

HOMOEOSIS, CANALIZATION, DECANALIZATION, 'CHARACTERS' AND ANGIOSPERM ORIGINS

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Reproductive structure is considered in the context of process morphology: the significance of homoeotic transformations is commented on in Araceae and other modern angiosperms. Disruption leads to the rearrangement of processes and destabilization of process combinations, or decanalization. This is apparently more readily achieved in certain extant angiosperms than in others; both environmentally triggered decanalization, including galling, and genetically prompted decanalization are discussed and illustrated with examples including those leading to the expression of 'lost' features. This is extended to a consideration of 'character' comparisons in extant angiosperms and possible pitfalls there. Finally, this approach is applied to the relationship of certain extant groups of seed-plants and their fossil allies and it is concluded that modern ones are (distantly) interrelated relics of a complex of 'hemiangiosperms' of the Triassic.

REPRODUCTIVE STRUCTURE

Insofar as it is not possible in plants to distinguish germline from the soma, reproductive structure, that is sexual reproductive structure, at its most simple conception, must be considered to be the series of transformations leading to cells undergoing meiosis and thus the formation of haploid gametes, followed by the paraphernalia of fertilization, which leads to the unfolding of a new generation. Such a series constitutes transformation of processes (an ontogenetic continuum) in the sense of Sattler (1992, 1993).

In classical morphological studies, the generally irrevocable change in a meristem leading to determinate growth manifest in floral primordia is the phase in the continuum after which 'reproductive characters' are recognized by taxonomists; these are the bases of much of the arrangement of angiosperms into families and higher taxa. Such an approach can often lead to the unsatisfactory attempted separation of the organism into fragments, which are labelled with essentialistic terms such as 'inflorescence' or 'bracts'. However, whole overground parts of herbaceous plants can in effect be photosynthesizing 'inflorescence' (Mabberley, 1974), for example in Liliaceae (sensu lato) *Asparagus* (annual overground parts), *Ruscus*, *Danae* (more or less perennial but hapaxanthic aerial shoots) and *Semele* (perennial and pleoanthic aerial shoots). Indeed, hapaxanthic organisms (or shoots) in general make clear the artificiality of sharp demarcation between reproductive and non-reproductive structure expressed in the static terms of classical morphology.

Instead we can view both vegetative and reproductive structure as integrated process involving a transition of changes in morphological and differentiation process parameters. This

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This paper is dedicated to B.L. Burtt on the occasion of his 80th birthday.

view is more organic than the classical view, the terminology of which may be commonly useful, if inadequate and, at times, quite distorting when structures are forced into categories. One such case may be the Araceae, in which it has been argued (Hay & Mabberley, 1991) that 'leaf', 'flower' and 'inflorescence' as static structural terms applied to a structural sequence (vegetative before reproductive) and hierarchy (flower as subunit of inflorescence) break down due to superimpositions caused by hypothesized homoeotic reorganization, leading to an apparent decanalization and proliferation of morphological novelty.

Liberated from the stranglehold of using rigid categories, it is possible to consider the concept of partial homology. With respect to flowers and inflorescences, the old divide between 'euanthia' and 'pseudanthia' (Arber & Parkin, 1908) could be argued to be merely the result of a pigeon-holing approach. Attempts at forcing all such reproductive structures into one or other category absolutely may well restrict our thinking about them. We have pointed this out with respect not only to aroids but also to *Houttuynia* (Saururaceae) and *Hedyosmum* (Chloranthaceae). Others have dealt with vegetative structures such as 'evergrowing' leaves like those in *Chisocheiton* and *Guarea* spp. (Meliaceae) similarly (Mabberley, 1979; Fisher & Rutishauser, 1990), proposing that they are partly homologous with shoots, partly with leaves (Sattler, 1993). For particular purposes it may be helpful to consider either one or the other, such attitudes being complementary. We want also to point the way to avenues of new thought in other extant groups, where a consideration of homoeotic transformations, once recognized as plausible, may help in elucidating evolutionary relationships. Finally we would now extend this further — to fossil groups.

'TRANSFERENCE OF FUNCTION', HOMOEOSIS AND CANALIZATION

Leavitt (1905) described a number of cases of teratology in angiosperms, where organs were formed in unorthodox positions, and considered such to be 'morphic translocations', later (1909) using the term homoeosis for such phenomena; the idea was developed in a different context by Corner (1958), who called it 'transference of function'. In zoology, particularly entomology, mutations promoting such translocations are known as homoeotic mutations. Sattler (1988) has provided a review of homoeosis in plants, while Coen & Meyerowitz (1991) and others have posited a genetic mechanism to account for mutants in flowers of *Antirrhinum* manifesting irregularities in the constitution of particular whorls. 'Crinkly petal' mutants in *Clarkia* are also considered to be homoeotic mutants (Smith-Huerta, 1992). Homoeotic mutants suggest that once-canalized structures, of easily inferrable homology, can be decanalized with a greater or lesser confusion of homology ('hybridity').

In *Saraca* (Leguminosae), one of Corner's original examples, Tucker (1992) has argued that the homoeotic transformation, where stamens appear in petal positions, is due to the primordia corresponding to petal primordia in allied plants becoming 'uncommitted' and differentiating into stamens, indicating an evolutionary disruption or decanalization. For Zingiberaceae, the 'fixing' of a homoeotic transformation has been posited as the explanation for floral evolution (Kirchoff, 1991) and, in Fagaceae, a hypothesis on the disputed origin of the cupule so typical of the family rests on a homoeotic event (Jenkins, 1993), while in Araceae partial homology is proposed between flower and floral organs and between perianth, spathe and leaf (Hay & Mabberley, 1991). In this last case, evolution of a prototypical aroid involves reconstitution of

an inflorescence in which the processes of floral differentiation are acted out twice, at two levels. The first is in a large floral apex most of which becomes the spadix, and the second is in what would otherwise have been floral organs, making what are conventionally regarded as the flowers. In addition the spathe is reconstituted by combining the processes of perianth formation with those of a foliage leaf. In this hypothesis, the homoeotic event leads to a disruption of the topography of the epigenetic landscape such that relationships between processes are rearranged and process combinations become destabilized, resulting in what has been called decanalization.

DECANALIZATION AND POSSIBLE MECHANISMS

In Leguminosae, Tucker (1992) also argued that the petal-less flowers of *Ceratonia siliqua*, which have a great variation in floral parts and other reproductive features, manifest the results of decanalization from an evolutionary point of view. A certain amount is now known about how this can be brought about in living plants. Canalization marks 'advanced' angiosperm groups when these are compared with 'primitive' groups such as Nymphaeaceae, within which transitions are found between elsewhere often canalized patterns — transitions between perianth and androecium, superior to inferior ovaries, orthotropous to anatropous ovules, 'ringed' or 'scattered' vascular bundles, etc., all within a group which is ecologically rather restricted. Canalization can, however, be overcome through mutation or environmentally.

ENVIRONMENTALLY TRIGGERED DECANALIZATION

Experimentally, surgery can affect the primordia in potato, to give rise to leaves or centric organs (Sussex, 1955) and is the stuff of successfully rooting cuttings, which cannot be effected in certain groups, e.g. many Coniferae, where other canalization phenomena include the perpetual horizontal growth of rooted branches of, for example, *Araucaria heterophylla*, and the occasional 'reverting' of *Sequoiadendron* cultivars of similar origin. Natural 'surgery' in the form of attack by predators, notably gall-insects, can produce organs intermediate between those generally produced — stems and leaves on a shoot for example — besides comparatively featureless tumour-like growths. Again, 'new' organs can be produced, like the branched hairs in *Solanum dulcamara* promoted by mite attack (Westphal, 1985) or, most spectacularly perhaps, the spiny galls of dipterocarps promoted by attack from coccids (Jenkins & Mabberley, 1994). In this last case, the most parsimonious explanation for the saltatory appearance of spines, organs otherwise unknown in the family Dipterocarpaceae, is that the insect in effect unmasks developmental routines otherwise suppressed and that the canalization of spinelessness can be overcome by the influence of the insect. The effect is to provide a fruit-like structure — the galls of *Hopea ponga* were long considered to be small breadfruits — as an armed home for the developing gall-insects, so that a reproductive routine for seed protection has apparently been hijacked by the parasite. As spines are features of related plant taxa, the action of the insect would appear to promote an atavism. Such 'genetic recall' (cf. Burt 1994) has been demonstrated in animals, notably in birds, where grafts of mammalian tissue in the embryo (Kollar & Fisher, 1980) promote the development of teeth, the presence of which is considered atavistic.

It may well be that the morphological effects are the work of differential proportions of the well-known plant-growth regulating substances. *Streptocarpus rexii* (Gesneriaceae), a phyllo-

morphic species manifesting remarkable morphological novelty (Jong & Burt, 1975), can be induced to produce what is thought to be an ancestral caulescent growth form; similarly, caulescent species can be induced to be phyllomorphic (Rosenblum & Basile, 1984). In at least one gall example, red-bean gall in willow (Higton & Mabberley, 1994), the control appears to be exerted by moieties in the colleterial fluid injected by the galling insect, in this case a sawfly, but whether these moieties are growth-substance analogues or whether they affect the synthesis of growth substances from precursor pools already present in the tissue is still to be clarified. Sawhney (1992) has shown how plant-growth regulators and temperature conditions affect the development of stamens in the stamenless-2 mutant of tomato and that these effects are modified through changes in proteins, including some specific enzymes. The primordia that normally form stamens can be induced to form either stamens or carpels, which incidentally shows how unisexuality could arise without primordial abortion of one sex.

Sawhney also demonstrated that plant-growth regulators and temperature affected the eventual 'fusion' of such organs, a condition known in the 'solanifolia' mutant where such 'fusion' is associated with the size of the apex and the number of organs. Whether environmental factors are responsible for the changing number of floral parts observed in many plants flowering over long periods (cf. Briggs & Walters, 1984: 45) or the appearance of vegetative parts in the flowers of *Rubus* (Rosaceae) late in the season (Obeso, 1987) and similar changes in *Calendula* (Compositae; Usha Rao & Mohan Ram, 1985) or the occasional occurrence of 'separate' petals in sympetalous groups, e.g. *Erica cinerea* var. *schizopetala* (Ericaceae) and *Convolvulus arvensis* f. *laciniata* (syn. var. *stonestreetii*) (Convolvulaceae) is still uninvestigated. Certain similar examples are known to be fixed mutants, however; for example, *Rhododendron stenopetalum* (the common cultivar of the wild '*R. macrosepalum*' (Ericaceae)) has an atypical deeply lobed corolla and leaves more linear than those of the wild plant.

GENETICALLY TRIGGERED DECANALIZATION

As far as genetically fixed mutants are concerned, some 'single-gene mutants' promoting major morphological changes may be of a type affecting combinations of developmental routines, for example architectural mutants (Hallé, 1978) such as foxtailing in pines. Certain other single-gene mutants may have a broad morphological effect by interrupting in a pervasive way meristematic activity throughout the life of an organism from vegetative to 'reproductive' phases, e.g. laciniate mutants of *Chelidonium majus* (Papaveraceae), where leaves and petals are similarly divided due to meristematic irregularities. This should be compared with apparently similar phenomena at the species level, e.g. the flowers but not the leaves of *Hibiscus schizopetalus* (Malvaceae), or at the generic level, e.g. the leaves and flowers of *Schizopetalon* (Cruciferae). Other examples of meristematic irregularities include the bizarre cup-shaped leaves of *Codiaeum variegatum* 'Nepenthifolium' (Euphorbiaceae) and *Ficus benghalensis* 'Krishnae' (Moraceae) or the cristate inflorescence forms of *Celosia argentea* (Amaranthaceae).

In *Plantago lanceolata*, Groenendaal (1985) describes what appears to be a hierarchy of developmental sequence controls. These have a varying susceptibility to perturbation, some being modifiable by environmental factors, others mainly by mutation. Indeed, the very plasticity of more or less stationary organisms could be viewed as one extreme of this continuum, the other being the rather inflexible sequences leading to floral features considered so important in classification.

The foregoing show that something is known of decanalization in terms of mutation and biochemical process and that the ready manipulation of developmental process by humans and other animals provides a model for the importance of the phenomenon in evolution. We would add that atavism may also be manifest after hybridization, a phenomenon of fundamental importance in plant evolution, if ruled out in that of most animals. Examples of such 'lost' features recovered artificially by hybridization in nurseries include the stipules of \times *Fatshedera lizei* (Mabberley, 1987: 224), when no species in either parental genus, *Fatsia* and *Hedera*, has stipules, though they are common elsewhere in their family Araliaceae: it would be of interest to look into the presence of such organs in *Viburnum elongatum* (Caprifoliaceae) in an otherwise stipule-less genus (Cronquist, 1988: 183). In flowers, '*Eranthis* \times *tubergenii*' (Ranunculaceae) has more carpels than either of its parents, *E. hyemalis* and *E. cilicica* (which are often considered conspecific!), as well as organs intermediate between the perianth segments and stamens (Mabberley, 1987: 209).

BIOLOGICAL FORM AND CHARACTERS

The study of 'inferior' ovaries and notably 'acarpellate gynoecea' (Sattler, 1974) has not only made 'explanations' such as 'fused carpels' otiose but has shown that the development of such structures, apparently similar at maturity, differs although the ecological effect may be similar. In *Calla* (Araceae), it has been suggested (Lehmann & Sattler, 1992) that the so-called etepalate condition has arisen by homoeotic transformation of tepals into stamens. In at least some of these homoeotic structures some phylloic growth occurs, so that the tepals do not seem to be completely lost. Codifying therefore requires some qualifying hypothesis, for it would be very differently carried out if the tepals were considered to have been lost and the outer stamens merely bigger. The conceptualizations required in describing organisms are not self-evident.

An example from vegetative structure is that of *Ficus* (Moraceae), where Corner (1967) showed that the simple elliptic leaf with a drip-tip, so typical of lowland rain forest trees, had arisen in various ways and that the history could be read in the venation. In other words, there have been several evolutionary-developmental solutions to an ecological problem leading to the same 'character state' in terms of leaf shape. In short, just as wings in birds, bats and bees may be functionally equivalent, the leaf outlines of the fig leaves need not necessarily be homologizeable from an evolutionary point of view: an obvious matter when the process of leaf formation is considered. In the fig leaves, the venation patterns of the mature leaves show that different meristematic regions are active to give the different patterns though the leaf shape is the same. It follows that if the genus *Ficus* is monophyletic with respect to the early *Ficus* species and their leaves, there has been a 'transference of function', in this case the generation of mesophyll cells, from one part of a developing leaf to another. Codifying structure in terms of 'character states' does not describe biological reality since the abstraction of, in this instance, shape, while being a perfectly good 'character', leads to a not only incomplete but also misleading picture in failing to portray the full array of processes that may lead to similarly categorized structures.

The dissection of organs and, indeed, organisms into bits for ease of data-handling has been criticized by Gould & Lewontin (1979) and, although a lot of what they have to say may appear to be more germane to the study of the more integrated development of motile animals, it has

become increasingly accepted that in plants it is better to consider an organism and what are perceived by many as its component parts at any one time as a snapshot in a dynamic transformation of growth, maturity and senescence, and that any particular perceived static structure is actually a phase of what Sattler (1992) has termed process morphology. That the scientific approach has been dissective is undeniable. But, due to the nature of perception in human beings, that approach, though empirical, does not disclose an objective reality. Rather, it, like process morphology, generates abstractions with a greater or lesser degree of adequacy of reference to reality. Process morphology, it is argued, is a more adequate approach since processes, though abstract, interlace. Organisms are described as combinations of processes, each significant in its relation to the others but not in itself alone, whereas the static view of fragment morphology (over)emphasizes dislocated topographic features at any one particular time in the dynamic continuum that is organism. These two endeavours, perhaps oversimplified as reductionist and holistic, have often been complementary as can also be seen in the history of ecological research, for example in succession (see Mabberley, 1992).

To a developmental biologist, homologous character states refer to conditions representing end-products of homologous developmental sequences. Such sequences are not biologically identical and they may not be identical according to abstract criteria such as relative position and/or special quality: 100% homology is not to be expected. Structure and process may be homologous to a varying degree (Sattler, 1984, 1994). Where such character-state differences are constant at what is perceived to be a high taxonomic level, process combinations ('developmental routines') are said to be canalized. To a systematist, the identification of constant character-state differences provides the basis for classification. Taxa are perceived as distinguishable by one or more diagnostic characters or by a suite of differential characters. Some taxa, such as the Nymphaeaceae (and sometimes individual organisms within them) express a range of character states, which are constant in other taxa afforded similar rank. From an evolutionist's point of view, the extent to which process combinations are constrained would appear to change with time, which is the explanation for the varying value of character-state differences within clades through time and between contemporary groups. It is clearly a mistake, therefore, to use character states across the boards of space and time: in palaeobotany, it would lead to the dissection of a fossil flora according to modern criteria, a sort of Whiggish interpretation of natural history (Mabberley, 1984). Moreover, character-state transformations (if one accepts this common but dubiously valuable metaphor (Hay & Mabberley, 1994; Sattler, 1994; Hay, submitted) cannot be considered uniformly across, say, all modern angiosperms: but how far down the taxonomic hierarchy is it necessary to go before one can be reasonably sure of dealing with equivalents? Would one be at the level of a particular taxon *and* its supposed 'outgroup' as used in cladistic analysis?

'CHARACTER STATES' AND ANGIOSPERM ORIGINS

The coding of, say, angiosperms in terms of 'character states' represents, in effect, an 'Urpflanze' or hypothetical type description of an abstracted idealized organism, a metaphysical summation of the relationship between contemporary organisms included within the group. It does not constitute the codification or reconstruction of a prototype. Does such a coding have anything to say about the evolution or origin of a group? The methodology of phylogenetic systematics, pace

pattern cladists, has nothing to say, yet those assessing for example the relationships of angiosperms and gnetopsids (e.g. Doyle & Donoghue, 1986) use that methodology to conclude that angiosperms have not been derived from gnetopsids.

As with now abandoned advancement indices, abstracted codings do not deal with organisms. Encoding angiosperms as a whole in the same way as, say, the living species *Welwitschia mirabilis* (Gnetopsida) is incongruous. However, if selected species were encoded in the context of particular comparisons this incongruity is avoided and better evolutionary insights might be generated.

Using such an approach with fossils would avoid the trap of having to assign them to pre-existing classificatory groups (cf. Hughes, 1976; Mabberley, 1984) which are meaningless outside the time-frame when they were recognized (Green, 1991). To continue with the angiosperm/gnetopsid saga, it is increasingly apparent that the three extant isolated genera referred to the modern group Gnetopsida are probably not closely allied (Eames, 1952; Martens, 1971). Beyond some pollen grains and one Cretaceous megafossil (*Drewria potomacensis*; Crane & Upchurch, 1987), there is apparently no fossil ancestry, though, long ago, Arber & Parkin (1908) suggested that this might be due to the fossils of the group being attributed to the 'angiosperms'. Indeed, with a more thorough examination of modern gnetopsids the so-called diagnostic characters of modern-day angiosperms, save triploid endosperm, are seen not to be so, such that the peddlers of the parallelism hypothesis (that all such features have arisen in parallel in gnetopsids and angiosperms) have an increasing credibility problem: vessel-elements (Macduffie, 1921; Muhammad & Sattler, 1982), chemistry (Gottlieb & Kubitzki, 1984), double fertilization and endosperm (Friedmann, 1990, 1992) and pollen-wall development (Zavada & Gabarayeva, 1991). Indeed, it seems most parsimonious to conclude that the angiosperms and gnetopsids of today represent the descendants of Jurassic seed-plants, Arber and Parkin's hypothesized 'Hemiangiosperms', not referable to either group in its modern sense, and that not only pigeon-holing fossils is thus futile but using such categories in a historical sense must mean that they represent paraphylies. In short, angiosperms are gnetopsids, or vice versa. Such an assertion removes problems (pseudoproblems) such as 'Were the angiosperms primitively vessel-less?', for it is reasonable to agree, in this context, with Carlquist (1987), who concludes in the very general context of wood 'evolution', 'If vessel specialization has occurred in a polyphyletic fashion, vessel origin has also occurred polyphyletically, because the two phenomena are intercontinuous'. Indeed, this argument can be extended, in the light of findings in the modern gnetopsids, that 'typical' angiosperm features have arisen independently resulting in reticulate relationships within the angiosperm-gnetopsid clade, a conclusion reached by Meeuse in 1990 (Meeuse, 1990).

The 'origin of the angiosperms' can thus safely be pushed back into the Jurassic and even earlier times, which chemical evidence (Martin et al., 1989) suggests to be the case. The work on the fossil *Sanmiguelia* from the Triassic (Cornet, 1989), a seed-plant neither monocot nor dicot (nor gnetopsid) in the modern sense, a weakly branched pachycaul of moist habitats (cf. Corner, 1966: 277), is therefore critical.

ACKNOWLEDGEMENTS

DJM is grateful to Professor Carrick Chambers for the award of a Trust Visiting Research Fellowship at the Royal Botanic Gardens Sydney in 1993, when this paper was written. We are indebted to Professor Rolf Sattler for his helpful comments on the manuscript. This is an extended version of a paper given in the symposium 'Systematic Aspects of Reproductive Structure' at the XVth International Botanical Congress, Tokyo; we thank Professor Klaus Kubitzki for his invitation to present it.

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