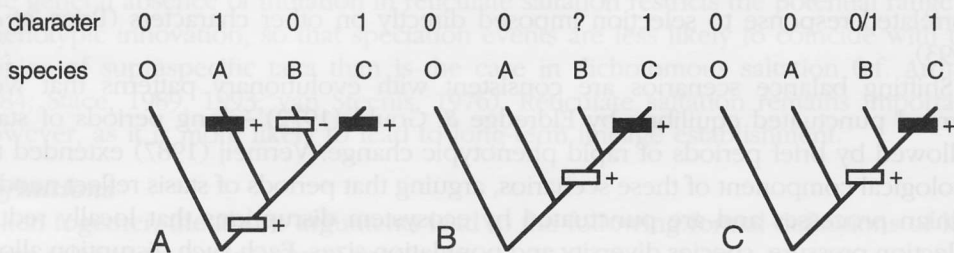

Figure 1 Three causes of ambiguity in the positions of character-state transitions on cladograms. **A** Character conflict. Because it is incongruent with other characters (not shown), this character is depicted as homoplastic. It undergoes two state changes: two origins under Deltran optimization (black boxes), and an origin and a loss under Acctran optimization (white boxes) (Swofford, 1993). **B** Missing value. Inability to score species B for this character results in arbitrary insertion of 0 under Deltran, yielding a late transition, or 1 under Acctran, yielding an earlier transition. **C** Polymorphism. An analogous situation to (B), but caused by the presence of both the primitive and the derived states in species B. Again, 0 is preferred under Deltran but 1 under Acctran.
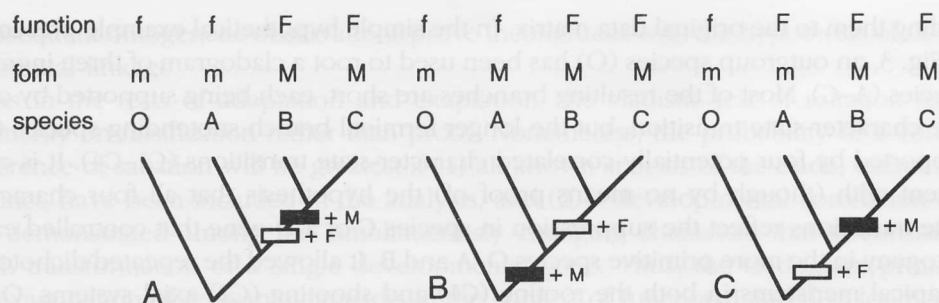
function	f	f	F	F	f	f	F	F	f	F	F	F
form	m	m	M	M	m	m	M	M	m	m	M	M
species	O	A	B	C	O	A	B	C	O	A	B	C

Figure 2 Cladograms as tests of adaptation and exaptation, illustrating the relative positions of transitions in a morphological character (m>M, black boxes) and its postulated function (f>F, white boxes). **A** Transitions in form and function coincide, a pattern consistent with a causal relationship involving selection-mediated adaptation. **B** Evolution of form precedes function, a pattern consistent with exaptation; the character did not evolve for its present function, but was later coopted. **C** Evolution of function precedes form, a pattern implying no significant correlation between the two observations. Adapted from Donoghue, 1989, fig. 3.

(Lauder, 1990). Fortunately, this is not a serious handicap to intepretation, as particular functions can be plotted on a cladogram *a posteriori* (mapped). (3) When attempting to infer evolutionary process from cladistic pattern, it is only possible to state that a particular process is consistent with a particular pattern. Demonstrating such a correlation requires additional biological data not coded into the original cladistic matrix.

To be consistent with a hypothesis of adaptation, a particular form and function must evolve on the same branch of the cladogram (Fig. 2A: Donoghue, 1989). A form appearing below the postulated function on the cladogram (Fig. 2B) is consistent with a hypothesis of exaptation; the form either (1) evolved non-adaptively, or (2) evolved adaptively but for a different function, only later acquiring its present function (Gould & Vrba, 1982). A form appearing above the putative function on the cladogram (Fig. 2C) refutes the hypothesis of positive correlation. We reiterate that arrangements of form and function consistent with adaptation or exaptation are not positive proof of such hypotheses; rather, the value of the cladograms is negative, allowing falsification of postulated correlations.

We argue that this same logic can be extended to allow cladistic tests of non-adaptive saltational hypotheses. These similarly rely on falsification, but the emphasis switches from demonstrating the simultaneous origin of a character state and its presumed adaptive function to demonstrating the simultaneous origin of several character states. This in turn focuses attention on long branches – those supported by several character-state transitions – and requires a literal (and thus controversial) interpretation of the cladogram as an evolutionary history. In this scenario, potentially developmentally correlated characters changing simultaneously on the cladogram are assumed to have changed simultaneously during evolution, most probably as the direct or indirect consequence of a single mutational event. In other words, saltation is regarded as the null hypothesis to explain certain types of long branch. (However, note that a long branch is consistent with any evolutionary process. Note also that long branches tend to be mutually attractive during tree-building, often yielding incorrect topologies: Hendy & Penny, 1989.)

Saltational hypotheses are tested most effectively by coding further species and

adding them to the original data matrix. In the simple hypothetical example presented in Fig. 3, an outgroup species (O) has been used to root a cladogram of three ingroup species (A–C). Most of the resulting branches are short, each being supported by only one character-state transition, but the longer terminal branch subtending species C is supported by four potentially correlated character-state transitions (C1–C4). It is consistent with (though by no means proof of) the hypothesis that all four character-state transitions reflect the suppression in species C of a D-gene that controlled early ontogeny in the more primitive species O, A and B. It allowed the repeated dichotomy of apical meristems in both the rooting (C1) and shooting (C2) axial systems. Once this ability was lost, only one reproductive cone could be generated (C3) at the end of the life history of the individual; the plant therefore became monocarpic (C4).

This initial saltational hypothesis was then tested by coding three additional species (D–F) that are closely related to species A–C. Analysis of the new expanded matrix could in theory alter the previous perception of the relationships of species A–C, though in Fig. 3 the original topology is supplemented rather than overturned by the addition of species D–F. Species D is attached to a branch irrelevant to the saltational hypothesis. Species E is attached to the relevant branch, but fails to dissociate the putatively correlated character states. However, species F is intercalated between the derived state of character 1 (which it possesses) and those of characters 2–4 (which it lacks). Following this reanalysis, suppression of meristematic division is perceived as two separate evolutionary events – the first in the root system and the second in the shoot system – though the remainder of the original saltational hypothesis pertaining to the shoot system (C2–C4) remains viable. Of course, this remains susceptible to refutation if yet more species can be added to the analysis of the clade, or if
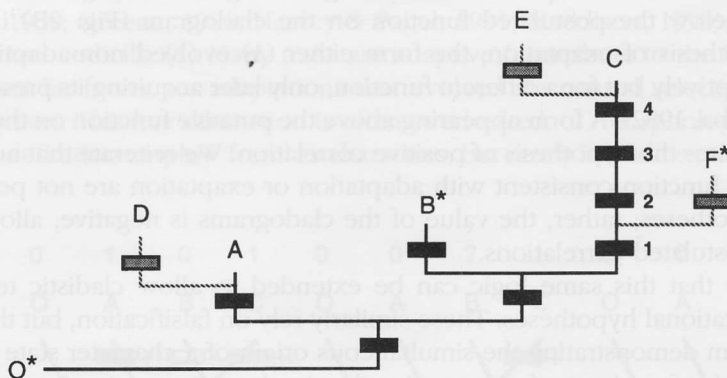

Figure 3 Cladograms as tests of saltation. The initial hypothetical analysis of outgroup species O and ingroup species A–C yields a single fully resolved topology. The relatively long branch subtending species C is supported by transitions in four potentially developmentally correlated characters: 1, suppression of dichotomy in root apical meristems; 2, suppression of dichotomy in shoot apical meristems; 3, switch from multiple to single reproductive cones; 4, switch from polycarpy to monocarpy. Simultaneous change in these four characters by saltation is assumed as the null hypothesis, and then tested by reanalysing the matrix with three additional ingroup species (labelled D–F). Species D is attached to an irrelevant branch. Although species E is connected to the relevant branch, it fails to dissociate the four correlated character-states. However, addition of species F separates character 1 from characters 2–4. This implies that the state transition occurred earlier in character 1 and thereby falsifies that part of the saltational hypothesis. Note that the fossil status of three of the species (asterisked) has no bearing on their analytical performance.

subsequent ontogenetic observations prove incongruent with the hypothesis of developmental linkage.

As in the tests of adaptation and exaptation, the cladistic test of saltation relies primarily on falsification rather than proof. Nonetheless, the probability of a correct inference of saltation will be greatest if (1) all known species of the clade, extant and extinct, have been included in the analysis, and (2) a developmental correlation can be demonstrated among the simultaneously changing characters that is consistent with transformation of a single developmental gene. Thus, the cladogram prompts re-examination of relevant characters in the context of functional and developmental integration. This requires direct observation of ontogeny and study of underlying genetic controls within a comparative framework. Even given this information, it is difficult to demonstrate that integration of the characters accompanied speciation, particularly if a considerable period of time separates speciation and observation.

LIFE AS A VASCULAR PLANT

Before further discussing plant evolution, it is desirable to review briefly what Darley (1990) graphically termed 'the essence of plantness'. The life history of an individual can be divided into the economic phenomena that govern the everyday activities of the plant within a particular generation, and the more temporally restricted reproductive phases that allow the transfer of genetic information to the next generation (Eldredge, 1989).

Physiology and ecology

In economic terms, plants are autotrophic primary producers. Able to synthesize energy-rich carbohydrates from carbon dioxide using solar radiation, they are basal to almost all food chains (the most notable exception is deep-sea hydrothermal vents). Plants also concentrate water, minerals and atmospheric oxygen. It should be emphasized that plants inherited these abilities from less derived groups. For example, photosynthesis characterizes many unicellular eukaryotes of the Protoctista and the prokaryotic cyanobacteria of the Monera. Plants first acquired chloroplasts as symbiotic cyanobacteria; earlier, a common ancestor of plants and animals had acquired mitochondria as symbiotic bacteria (e.g. Fernholm et al., 1989; Knoll, 1992; Margulis, 1993; Margulis & Schwartz, 1988; Woese et al., 1990). Multicellularity, and thus tissue differentiation, evolved independently in plants and animals.

Much of the subsequent evolution of plants has improved physiological efficiency. Planar megaphyllous leaves borne in Fibonacci phyllotaxis increase incident light, while their cuticle and stomata enhance water conservation and gaseous exchange. Specialized vascular tissues allow rapid transport of nutrients and hormones around the plant body, driven by passive transpiration tension in the acropetally conducting xylem but an active process in the basipetally conducting phloem. Xylem transport helps to maintain the turgor pressure that is the primary support mechanism of plant tissues. Turgor is generated in cell vacuoles, which are constrained by the primary cellulose walls of cells that are mutually adhesive (Wiebe, 1978). Later in ontogeny this 'hydraulic skeleton' becomes inadequate and secondary cell walls are laid down, providing structural reinforcement at the expense of suppressing the potential for

further cell division or expansion. Roots anchor the plant to the substrate and increase surface area for absorption of water and nutrients, thereby confining the organism to a sedentary, sessile life-style. Thus, motility in vascular land plants is passive and largely restricted to aquatic species, in contrast with the active motility of flagellate photosynthetic protoctistans (e.g. *Euglena*) and chlorophyte algae (e.g. *Volvox*). It should be noted that the sessile life-style, like photosynthesis, probably preceded the conquest of the land by plants (cf. DiMichele *et al.*, 1992; Kenrick & Crane, 1991; Selden & Edwards, 1989).

Meristems and architecture

Another major factor constraining the evolution of form in plants is the restriction of all cell division and most cell expansion to a small proportion of the plant body, in regions that are termed meristems. These permit indeterminate ('open') growth throughout the life history of most vascular plant species. Early land plants possessed only axial apical meristems that allowed elongation of shoots and roots, but these subsequently diversified to generate more specialized shoot meristems for the pro-duction of leaves and sporophylls, and lateral meristems that enabled secondary growth (vascular cambium). This led to greater numbers of plant organs possessing greater degrees of physiological independence; in some species most organs are dis-pensable, provided that at least one indeterminate meristem is retained by the plant (Bazzaz & Carlson, 1979; White, 1979). Best known for allowing organ abscission during ontogeny, this property also confers remarkable resilience to physical damage and the opportunity for various modes of meristem-mediated asexual reproduction. The more advanced vascular plant clades evolved embryonic bipolarity of meristems to generate distinct shoot and root axial systems (Bateman, in press). Architectural flexibility in plants is largely confined to variations in the type, number, spatial arrangements and branching patterns of meristems (e.g. Hallé *et al.*, 1978).

Darley (1990) convincingly argued that the relatively complex growth patterns of higher plants are largely a substitute for motility, maximizing potential responses to environmental perturbations within this severe economic constraint. Most interactions among plants, both infraspecific and interspecific, are indirect – they are mediated by the environment. Sophisticated hormonal systems remain essential to regulate growth and metabolism (Cheplick, 1989; Poethig, 1990), but chemical interactions among plants are uncommon (exceptions include certain phytotoxins and 'phytopheromones'). Physicochemical interactions, notably mycorrhizal associations, are more common. Some species have saprophytic or parasitic life histories. Other interspecific relationships are purely physical, such as epiphytism and lianescent strangulation. Moving on from economic to reproductive interactions, sexual repro-duction requires an intermediate environmental or animate vector for dissemination of at least one gender of gamete and often of the resulting zygote. Such disseminules involve periods of low metabolic activity and thus allow a resilience to environmental catastrophes greater than that observed in higher animals (e.g. Boulter *et al.*, 1988). Furthermore, plants lack the complex central nervous systems and consequent inter-active behaviours of higher animals; for example, choice of mate is purely physiologi-cal and generally *ad hoc* within the population. Sadly, intelligent vegetables remain the preserve of science ficition (e.g. Wyndham, 1951).

Thus, plants compete primarily with the environment rather than with each other,

and where they do interact they do so unconsciously – key points that we will develop later.

PLANT DEVELOPMENT AND ARCHITECTURE

Intraspecific description

The largest scale and thus most obvious aspect of the shape and form of vascular plants is their overall architecture. Body shape and size are among the most biologically significant aspects of a plant, as they strongly influence life history and ecological role (e.g. Hallé *et al.,* 1978; Phillips & DiMichele, 1992). We define architecture as the idealized, genetically determined morphology of a plant. Architecture is subject to varying degrees of non-genetic, ecophenotypic modification to generate the observed phenotypic growth habit: the ultimate form of a plant as expressed in its physiognomy (Bateman & DiMichele, 1991; Gottlieb, 1984, 1986; Hallé *et al.,* 1978; Meeuse, 1986; Mosbrugger, 1990; Tomlinson, 1982, 1987). Other classifications of form are more nebulous, such as the distinction among tree (large bodied, non-recumbent), shrub (medium bodied, non-recumbent), pseudoherb (small bodied or recumbent, woody), and herb (small bodied or recumbent, non-woody) (Bateman & DiMichele, 1991; Bateman *et al.,* 1992).

The plant body is a composite of modular constructional units generated by various types of meristem (a metapopulation *sensu* White, 1979; see also Buss, 1987; Harper *et al.,* 1986; Tomlinson, 1982). Appendages borne on axes are generally produced by determinate meristems as repeatable (and often dispensable) units (Hallé, 1986; Hardwick, 1986). However, evolution can blur the axis–appendage distinction. For example, the megaphyllous leaves of ferns and seed plants are positionally appendicular but share a developmental programme with axes; leaves of many early tracheophytes resemble dichotomous axial branching systems and were termed telomes and telome–mesome aggregates (Stewart & Rothwell, 1993; Stidd, 1987; Zimmermann, 1959). A plant is characterized primarily by the number of types of such modules present and by their spatial arrangements. Variations in the size, shape and relative numbers of such modules are less profound (Bateman, in press).

Moreover, the ultimate expression of the genotypically mediated body form of an individual plant is strongly influenced by chance factors such as disturbance, predation and proximity to limiting resources (Tomlinson, 1982). Plant form permits opportunistic responses to local conditions and events; such flexibility is crucial, given their inability to relocate when subjected to stress. Thus, genetically determined architectures incur a strong stochastic overprint, perturbing the idealized form.

Interspecific comparison: evolutionary developmental change

Conceptual aspects of comparative development have long been dominated by zoologists (e.g. Alberch *et al.,* 1979; Arthur, 1984, 1988; de Beer, 1940; Gould, 1977a; Haeckel, 1868; Kauffman, 1993; Kluge & Strauss, 1985; McKinney, 1988; McKinney & McNamara, 1991; Raff & Kaufman, 1983; Riedl, 1979; von Baer, 1828; Wake, 1989). Neobotanical applications have been relatively few (e.g. Gottlieb & Jain, 1988; Guerrant, 1982; Iltis, 1983; Kellogg, 1990; Sattler, 1988, 1993; Takhtajan, 1972; Weston, 1988; Williams *et al.,* 1990) and palaeobotanical applications even fewer (Bateman, in press;

Bateman & DiMichele, 1991; Bateman *et al.*, 1992; Doyle, 1978; Meyen, 1988; Rothwell, 1987; Stidd, 1980). Much is owed to Gould (1977a) for rigorously defining a set of descriptive terms, Alberch *et al.* (1979) for translating those definitions into semi-quantitative plots of shape against time (or against its crude proxy, size), and Fink (1982) for developing cladistic tests of hypotheses of developmental transitions.

Broadly (and somewhat superficially), changes in development between ancestor and descendant can be attributed to heterotopy – a spatial (positional) change in the expression of a trait – and heterochrony – a temporal change in the expression of a trait. Changes in the relative times of onset or offset of growth, or of the rate of morphological development, can be used to define six end-member modes of heterochrony that can be assigned to two main categories: relative to the ancestor, the descendant shows more morphological change if peramorphic and less morphological change if paedomorphic (Alberch *et al.*, 1979). Allometric changes that alter size but not shape (giantism and dwarfism) lie outside the formal definition of heterochrony (Alberch *et al.*, 1979; Gould, 1977a). Bateman (in press) argued that changes in whole-organism traits such as the timing of onset of sexual maturity and the number of definable developmental stages in the ancestral and descendant ontogenies should also be excluded from heterochrony *sensu stricto*. He preferred to coin the broader collective term evolutionary developmental change for these phenomena, and suggested that architectural comparisons among plants are best made at the level of definable organs rather than entire organisms.

Terminology developed to describe changes in the number or nature of developmental stages in compared ontogenies also presents difficulties. Each change can be an addition, deletion or substitution, which can be terminal or non-terminal in the ontogenetic sequence (O'Grady, 1985). Unfortunately, a change in a single gene can affect more than one developmental stage, either by pleiotropism, epigenesis, or mere cascade effects; parity between cause and effect cannot be assumed. Another problem is presented by morphological simplification; whether due to heterochronic paedomorphism or stage deletion, this can undermine cladistic analyses (Bateman, in press; Bateman *et al.*, 1992).

To summarize, comparative plant development suffers from the same conceptual deficiencies as descriptive plant development. When torn from their zoological roots in order to be applied to higher plants, and when shoe-horned into a cladistic framework, those concepts clearly require reappraisal (Bateman, in press; Sattler, 1988, 1993). Such revisions are now underway.

CASE STUDIES OF SALTATION IN PLANT ARCHITECTURE

The following case studies were selected from among the few cladistic analyses of vascular plants performed to date within a single taxonomic order. The range of appropriate studies was further restricted by several *a priori* requirements for the nature of the data matrix (cf. Bateman, in press). Studies coding species rather than infraspecific or supraspecific taxa were preferred. The matrix should lack both polymorphic coding (i.e. each character of each species should be represented by a single character state) and large tracts of missing values. Characters should be dominantly morphological and some should describe overall architecture. Interestingly, architectural characters were omitted from a surprisingly large proportion of morphological

cladistic studies. On the rare occasions when they were included they proved unusually homoplastic, thereby decreasing the resolution of the analysis (e.g. Bateman, in press; Bateman *et al.*, 1992; Funk, 1982; Hill & Camus, 1986). Recognition of their problematic nature led to their deliberate *a priori* omission from many studies.

The following case studies were selected from among the few analyses that conform to the above criteria. The chosen clades differ greatly in taxonomic affinities and in the relative proportions of living and fossil species. These brief summaries focus on relevant aspects of the interpretations; further analytical details should be sought in the original publications.

Montanoa (Asteraceae: Angiospermales)

Funk (1982) performed a morphological cladistic analysis of 25 exant species of the predominantly tropical American asteracean genus *Montanoa*. Most were small-bodied shrubs or lianas, but five species were woody trees reaching about 30 m. Mapping of habitat preferences across the cladogram showed that the five arboreous (tree-sized) species differed from the remainder in favouring high-altitude cloud forests; moreover, three of the five species were studied karyotypically and all proved to be high-level polyploids. Had chromosome counts been obtained from all 25 species analysed, precise correlations and co-occurrences could have been calculated between karyotype, habitat and morphological characters such as body size (Harvey & Pagel, 1991). Even with the present incomplete evidence, the association of the three parameters is clear-cut. Funk (1982) and Funk & Brooks (1990) argued that in the Asteraceae polyploidy frequently promotes arboreousness; this in turn leads to unusually inefficient vascular conductance; and this in turn confines composite trees to perpetually humid habitats such as cloud forests. Interestingly, a similar pattern has been documented in *Lobelia*, which shows repeated origins of woody tetraploid and hexaploid species from putative ancestors that are both diploid and herbaceous (Knox *et al.*, 1993).

The *Montanoa* cladogram (Fig. 4) shows that four independent origins of arboreousness are required to explain the phylogenetic positions of the five tree species (unlike the lycopsid example below, no evolutionary transitions from tree to shrub are required). Together, these observations are consistent with frequent generation of arboreous prospecies by *ad hoc* polyploidy events among the diploid, low-altitude species of *Montanoa*. Only polyploid seeds – embryonic hopeful monsters – that fortuitously reach cloud forest habitats have any chance of establishing evolutionarily significant populations (differential habitat preferences render the polyploids allopatric relative to their ancestors). Although most polyploid *Montanoa* seeds presumably fail even in appropriate habitats, at least four of the saltationally generated prospecies achieved historical continuity, and one ((3) on Fig. 4) apparently underwent at least one additional speciation event without further change in ploidy. This illustrates another important point. Stace (1989, 1993) estimated that perhaps the majority of all living angiosperm species are polyploid. However, this does not mean that half the extant species owe their origin to polyploidy events; given that speciation occurs frequently among polyploids, far fewer ploidy changes are required to explain their evolution.
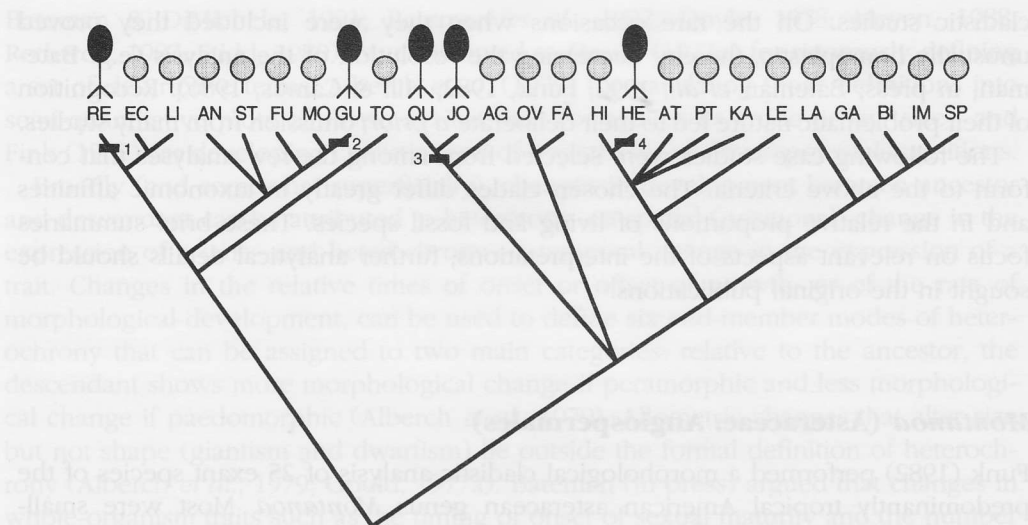
Figure 4 Incompletely resolved preferred most-parsimonious cladogram of 25 extant species of the composite genus *Montanoa*, showing four independent origins (1–4) of large-bodied trees from smaller-bodied shrubs and lianas. The origin of arboreousness coincides with polyploidy events (reticulate saltation) and with ecological transitions from low- to high-altitude tropical forest habitats. Species as follows: RE, *M. revealii;* EC, *M. echinacea;* LI, *M. liebmannii;* AN, *M. andersonii;* ST, *M. standleyi;* FU, *M. frutescens;* MO, *M. mollissima;* GU, *M. guatemalensis;* TO, *M. tormentosa;* QU, *M. quadrangularis;* JO, *M. josei;* AG, *M. angulata;* OV, *M. ovalifolia;* FA, *M. fragrans;* HI, *M. hibiscifolia;* HE, *M. hexagona;* AT, *M. atriplicifolia;* PT, *M. pteropoda;* KA, *M. karwinskii;* LE, *M. leucantha;* LA, *M. laskowskii;* GA, *M. grandiflora;* BI, *M. bipinnatifida;* IM, *M. imbricata;* SP, *M. speciosa.* Data from Funk, 1982; figure adapted from Funk & Brooks, 1990, fig. 102.

Rhizomorphales (Lycopsida)

The rhizomorphic lycopsids are the most derived portion of the lycophyte clade (lycopsids plus zosterophyllopsids), which is sister group to the remainder of the eutracheophytes (e.g. Crane, 1990). They evolved independently many of the features generally regarded as characterizing the early seed plants, including bipolar embryonic growth, secondary growth producing wood and periderm, the arboreous growth form, and indehiscent integumented megasporangia (Bateman, in press; Bateman *et al.*, 1992; Phillips & DiMichele, 1992). Observable anatomical differences highlight the non-homology of these features between the two clades. Appendages are comparatively poorly developed in the rhizomorphic lycopsids; microphylls, sporophylls and rootlets are all supplied by a single, narrow vascular strand. More significantly, their bipolar growth exhibited much stronger developmental parallelism between the rooting and shooting axial systems than that documented in seed plants. Also, the apical meristems followed an animal-like developmental pattern of closed, determinate growth. Consequently, individual growth modules experienced high degrees of physiological independence and thus were unusually well defined. This in turn meant that the idealized genotypic architecture was unusually faithfully reproduced in the actual growth habitat observed in the phenotype (Bateman & DiMichele, 1991).

A detailed experimental cladistic analysis was performed on the group by Bateman *et al.* (1992), and its implications for evolutionary developmental change in architec-

ture were explored in detail by Bateman (in press). Sixteen adequately reconstructed fossil species, comprising ten genera, were included; they were scored for 12 binary architectural characters. A simplified version of the preferred most-parsimonious tree, reduced to generic level, is reproduced in Fig. 5. This reveals a tremendous range of body size and architectural plans; only one triplet and one pair of genera possess identically coded architectures, and of these only the most derived pair is depicted as monophyletic. However the phylogenetic relationships and character-state changes are interpreted, the architectural history of the group appears anarchic. On several occasions similar architectures evolved in parallel. Trees alternate with far smaller-bodied genera, and isotomous, exclusively terminal crown-branching alternates with anisotomous, at least partially non-terminal lateral branching. Loss of organs is an iterative theme, occurring as morphological simplification via the suite of heterochronic phenomena that are collectively termed paedomorphosis.

Bateman (in press) argued that the remarkable frequency and radical nature of these architectural transitions, combined with the determinate modular growth and presumably relatively simple genetic control of development, render this an especially
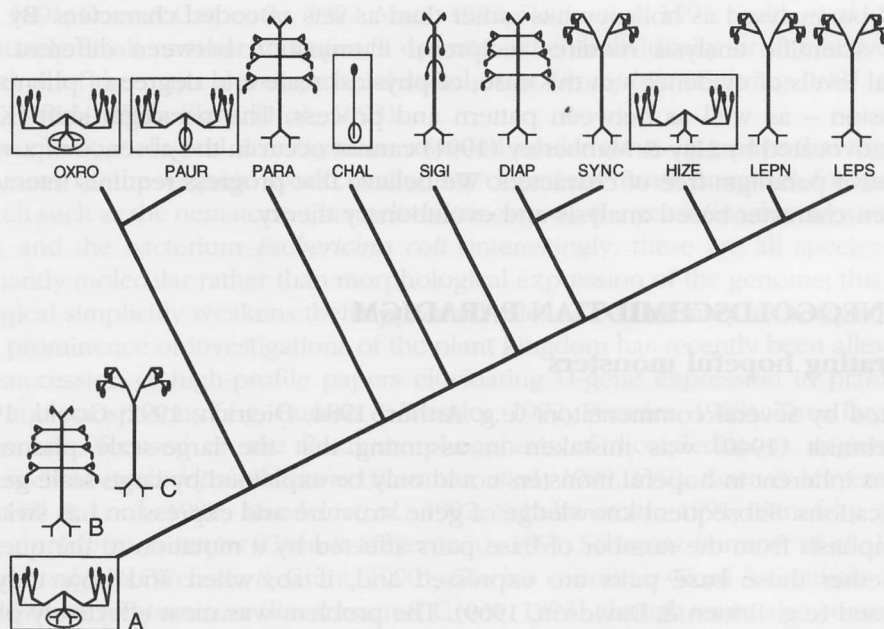

Figure 5 Fully resolved preferred most-parsimonious cladogram of 16 extinct species of rhizomorphic lycopsid, subsequently collapsed to ten monophyletic genera for ease of interpretation. Note the radical differences among mature growth architectures, which require hypotheses of convergence, reversible architectural transitions, loss of entire growth modules, and repeated origins of shrubs from trees (small-bodied, non-tree genera are boxed; ellipses denote compact, 'cormose' rootstocks). These radical architectural transitions are consistent with mutation-driven dichotomous saltation. The cladogram was rooted using an *Oxroadia*-like (A) hypothetical ancestor, though credible alternative hypotheses detailed by Bateman (in press) would allow rooting using *Paralycopodites*-like (B) or *Synchysidendron*-like (C) architectures. Genera as follows: OXRO, *Oxroadia*; PAUR, *Paurodendron*; PARA, *Paralycopodites*; CHAL, *Chaloneria*; SIGI, *Sigillaria*; DIAP, *Diaphorodendron*; SYNC, *Synchysidendron*; HIZE, *Hizemodendron*; LEPN, *Lepidodendron*; LEPS, *Lepidophloios*. Data from Bateman *et al.*, 1992; figure adapted from Bateman, 1992, fig. 12.

plausible example of repeated, profound (and presumably dichotomous) saltational evolution.

Summary

Overall architecture is the largest-scale phenotypic expression of a plant, largely reflecting the relative sizes and spatial relationships of various types of meristem and thereby encapsulating much of its ontogenetic history. There is strong positive feedback between changes in architecture and changes in smaller-scale features of the plant, which may render architectural characters particularly susceptible to non-adaptive (and often ultimately non-directional) saltational evolution.

Their flexibility and scale should not routinely excuse architectural characters from inclusion in cladistic analyses; indeed, we find them particularly illuminating. They are a useful reminder that, despite the large degree of physiological and evolutionary independence enjoyed by particular growth modules, plants nonetheless act primarily as holistic individuals. This point was emphasized in a saltational context by Hay & Mabberley (1991), though we fundamentally disagree with their conclusion that plants should be analysed as holistic units rather than as sets of coded characters. By definition, scientific analysis requires reciprocal illumination between different hierarchical levels of evidence – in this case, of physical scale and degree of phenotypic expression – as well as between pattern and process. The paradigm shift (Kuhn, 1962) advocated by Hay & Mabberley (1991) cannot occur in the absence of a viable alternative paradigm free of characters. We believe that progress requires interaction between character-based analysis and evolutionary theory.

THE NEOGOLDSCHMIDTIAN PARADIGM

Generating hopeful monsters

As noted by several commentators (e.g. Arthur, 1984; Dietrich, 1992; Gould, 1982), Goldschmidt (1940) was mistaken in assuming that the large-scale phenotypic changes inherent in hopeful monsters could only be explained by large-scale genetic modifications. Subsequent knowledge of gene structure and expression has switched the emphasis from the number of base pairs affected by a mutation to the question of whether those base pairs are expressed and, if so, when and how they are expressed (e.g. Britten & Davidson, 1969). The problem was most effectively placed in a developmental genetic context by Arthur (1984), who focused on enzyme-producing structural genes that are in turn controlled by regulatory genes. If the enzyme in question affects only biochemical maintenance of cells, the relevant structural genes are termed S-genes and the regulatory genes R-genes. If, on the other hand, the enzyme is a morphogen affecting ontogeny, both the structural and regulatory genes are termed D-genes. These were in turn divided by McKinney & McNamara (1991) into type I D-genes, which control intercellular development (i.e. rearrange cells), and type II D-genes, which control intracellular development (i.e. determine cell type). As already noted, following their generation by meristems, plant cells rapidly coalesce into more-or-less fixed spatial arrangements; thus, the saltational spotlight becomes firmly fixed on type II D-genes. Although biologically simplistic, this dynamic classification of genes is heuristically useful.

Certainly, D-genes are no mere hypothetical construct. The best-known studies of developmental gene expression focused on the fruit-fly *Drosophila* (e.g. Ashburner, 1989; Duncan, 1986; Gehring, 1987; Lawrence, 1992). A typical arthropod, *Drosophila* consists of repeated segments bearing serially homologous appendages that show differing degrees of functional specialization. Although this modular construction is analogous to vascular plant architecture, *Drosophila* has far fewer degrees of developmental freedom, being confined to three pairs of legs and the inevitable bilateral body symmetry of vagile terrestrial animals. Also, the stepwise metamorphic ontogeny of *Drosophila* contrasts starkly with the gradual ontogeny of plants. Many teratological mutant types have been documented in *Drosophila* that involve either (1) a change in the number of compartmentalized segments or appendages (heterochrony *sensu lato*) or (2) a spatial change in the segment on which a particular appendage is expressed (heterotopy). Most such mutations have been tied to specific type II D-genes, which can be suppressed by inserting short lengths of transposable DNA (transposons). Sequencing of several homeotic genes – notably the homeobox family – has shown that all consist of relatively short lengths of DNA and for much of their lengths have similar base pair sequences, suggesting a common origin (cf. Coen, 1991; Coen & Carpenter, 1992; Marx, 1992; Slack *et al.*, 1993; Smith *et al.*, 1992). A relatively small number of D-genes operate either individually or interactively to control all of the major developmental switches in *Drosophila* (Gehring, 1987; Gehring & Hiromi, 1986; Slack *et al.*, 1993).

Subsequent zoological investigations revealed similar genes in groups that together span most of the organic world, including organisms most favoured for genetic research such as the nematode *Caenorhabditis elegans*, the yeast *Saccharomyces cerevisiae*, and the bacterium *Escherichia coli* (interestingly, these are all species with dominantly molecular rather than morphological expression of the genome; this morphological simplicity weakens their appointed roles as evolutionary archetypes). The lesser prominence of investigations of the plant kingdom has recently been alleviated by a succession of high-profile papers elucidating D-gene expression in plants via terata and transposons (e.g. Bureau & Wessler, 1992; Wessler, 1988). Thus far, such studies have focused on the floral morphogenesis of dicotyledonous angiosperm herbs such as *Arabidopsis thaliana* (Bowman *et al.*, 1989, 1991; Coen & Meyerowitz, 1991; Hill & Lord, 1989; Mandel *et al.*, 1992; Schultz *et al.*, 1991; Yanofsky *et al.*, 1990), *Antirrhinum majus* (Coen & Meyerowitz, 1991; Schwartz-Sommer *et al.*, 1990), *Primula vulgaris* (Webster & Grant, 1990), *Clarkia concinna* (Ford & Gottlieb, 1992) and *Solanum lycopersicum* (Rasmussen & Green, 1993), though terata also commonly occur among monocots (e.g. orchids: Bateman, 1985; McCook & Bateman, 1990), gymnosperms (e.g. Long, 1977; T. L. Phillips, personal communication, 1993) and pteridophytes (e.g. Leavitt, 1909; Page, 1972). (See also Meyer, 1966; Worsdell, 1916.)

Although environmental modifications can generate teratological flowers (Crozier & Thomas, 1993), most studies have revealed that the expression and differentiation of each whorl of floral appendages (sepals, petals, stamen, carpels) can be explained in terms of control by one or two factors that probably reflect particular D-genes; some are specific to a single whorl, whereas others are more widely expressed (Coen, 1991; Coen & Carpenter, 1992; see also Endress, 1992; Hilu, 1983). Moreover, the floral genes of plants share substantial sequences of base pairs with genes found in species belonging to other kingdoms, suggesting that this family of key developmental genes originated during the earliest stages of life on Earth. They have been progress-

ively modified and coopted for different tasks (not always developmentally related) during major phylogenetic radiations; most homoeotic genes are members of ancient families of D-genes, although their present roles in particular species are often relatively recent. Studies of the genetic control of exclusively vegetative morphogenesis in plants are less advanced (e.g. Aeschbacher *et al.*, 1992; Poethig, 1990; Smith *et al.*, 1992), but similar control of the all-important meristems by very small numbers of D-genes is highly likely.

To summarize, recent studies have demonstrated conclusively that plant development parallels that of animals in being controlled by a small number of key D-genes. Their importance lies not in their size but in the ontogenetic timing and magnitude of their phenotypic expression. Accumulating molecular data increasingly reveal species radiations involving significant morphological differentiation but little molecular change – a much debated example of East African cichlid fishes (cf. Avise, 1990; Greenwood, 1981; Kenleyside, 1991; Meyer *et al.*, 1990) overshadowing equally informative studies of the Hawaiian asteraceans *Tetramolopium* (Lowrey, 1993; Lowrey & Crawford, 1985); and silverswords (Baldwin, 1992; Baldwin et al., 1990, 1991; see also Doyle, 1993). Moreover, the relative simplicity of developmental control reduces the potential of the genome to buffer the effects of D-gene mutations, and increases the likelihood of genetic parallelism – different mutation events having the same effect on the same gene within the same species. Thus, many similar hopeful monsters can occur sporadically throughout the range of their 'ancestral' species. Although exciting, reports of breakthroughs in the understanding of plant developmental control have lacked discussion of the profound evolutionary significance of D-gene mutations. In order to complete the saltational paradigm it is necessary to switch emphasis from the evolutionary play to the ecological theatre.

Establishing hopeful monsters

The architectural development of higher organisms is probably controlled by few D-genes, and like all genes these are susceptible to mutation. Thus, each species constantly generates hopeful monsters throughout its life-span. The limiting factor is not the availability of hopeful monsters but their establishment. This second phase of saltational evolution depends on the interaction between phenotype and environment.

The second fundamental flaw of Goldschmidt's paradigm noted by Gould (1982) was the requirement that successful hopeful monsters should emerge from the saltation event already possessing a level of fitness sufficiently high to compete with other sympatric organisms, both interspecific and intraspecific and including the parent(s) of the monster. This hypothesis appears untenable; organisms arising by saltation will not be competitive with organisms already honed to local optima of fitness by natural selection. Rather, they are faced with 'unwanted' changes that significantly decrease their fitness, and must survive their handicaps as best they can. The solution to their dilemma lies in ecology; specifically, the need to temporarily release the mutant lineage from selection (Arthur, 1984, 1987, 1988; Carson, 1985; DiMichele *et al.*, 1987; Erwin & Valentine, 1984; Levinton, 1988; Valentine, 1980; van Steenis, 1976; Waddington, 1957).

We recognize four establishment thresholds, listed in order of increasing levels of fitness: (1) the lowest threshold is the minimum fitness level necessary for economic establishment of the hopeful monster in its habitat – in the case of a seed plant, germination and growth to maturity. (2) Once the plant reaches maturity it must be capable of generating viable progeny, however inefficient the reproductive process. (3) Further generations are required to achieve continuity of the mutant lineage and to expand its biogeographical and ecological influence. This requires an even higher level of fitness, to compete successfully with sympatric organisms actually occupying the contested niche. (4) There is a theoretical threshold of even greater fitness that would have to be exceeded to outcompete the fittest potential occupant of the niche (because of the non-motility of plants, there is a strong *ad hoc* element to the species that actually occupies a specific niche in a specific habitat at a specific moment in time).

Factors determining establishment are summarized conceptually in Fig. 6. This scenario involves a landscape of five habitats (A–E), each offering one niche for a tree and one for a shrub. Habitats A, B and C–E differ considerably in relative levels of intrinsic stress (S1–S3), which determines fitness thresholds for the successful establishment of plant lineages in the absence of competition (essentially threshold (2) above). Initially, the landscape is occupied by three species of rhizomorphic lycopsid, each already honed by natural selection to a local optimum of fitness in its preferred habitat: a laterally branched tree and an unbranched shrub in habitats B and C, and a laterally branched tree only in habitat D. The parental tree in habitat D continuously produces by mutationally driven saltation two types of teratological propagule, of equal fitness among themselves but of lesser fitness than the pre-existing species in habitats B and C and the parent in habitat D. The first type of hopeful monster, crown-branched trees, are produced by suppression of lateral branching and are potential occupants of the tree niche. The second type of hopeful monster, crown-branched pseudoherbs, are produced by suppression of lateral branching plus profound paedomorphosis, and are potential occupants of the shrub niche. All are of an equal fitness ($\omega1$) that is appreciably lower than the shared fitness of the adaptively honed pre-existing species ($\omega2$), and all are dispersed evenly across the landscape.

Figure 6 documents the fates of identical monsters in habitats that differ in intrinsic stress levels and niches that differ in whether they are occupied or vacant (cf. Arthur, 1984; Stanley, 1979). Habitat A offers the highest intrinsic stress (it could be a desert); it exceeds the abilities of both the hopeful monsters and their adaptively honed predecessors to grow and/or reproduce in either niche; thus, the organisms suffer economic or reproductive failure. In contrast, habitat C offers an attractively low level of intrinsic stress; consequently, both niches are already occupied by adaptively honed species. The hopeful monsters may germinate and even reproduce in the habitat, but their long-term prognosis is poor; they will eventually be excluded from both niches by interspecific competition. In habitat D, the hopeful monster is excluded from the tree niche by its own parental stock, but the shrub niche is vacant and the hopeful monster has sufficient fitness to transcend successfully the establishment threshold determined by intrinsic stress. Habitat E also offers low intrinsic stress but nonetheless both niches are vacant due to chance factors (for example, the habitat is a recently formed island or a volcanically sterilized landscape). Thus, any hopeful monster can become established here, irrespective of niche. Lastly, habitat B illustrates the potential for incorrect interpretations of causation. The situation appears identical to that in habitat C,
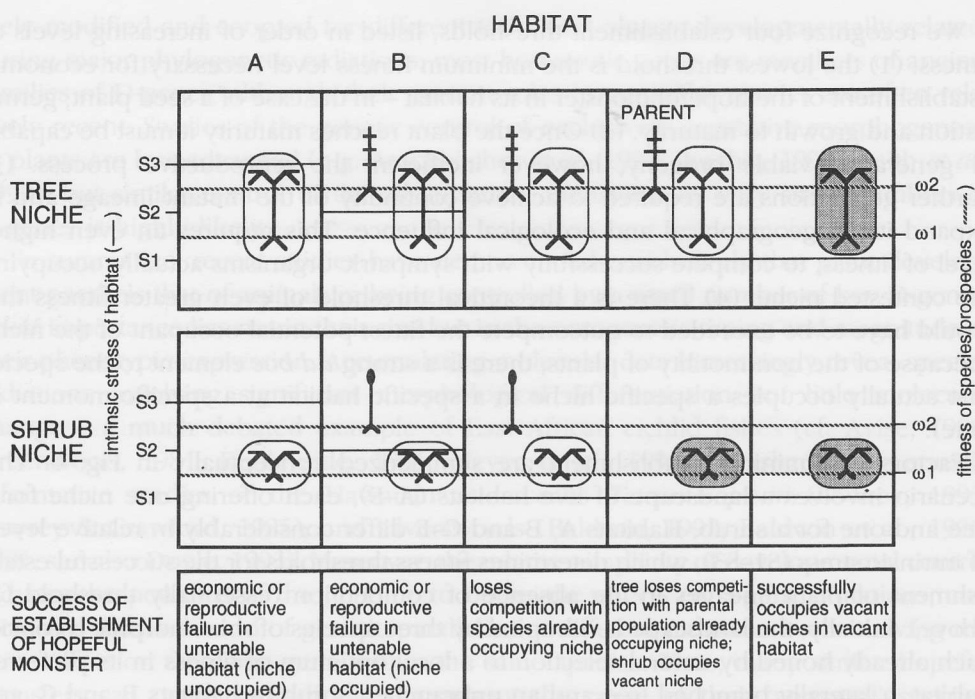
Figure 6 The key role of ecology in the neoGoldschmidtian paradigm. The simple ecological system depicted is a landscape of five habitats (A–E), each offering single niches for a tree and a shrub. These differ in relative intrinsic stress (S: solid line); low-stress habitats are more easily colonized by individuals of low fitness. Initially, the landscape is occupied by three species of rhizomorphic lycopsid: a laterally branched tree and an unbranched shrub in habitats B and C, and a laterally branched tree only in habitat D. These species have been honed by natural selection in their preferred habitats to local optima of fitness (coincidentally the same level for all three species: upper dashed line, ω2). In this scenario, the parental tree in habitat D continuously produces two types of hopeful monster by mutationally driven saltation: crown-branched trees by suppression of lateral branching, and crown-branched pseudoherbs by suppression of lateral branching plus profound paedomorphosis. Again, all are of the same fitness (lower dashed line, ω1), which is appreciably less than that of the pre-existing species. The fates of identical monsters in different habitats are documented. Note that succcessful establishment (stippled) requires vacant niches of relatively low intrinsic stress; any interspecific competition eliminates the monsters due to their suboptimal fitness, which reflects lack of selective honing (see text).

prompting a similar interpretation of competitive exclusion of the hopeful monsters by the incumbents. However, the intermediate stress level of the habitat (S2) means that it is tenable for the adaptively honed species (ω2) but untenable for the hopeful monsters (ω1); the true cause of their failure is intrinsic stress rather than competitive exclusion.

Obviously, the model outlined in Fig. 6 is simplistic. Firstly, many more than two plant niches can be recognized in any one habitat. Secondly, contrasting niches within a particular habitat differ in intrinsic stress; for example, stress was often higher in the shrub niches than the tree niches of many Carboniferous lycopsid forests due to periodic flooding and consequent inundation of smaller-bodied species. Thirdly, the uniformity of fitnesses among species implied here is not mirrored in nature, where

fitness is a variable, dynamic, and arguably unmeasurable parameter. Fourthly, the relationship between vegetation and environment is more intimate than the model suggests; plants can profoundly modify their habitats (Lewontin, 1993), thereby often reducing intrinsic stress levels that they encounter.

Nonetheless, we are confident that the basic assumptions of the model are valid. Successful establishment of hopeful monsters requires vacant niches of relatively low intrinsic stress; any interspecific competition eliminates the monsters due to their suboptimal fitness, which reflects lack of selective honing. Thus, the environment acts initially as a passive filter of hopeful monsters rather than the active agent of their evolution. Subsequent imposition of selection stabilizes phenotypic expression, thereby increasingly canalizing the new developmental programme (Carson, 1985; Carson & Templeton, 1984; Iltis, 1983; Valentine, 1980).

Canalization, character loss and complexity

It has long been recognized that major developmental events become increasingly canalized within lineages as they evolve (Levinton, 1988; Rachootin & Thomson, 1981; Waddington, 1942). In particular, developmental control becomes increasingly integrated and interdependent. Also, structures formed later in ontogeny become dependent on earlier events, increasing the burden on the earlier-formed (and generally physically larger) structures. Theoretically, canalization is of adaptive benefit to the long-term survival of the species (Kerszberg, 1989), but it also reduces the chances that the species in question will generate further distinct species by neodarwinian processes, given its declining ability to accommodate developmental variation.

Saltation breaks that canalization, toppling the hopeful monster from the adaptive optimum of its parent(s) but also freeing the potential lineage for radical reorganization of form (Arthur, 1984, 1988; Bateman, in press; Carson, 1985; Erwin & Valentine, 1984; Goldschmidt, 1940; Levinton, 1988; van Steenis, 1976). Rather than creating new D-genes, most mutationally driven saltational events involve the suppression of one or more pre-existing D-genes, resulting in the loss of features coded for by those genes (e.g. Tucker, 1988). Other features that develop later in ontogeny and are attached to the suppressed feature are also liable to be lost in consequence (the 'domino effect' of Bateman, in press), leading to a decrease in overall morphological complexity (cf. Atchley & Hall, 1991; McShea, 1991; Wimsatt & Schank, 1988). In some cases, these secondary losses are avoided by epigenetic readjustment; gene interactions may allow the dependent features to be expressed elsewhere on the body plan (heterotopy). Pleiotropy has the converse effect; suppression of a gene expressed in several parts of the body is likely to have particularly profound effects on morphogenesis, and should generally lead to considerable simplification of form.

Superficially, such character losses appear improbable agents for innovative evolutionary change. However, by breaking canalization and simplifying development, they clear the evolutionary palette for future adaptive innovation. The 'development ratchet' (Levinton, 1988; Vermeij, 1987) is reset at a lower level, leaving a combination of adaptation and contingency to define a new evolutionary trajectory for the lineage should it survive the establishment bottleneck. Indeed, simplification proved to be the most powerful of several forces driving the evolution of architecture among the rhizomorphic lycopsids (Bateman, in press; Bateman *et al.*, 1992). It is difficult to envisage centralized determinate growth and secondary thickening as adaptive in

smaller-bodied rhizomorphic lycopsids such as *Isoetes*. Rather, these characters represent a significant waste of resources, and make biological sense only if they are perceived as unbreakable developmental constraints that refelect evolution from large-bodied trees – trees that benefited greatly from the increased fitness conferred by these characters (Bateman, 1992, in press). Similarly, morphological (Mayo, 1993) and cpDNA (French *et al.*, 1993) cladograms concur that the minute aquatics of the Lemnaceae are nested well within the Araceae; this can only be interpreted as an example of extreme paedomorphosis and ecological specialization.

One last point should be made about D-gene suppression. Clearly, a particular gene can be suppressed in many different ways (for example, transposons could be inserted at different points within the active region of the same gene in different genomes), but the net result may be identical in terms of phenotypic expression. Such 'polyphyly' of hopeful monsters is suspected in the case of widespread occurrences of pseudopeloria in the insect-mimicking orchid *Ophrys apifera* (Bateman, 1985), and is probably a more general phenomenon. It constitutes parallelism as restrictively defined by Kellogg (1990). Thus, two or more saltational prospecies may appear morphologically indistinguishable.

Summary

Figure 7 summarizes the neoGoldschmidtian paradigm advocated in this paper, integrating genomic changes, organismal demographics and ecological niches. In this example, a key D-gene promoting the development of a major growth module is suppressed by mutation in a germ-cell lineage (animals) or reproductively potentiated meristem (plants) of a single ancestral individual. The resulting hopeful monster is dispersed as a mutant propagule, and by good fortune germinates in a vacant niche that presents no competition and a tolerably low degree of intrinsic stress. During the ontogeny of the monster, it becomes apparent that it has lost the ability to produce a particular ancestral growth module; this in turn means that smaller-scale features usually occurring on that module can no longer be expressed. Loss of the module also prompts epigenetic and/or pleiotropic readjustment to accommodate the remaining modules.

The reproductively isolated hopeful monster (prospecies) then successfully reproduces. Initially, the population is small. In effect, saltation constitutes an extreme genetic bottleneck that will be reflected in greatly reduced genetic diversity relative to the parental population – a potentially sympatric parallel of the allopatric founder effect. The small size of the population will also render it susceptible to genetic drift (e.g. Ayala & Valentine, 1979). Nonetheless, successful reproduction marks a switch from a non-adaptive saltational mode to a potentially adaptive gradual mode (Carson, 1985; Davis & Gilmartin, 1985; Iltis, 1983). Expansion of the radical new species and/or invasion of its niche by other species gradually introduce the population to competitive selection, thereby reforming coadapted gene complexes. This prompts equally gradual population-level changes in the gene pool; some features initially retained by the hopeful monsters have lost any function and can be eliminated, whereas others have changed their function and can be appropriately modified. Eventually, a large, viable population (taxonomic species) is established. Thus, classical neodarwinism has a significant role to play in the saltational paradigm, by honing
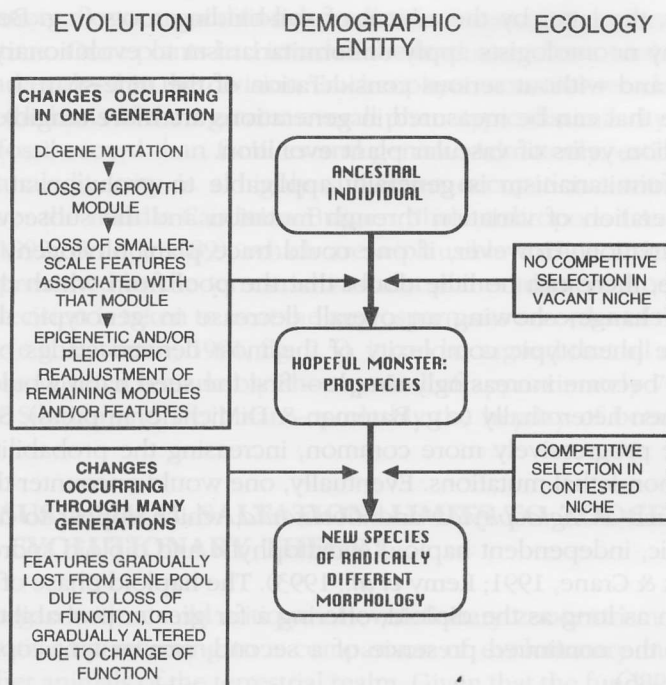
EVOLUTION	DEMOGRAPHIC ENTITY	ECOLOGY

CHANGES OCCURRING IN ONE GENERATION

D-GENE MUTATION
▼
LOSS OF GROWTH MODULE
▼
LOSS OF SMALLER-SCALE FEATURES ASSOCIATED WITH THAT MODULE
▼
EPIGENETIC AND/OR PLEIOTROPIC READJUSTMENT OF REMAINING MODULES AND/OR FEATURES

ANCESTRAL INDIVIDUAL

NO COMPETITIVE SELECTION IN VACANT NICHE

HOPEFUL MONSTER: PROSPECIES

CHANGES OCCURRING THROUGH MANY GENERATIONS

FEATURES GRADUALLY LOST FROM GENE POOL DUE TO LOSS OF FUNCTION, OR GRADUALLY ALTERED DUE TO CHANGE OF FUNCTION

COMPETITIVE SELECTION IN CONTESTED NICHE

NEW SPECIES OF RADICALLY DIFFERENT MORPHOLOGY

Figure 7 Summary of the neoGoldschmidtian paradigm, integrating genomic changes, organismal demographics and ecological niches. In this example, a key gene controlling early development (D-gene) is suppressed by mutation in a germ-cell lineage of the ancestral individual. The resulting hopeful monster is dispersed as a mutant propagule, which by good fortune germinates in a vacant niche that presents no competition and a tolerably low degree of intrinsic stress. During the ontogeny of the monster it becomes apparent that it has lost the ability to produce a particular ancestral growth module; this in turn means that smaller-scale features usually occurring on that module can no longer be expressed. Loss of the module also prompts epigenetic and/or pleiotropic readjustment to accommodate the remaining modules. The hopeful monster (prospecies) then successfully reproduces, eventually establishing a large, viable and reproductively isolated population (taxonomic species). Expansion of the radical new species and/or invasion of its niche by other species gradually introduce the population to competitive selection, altering or removing features by classic neodarwinian, population-level changes in the gene pool and thereby honing the new lineage to a local fitness optimum.

the saltationally generated lineage to a local fitness optimum. Saltation is supradarwinian rather than antidarwinian.

LIVING VERSUS FOSSIL PLANT SALTATION: LIMITS TO UNIFORMITARIANISM IN EVOLUTIONARY THEORY

Uniformitarianism – the constancy of processes through time – has long been a fundamental principle of geology (Gould, 1990; Hallam, 1983; Lyell, 1830–33). Most physical contraventions of the principle, such as long-term changes in atmospheric composition and in terrestrial weathering rates, can be attributed largely to non-uniformitarianism in the Earth's biota – the former prompted by the evolution of

photosynthesis, the latter by the advent of soil-binding roots (e.g. Behrensmeyer *et al.*, 1992). Many neontologists apply uniformitarianism to evolutionary theory, often unconsciously and without serious consideration of the time-span at their disposal; periods of time that can be measured in generations are more tangible than the estimated 420 million years of vascular plant evolution.

Indeed, uniformitarianism is generally applicable to evolution at the molecular level – the generation of variation through mutation and the subsequent history of that genetic variation. However, if one could trace plant phylogeny back through geological time, there can be little doubt that the pool from which that variation is drawn would change, showing an overall decrease in genotypic diversity and a decrease in the phenotypic complexity of the most derived clades present. Reproduction would become increasingly simple – first the seed habit would be lost, then heterospory, then heterothally (e.g. Bateman & DiMichele, in press). Self-fertilization would become progressively more common, increasing the probability of historical continuity for non-lethal mutations. Eventually, one would encounter the earliest vascular plants, such as *Aglaophyton* and *Cooksonia*, which appear to have possessed near-isomorphic, independent haploid gametophytic and diploid sporophytic generations (Kenrick & Crane, 1991; Remy *et al.*, 1993). The haploid phase of the life history may have been as long as the diploid, offering a far greater probability of mutations unbuffered by the continued presence of a second, non-mutant copy of the allele (Knoll *et al.*, 1986).

This reproductive simplification is paralleled by developmental simplification; although the number of D-genes is modest in the more derived extant clades, it was probably still fewer in primitive fossil groups such as the 'rhyniophytes'. This would increase the average phenotypic effect of D-gene mutations, by reducing the probability of alternative developmental pathways and of epigenetic readjustment to compensate for the genomic change.

However, the most profound contraventions of biological uniformitarianism are ecological. Neobotanical ecology focuses heavily on angiosperms, acknowledging their remarkable species-level diversity. We believe that this largely reflects unusually fine niche partitioning. We further believe that this in turn reflects unusually high frequencies of intimate coevolutionary relationships (for example, with pollinators, herbivores and mycorrhizae) rather than the greater genomic 'rigidity' of non-angiosperms invoked by van Steenis (1976). However, passing back through time, the small-scale niche partitioning of the angiosperms would gradually give way to less diverse communities dominated by non-angiosperms (Bateman, 1991; Behrensmeyer *et al.*, 1992; Niklas *et al.*, 1985). The strengths of interspecific links may remain strong, but the potential total number is greatly reduced. By the time one reached the mid- to late Devonian, the ecological scenario presented in Fig. 6 of two-niche ecosystems would be far less of a parody. There was more opportunity for partitioning existing niches and for increasing connectivity among the species occupying those niches. Moreover, many more niches, and even entire habitats, were vacant at any one moment in time. Opportunities for temporary release from selection, allowing the establishment of hopeful monsters, were far more common. In short, a higher frequency of generation of hopeful monsters in the past is possible, but a far higher frequency of their establishment is certain. The further back in time one travelled, the greater would be the significance of non-adaptive saltation relative to adaptive selection.

The observation allows an additional prediction – one of fractal evolutionary patterns through time. Once plants had invaded the land and a basic tool-kit of terrestrial adaptations had evolved in the division Tracheophyta, taxa that we classify as classes and orders on the basis of their greater overall phenotypic dissimilarity should appear earlier in the fossil record than families and genera. Admittedly, estimation of high-level architectural diversity is a highly subjective occupation – witness the recent controversy over the middle Cambrian Burgess Shale arthropods (*Auct. Mult.*, 1992; Briggs *et al.*, 1992; Gould, 1989), which are a plausible marine animal analogue to the problems presented by the terrestrial vascular plant radiation. Nonetheless, if the controversial decision is taken to treat the angiosperms as an order of the class Gymnospermopsida (e.g. Bateman, 1991, fig. 2.5), it can be argued that all eutracheophyte classes originated over a remarkably short period of approximately 70 million years during the late Silurian and Devonian – probably the heyday of botanical saltation.

PLANT VERSUS ANIMAL SALTATION: LIMITS TO ZOOCENTRIC HOLISM IN EVOLUTIONARY THEORY

This chapter began with a mild critique of evolutionary zoocentrism. We now conclude the narrative by returning to a comparison of evolutionary modes in higher plants and higher animals of the terrestrial realm. Given that the fundamental genomic controls of development in animals and plants are similar, any contrasts must reflect differences in (1) frequencies of mutation and polyploidy, (2) modes of gene expression (both determining the generative phase), and/or (3) different ecological roles (determining the establishment phase). Linking the generative and establishment phases is the sessile life-style of plants, and their consequent reliance on numerous localized meristems for open, additive growth and differentiation. This contrasts starkly with the vagile life-style of higher animals; their generalized, closed and often replacive growth (typically involving a greater number of tissues), and their complex, neurally mediated behaviours.

Beginning with the relative frequency of saltational genetic changes, most plants possess numerous meristems that offer greater scope for both polyploidy and mutation; different branches of the same individual often prove to be genetically dissimilar (e.g. Thomson *et al.*, 1991). This is particularly important with respect to germ lineages. In contrast with vertebrates, the gametes or gamete-producing organs of plants are not sequestered early in development. Any one of the many meristems in any one individual is capable of differentiating into reproductive structures that can pass on mutations acquired during normal somatic growth (e.g. Buss, 1987; Darley, 1990). Indeed, plants appear to have developed specific mechanisms to eliminate, or at least buffer the accumulation of, detrimental mutations (Klekowski *et al.*, 1985).

Differences in gene expression are more problematic. Firstly, meristematic growth offers few commands for apical behaviour and these are generally of the binary, 'on-off' variety (Bateman, in press; Borchert, 1983; Borchert & Honda, 1984). The meristem is either indeterminate or determinate, either it divides or it does not, and either it divides isotomously or anisotomously. There is some scope in plants for intermediate responses that would allow gradual, directional evolution of form, notably by positional interplay between appendicular organs and the axial apical meristems via hor-

monal gradients and/or glycoprotein receptors. Nonetheless, such responses are far more compatible with the generalized growth and cell mobility evident in the more holistic ontogenies of animals. In this context, it is noteworthy that among animals saltation is most easily recognized in arthropods, whose stepwise metamorphic ontogenies and modular segmented growth most closely resemble plant development. Because saltation causes a greater average decrease in fitness among animals than among plants (see later), selection pressures are presumably greater for post-transcriptional and epigenetic flexibility, albeit within heavily prescribed architectural constraints (cf. Gallie, 1993; Goodwin, 1984, 1988, 1993; Goodwin & Saunders, 1992; Løvtrup, 1973; Stebbins, 1992). Furthermore, physiological abortion of hopeful monsters during ontogeny is probably less common in plants than animals; for example, seed plants are presumably more tolerant of developing mutant embryos (including polyploids) than are placental mammals.

The greatest differences between plants and animals concern ecologically mediated establishment; specifically, the theoretical level of fitness required for successful establishment in a particular habitat if vacant, and the actual (higher) level of fitness required for successful establishment in that habitat under specific conditions of competition.

Firstly, intrinsic functional constraints require consideration. In vagile terrestrial animals there is clearly an enormous adaptive advantage to a bilaterally symmetrical body that consists of a core framework subtending paired appendages. Other architectures are frequently generated as hopeful monsters and many transcend the lower, non-competitive fitness threshold for establishment. Unfortunately, the non-competitive threshold is less often relevant for vagile animals than sessile plants. Inevitably, vagile hopeful monsters are immediately assailed by the full force of active and direct competition, for resources such as food and mates, from far fitter organisms.

Plants too have a fundamental architectural constraint, imposed by the facts that (1) their development is centrifugal from a point of origin (prothallus in pteridophytes, seed in spermatophytes) that generates at least one primary axis (stem), and (2) they require distinct negatively geotropic organs for photosynthesis and reproduction, and positively geotropic organs for absorption of water and nutrients; the latter are attached to the former as repeated modular units in unipolar plants, but as a single unit (rootstock) in bipolar plants. Nonetheless, within this constraint lies an enormous range of potential architectures that reflect great flexibility in the meristematic expression of particular organs.

Ecologically, this argument can be placed in a framework of four progressively more stringent thresholds of establishment. Many of these architectures are capable of surpassing the non-competitive establishment threshold for germination and growth (threshold 1). More importantly, the indirect nature of competition among plants gives the hopeful monster a far greater probability of reaching reproductive maturity (threshold 2), decreasing the differential between the non-competitive and actual competitive thresholds (3). Moreover, the potential range of competitors is more restricted due to the slow pace and *ad hoc* unconscious migration of plants relative to animals within particular habitats, as they attempt to accommodate to local changes in resource availability (threshold 4). Thus, competitive displacement is far less common among plants that animals, requiring an environmental perturbation to upset the local ecological equilibrium (DiMichele *et al.*, 1987, 1992). Yet more significantly, all four establishment thresholds for the average plant are lower than for the average

animal, and the differentials among those thresholds are also less. Thus, the degrees of freedom for non-selective experimentation in form (the 'patio ludens' of van Steenis, 1976) are far greater in plants than animals; at any one moment in time, far more of their characters are likely to be adaptively neutral. This is turn leaves much greater opportunity for canalization into a particular suite of developmental constraints that owe their origin to historical accident rather than vectorial adaptation (contingency sensu Gould, 1989). Comparison of plant and animal cladograms suggests that architectures are much less likely to be evolutionarily conserved in plants than in animals.

The modular growth of plants and differentiation into permanent core organs and transient appendages renders them far less integrated and holistic than animals (cf. Hay & Mabberley, 1991). Many plant organs, notably appendicular organs such as rootlets, leaves, and reproductive organs but also non-appendicular stems in seed plants possessing axillary branches, terminate ontogenetic cascades. Reiterated and to a large degree independent, they can be evolutionarily modified without a resulting domino effect on other organs formed later in development. Such organs have high degrees of physiological and developmental independence; they can become individually canalized. This in turn permits evolutionary independence in the form of mosaic evolution; differential rates of evolution and degrees of character conservation among different organs (Knoll et al., 1984; Meyen, 1987; Thomas & Spicer, 1987). Bateman (in press) used the rhizomorphic lycopsid phylogeny (Fig. 5) to demonstrate that cladograms offer the opportunity to quantify such mosaicism. He noted that intermediate-scale characters such as vascular anatomy and cone morphology were more highly conserved than large-scale architectural features under pleiotropic control (a few D-genes control the development of many characters) and small-scale features such as spore ornamentation that are unlikely to be subject to strong selection pressures.

Whether these conclusions can be generalized to other clades remains a moot point. Certainly, arguments have been made for the non-adaptive evolution of vascular morphology of extinct progymnosperms (Wight, 1987), and successful saltational changes in angiosperm floral morphology have been well documented among extant Orchidaceae (Bateman, 1985; Leavitt, 1909; McCook & Bateman, 1990). Some occur iteratively, as mutant individuals within widely distributed populations of the 'wild type' morph (e.g. pseudopeloric individuals of Ophrys apifera: Bateman, 1985). Others are more abundant, form homogeneous interbreeding populations, and become recognized as species (e.g. the pseudopeloric species Phragmipedium lindenii). Yet others originate by saltation but subsequently experience repeated speciation events, potentially by neodarwinian processes (e.g. the type B peloric genus Thelymitra).

Vagility and cerebralization also allow mate selection in higher animals, whereas sedentary plants rely on ad hoc dispersal of gametes; any incompatibility is purely physiological rather than behavioural. Moreover, most plant species consist of hermaphroditic individuals, and many of these are self-compatible, particularly among the more primitive clades. Thus, many teratological plants have the potential to establish their own mutant lineages without the aid of a partner, nullifying the improbable requirement for two compatible and mutually attracted hopeful monsters that led to the ridicule of Goldschmidt's (1940) original zoological formulation of saltation and continues to preoccupy zoological saltationists (e.g. Arthur, 1984).

Thus, the most important difference between evolutionary modes in higher animals and higher plants is the presence and absence respectively of direct competition, not only for resources but also for reproductive partners. This greatly diminishes the relevance of Malthusian concepts to plant evolution, and thereby of the scenarios of competitive selection that drive modern evolutionary zoology (cf. Eldredge, 1989; Knoll, 1984; Levinton, 1988; Vermeij, 1987). Nonetheless, saltation has undoubtedly also played a major role in the evolution of many animal lineages (e.g. Ahlberg, 1992; Mooi, 1990).

THE SALTATIONAL PARADIGM IN A BROADER EVOLUTIONARY CONTEXT

Figure 8 summarizes our view of a typical pattern of vascular plant evolution through time. Neodarwinian vicariance emphasizes population-level divergences, often of small allopatric or parapatric groups. NeoGoldschmidtian saltation, both dichotomous (mutational) and reticulate (allopolyploid), emphasizes individuals that are often sym-
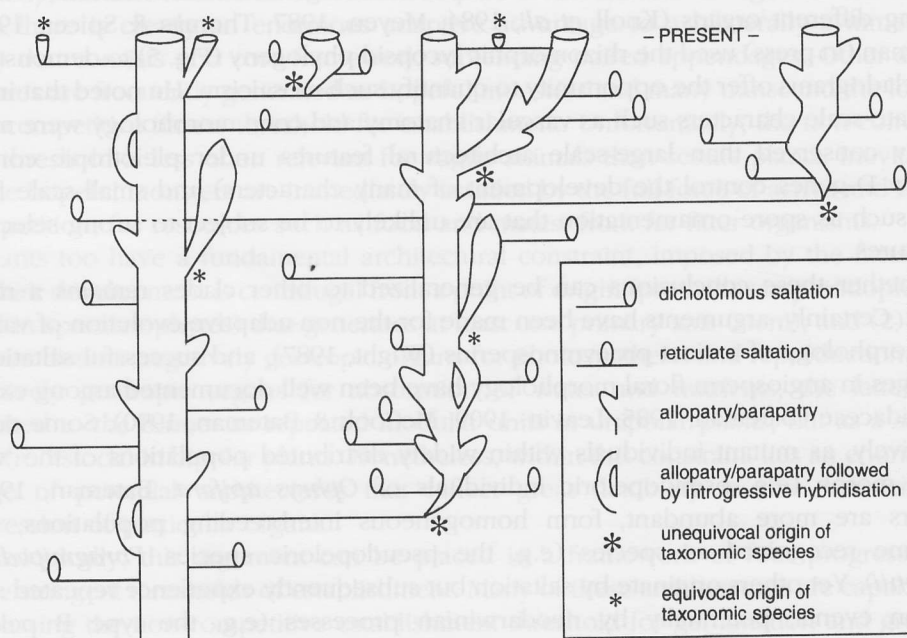

Figure 8   A typical pattern of evolution in vascular plants, viewed as phenotypic changes through time. Prospecies are produced frequently by neodarwinian allopatric vicariance and by both dichotomous (mutational) and reticulate (allopolyploid) neoGoldschmidtian saltation. Most prospecies become extinct rapidly, often by introgressive hybridization in the case of vicariant gradualist lineages. Very few prospecies pass the dual tests of increased abundance and long-term continuity necessary for recognition as taxonomic species (large asterisks). Note that some lineages are difficult to categorize (small asterisks), either because they achieved intermediate population maxima and longevities or because they evolved too recently to assess their longevities. We believe that the ratio of successful to equivocal plus unsuccessful taxonomic speciation events shown in this diagram (4:44) is unrealistically high.

patric with their parent(s). All three mechanisms generate vast numbers of prospecies, though most terminate after a few generations. Termination usually occurs by extinction but can also be caused by introgressive hybridization, particularly in the case of vicariant gradualist lineages. Very few prospecies pass the tests of increased abundance and long-term continuity necessary for recognition as historically significant taxonomic species, and even fewer generate further taxonomic species. Thus we support the emphasis placed on specification and reproduction in the species selection evolutionary model of Futuyma (1987) and Gould & Eldridge (1993), but argue that a new species can be born instantaneously and *in extremis* consist only of a single organism.

Dichotomous saltation is more likely to produce radical new lineages than are reticulate saltation or vicariance, though the magnitude of its maximum effect has diminished through time due to increased developmental canalization and ecological saturation. Nonetheless, saltation may remain the most frequent mode of speciation among vascular plants (van Steenis, 1976). This implies a strong element of chance in evolutionary patterns, and reinforces Gould's (1989) emphasis on contingency; replaying the history of life on Earth would presumably generate a very different biota.

These evolutionary hypotheses require testing by interspecific comparison in a rigorous conceptual framework. At present, comparative biology is pursued on two very different scales – morphological and molecular – that are in practice treated as mutually independent. Morphological phylogenies have the potential to describe the phenotype of the whole organism, but they tend to be static (describing only reproductively mature individuals) and cannot accurately represent underlying genotypic changes. Comparisons of base pair sequences, such as the approximately 1428 base pairs of the phylogenetically popular *rbc*L gene, consider only a tiny proportion of the total genome (i.e. of the available evidence), and only a small proportion of any set of coded sites vary among species and thus are phylogenetically informative. Moreover, many such studies fail to distinguish phenotypically expressed base pairs from the inactive bulk of the genome.

It has long been accepted that the fundamental unit of evolutionary change is the gene but that such changes are mediated via the phenotype of the host organism (the replicators and interactors respectively of Dawkins, 1982, 1986, 1989). Recent studies of D-gene expression in plants (e.g. Coen, 1991; Coen & Carpenter, 1992; Meyerowitz *et al.*, 1992) provide a vital causal link between genotype and phenotype – replicator and interactor – that allows reciprocal illumination between these two contrasting manifestations of the evolutionary process. D-genes can be coded cladistically in order to make the crucial distinction between primitive and derived states and, as we have shown, the resulting cladograms can be used to test competing hypotheses of underlying evolutionary mechanisms. Despite recent advances (Chasan, 1993), biologists have been surprisingly slow to combine relevant concepts of gene expression, developmental control, phylogeny reconstruction, ecological filtering of phenotypes, and evolutionary theory into a truly integrated evolutionary synthesis. This problem has been exacerbated by over-enthusiastic generalization from parochial studies of a few 'flagship' species to all-embracing evolutionary theories. Nonetheless, we are confident that future syntheses will confirm our opinion that plants have their own distinct approach to the evolution of shape and form.

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