

# Transference of function, heterotopy and the evolution of plant development

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## ABSTRACT

The concept of transference of function, developed by E. J. H. Corner, refers to situations in which a particular ecological function carried out by one part of an ancestor is transferred to another spatial location in a descendant species. Under this view it is necessary that both the ancestral and derived structures fulfill the same biological role and that there be phylogenetic continuity between the use of the ancestral and derived structures. Transference of function can entail heterotopy, where a genetic program formerly expressed in the ancestral location comes to be expressed in the derived location. We refer to transfer of function via heterotopy as homologous transference of function, because the expression of genes typical of one structure in another structure constitutes the sharing of genetic identity between those structures. We distinguish "homeoheterotopy," the transfer of genetic identity among pre-existing structural modules, which can explain transference of function, from "neoheterotopy," the production of a module in a novel location, which cannot. We discuss the hypothesis that transference of function generally involves structures in close physical proximity, briefly explore the consequences of homeoheterotopy for concepts of homology, and consider the possibility that certain groups of organisms, such as angiosperms, are especially prone to homeoheterotopy and transference of function.

## 4.1 Introduction

The great tropical botanist E. J. H. Corner was a keen observer of plant structure and diversity. In the course of his work he observed a pattern that he considered noteworthy because of its implications for the mode of morphological evolution. He noticed that among closely related plants one often finds that different species fulfill the same ecological function through the elaboration of different organs. For example, fleshy structures associated with seeds can be derived from quite different organs yet fulfill the same role of attracting vertebrate dispersers (Corner, 1949a, b). In a paper presented to the Linnean Society to commemorate the 100th anniversary of the Darwin and Wallace presentations on natural selection, Corner (1958) enumerated many putative examples of transference of function (Table 4.1) and discussed developmental mechanisms that might underlie this phenomenon. At that time, however, too little was known about phylogenetic theory and mechanisms of

Table 4.1 Examples of transference of function proposed by Corner (1958)

Function	Alternative locations	Taxa involved
Anthocyanin production	Leaf underside; petiole; node; internode; young leaves; old leaves	Angiosperms
Petal function	Petals; calyx <sup>1</sup>	<i>Saraca</i> vs. <i>Pahudia</i> (Fabaceae)
Initiation of flowers	Leaf axil; leaf primordium itself	Angiosperms vs. Brassicaceae ( <i>Capsella</i> ) <sup>2</sup>
Flower	Flower; inflorescence	<i>Euphorbia</i> , Asteraceae etc.
Compound fruit	Infructescence; simple fruit	<i>Parkia</i> vs. <i>Archidendron</i> (Fabaceae) <sup>3</sup>
Production of ovules	Carpels; receptacular tissue or sepal internodes	Apocarpous vs. syncarpous angiosperms
Fleshy fruit-associated structures	Peduncle; pericarp	<i>Anacardium</i> vs. <i>Mangifera</i> (Anacardiaceae)
	Pericarp; receptacle	<i>Rubus</i> vs. <i>Fragaria</i> (Rosaceae)
	Pericarp; sepals; inflorescence axis	Unspecified Moraceae vs. <i>Morus</i> vs. <i>Artocarpus</i>
	Pericarp; inflorescence axis	<i>Carludovica</i> (Cyclanthaceae) or <i>Monstera</i> (Araceae) vs. Araceae
	Pericarp; sepals; receptacle	<i>Pernettya</i> vs. <i>Gaultheria</i> vs. <i>Vaccinium</i> (Ericaceae) <sup>7</sup>
Wings	Seeds; fruit	Species of <i>Ricotia</i> (Brassicaceae)
	Seeds; fruit	<i>Sterculia alata</i> vs. <i>Tarrietia</i> (Malvaceae, Sterculioideae)
	Carpel ridges; persistent sepals	<i>Rheum</i> vs. <i>Rumex</i> (Chenopodiaceae)
Viscin layer	External vascular bundles	Loranthoideae vs. Viscoideae (Loranthaceae)
Accumulation of fibers, crystals and specialized cells	Outer integument of seed; "middle" integument	Various Annonaceae <sup>4</sup>
Malpighian cells (macroclereids)	Outer seed epidermis; hypodermis; outer integument; inner integument	Fabaceae vs. Cucurbitaceae vs. Myristicaceae vs. Malvaceae s.l., Euphorbiaceae, etc.
Fleshy seed-associated structures	Sarcotesta; funicular aril; micropylar aril; chalazal aril; aril borne on the seed opposite the chalaza	Various angiosperms <sup>5</sup>
Leaf development	Leaf; shoot	Phyllanthaceae (Euphorbiaceae)
Primary stem development	Primary SAM; cotyledon	Most angiosperms vs. some Fabaceae
Bearing of inflorescences	axillary SAM	Most angiosperms vs. <i>Taeniophyllum</i> (Orchidaceae)
Photosynthesis	Shoot; root	Most angiosperms vs. some Orchidaceae
Bearing of flowers and roots	Leaves; roots	Most Gesneriaceae vs. some <i>Streptocarpus</i> <sup>6</sup>
Mesophyll production	Stem; cotyledon	Most dicots vs. e.g. <i>Plantago</i>
Light interception	Leaf lamina; petiole	
	Leaflets; petiole; stipules	Different species of <i>Lathyrus</i>
	Leaves; stems	Most dicots vs. Cactaceae

### Notes:

- Specifically Corner emphasizes the transfer of vascular supply.
- Corner's interpretation is contradicted by recent studies suggesting that the flower meristem remains axillary but the subtending leaf is suppressed (McConnell and Barton, 1998).
- Archidendron* has several free carpels per flower and, in fruit, resembles the infructescence of *Parkia*.
- Discussed in more detail by Corner (1949a).
- Discussed in more detail by Corner (1949a, b).
- There have been several independent origins of the phyllo-morph condition (Jong and Burt, 1975; Möller and Cronk, 2001).
- See the phylogenetic analysis of Powell and Kron (2001).

plant development for transference of function to be framed as a testable evolutionary-developmental hypothesis. Our aim in this chapter is to revisit Corner's idea with the help of a phylogenetic perspective and an improved understanding of plant developmental genetics. We clarify the definition of transference of function and related concepts, and then speculate on the importance of these phenomena in plant evolution.

## 4.2 Definition of transference of function

Corner (1958: 33) provided the following description of transference of function:

a property which occurs in an organ, tissue or cell-layer in one case may occur in other parts of the body in other cases. The property is the same, but its site of development has shifted ... the transference of function, as I have called the process, is a method of evolution.

In trying to provide a modern redefinition of transference of function we faced a difficult decision. One option would be to follow Corner's likely intent and define the concept so as to require the transfer of some developmental program between structures. However, to evolutionary biologists the term "function" refers to a biological role fulfilled by a structure, often with the further implication that the structure evolved by natural selection to fulfill that biological role (Gould and Vrba, 1982). Bearing this in mind, one could instead use the term "transference of function" to refer to cases in which biological roles are transferred among structures regardless of whether any developmental programs have been transferred.

To clarify these two alternative definitional schemes, consider a hypothetical case in which there is a transition from wind-dispersed fruit endowed with a pappus of feathery (calyx-derived) hairs to fruit with (receptacle-derived) wings. Assuming that this transfer did not involve the transfer of any genetic programs from hairs to wings (which is likely because the properties that make a hair an efficient aid to dispersal are not the same properties as are relevant in the case of a wing), should this event be considered "transference of function?" Given the literal reading of the phrase, the answer is "yes," since an ecological function, namely dispersal, has been transferred. Given a genetic view, the answer would be "no," since no heritable properties have been transferred from the calyx to the receptacle.

We propose framing the definition of transference of function in terms of the biological roles fulfilled by structures:

Transference of function from structure A to structure B means that an ecologically meaningful biological role is carried out by structure A in species *a* and structure B in species *b*, and there was a direct transition from using A to using B in an ancestor of *b*.

Direct transition could (and probably will often) entail a transitional stage during which the function is fulfilled by both structure A and B. To accommodate those cases in which transfer of function is accomplished by the transfer of genetic identity we recognize a subcategory, homologous transfer of function (see Section 4.5.1).

## 4.3 Testing hypotheses of transference of function

The concept of transference of function is a useful tool when interpreting plant diversity. Corner expected little more than this from the concept. Nonetheless, much more will be gained if transference of function is framed in terms of testable hypotheses. Given our definition, a hypothesis of transference of function can be subjected to two phylogenetic tests. These are comparable to tests used in the study of adaptation, in that one test deals with historical genesis and the other with current utility (Gould and Vrba, 1982; Baum and Larson, 1991).

### 4.3.1 Phylogenetic continuity

The definition of transference of function requires that there be a direct transition from the use of the donor to recipient structure. This requires, first, that all intervening ancestors should have carried out the ecological function with one or the other or both structures (Figure 4.1). Additionally, it is necessary that the common ancestor of the focal species should have used one or the other structure, *but not both*. This follows because otherwise there was not transference of function but differential contraction of function (Figure 4.1d). These two criteria can be evaluated using phylogenetic information about the taxa in question combined with methods of ancestral-state reconstruction (e.g. Schluter *et al.*, 1997; Ree and Donoghue, 1998). Below, we use two examples to illustrate the two ways in which phylogenetic data can refute a hypothesis of transference of function.

*Fragaria* (strawberries) and *Rubus* (including blackberries and raspberries) both have colorful, palatable tissues associated with the fruit that facilitate endozoochory. In *Rubus* the walls of the free carpels fulfill this function, whereas in *Fragaria* it is the swollen receptacle. Corner (1958) hypothesized that this represented transference of function. Current knowledge of the phylogeny of Rosoideae (Eriksson *et al.*, 1998), however, implies that *Rubus* and *Fragaria* are only distantly related: *Fragaria* is nested within *Potentilla* (a genus whose traditional circumscription makes it massively paraphyletic), whereas *Rubus* is affiliated with the genera *Geum*, *Fallugia* and *Waldsteinia*. Given that *Potentilla* (with one possible exception) and all remaining Rosoideae have dry fruits, the reconstruction of ancestral states using simple parsimony suggests that the common ancestor of *Rubus* and *Fragaria* had neither a fleshy pericarp nor a swollen receptacle. It is necessary to weight gains over losses more than 4:1 in generalized parsimony reconstruction before the ancestral state is switched to fleshiness. If we conclude on this basis that fleshiness did in fact evolve independently in blackberries and strawberries, this would serve to refute Corner's (1958) hypothesis of transference of function.

Another example can be used to illustrate the idea that the ancestral function should be restricted to one or the other structure in order to imply transference of function. Corner (1958) hypothesized that the swollen, fleshy, brightly-colored peduncle (hypocarp) of the cashews (*Anacardium* spp.) arose by transference of function from the fleshy fruit wall (pericarp) that attracts dispersal agents in mangoes (*Mangifera*). Based on molecular data (Pell, pers. comm. 2000), *Mangifera* and *Anacardium* fall in a well-supported clade with three other genera of Anacardiaceae: *Semecarpus*, *Gluta* and *Sorindeia*. The topology of this clade is resolved convincingly as (*Semecarpus*(*Anacardium*(*Gluta*(*Mangifera*,*Sorindeia*))))).

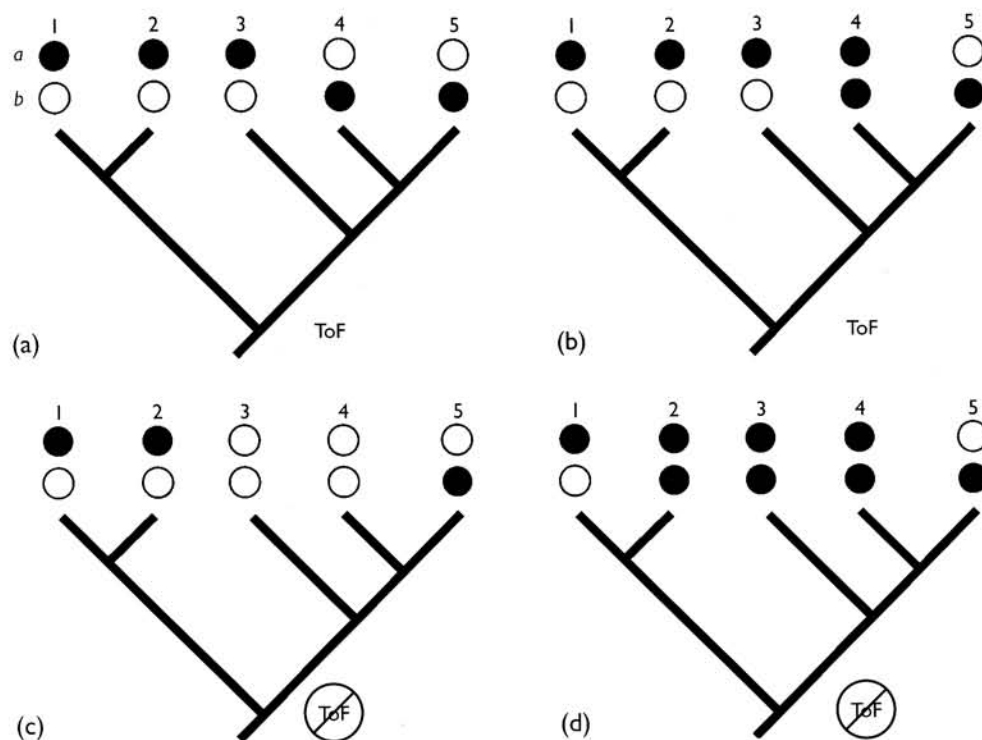


Figure 4.1 Hypothetical examples to illustrate the criterion of phylogenetic continuity in tests of transference of function (ToF). Five species (1–5) are related as shown. Taxa 1 and 5 differ in that taxon 1 uses structure *a* whereas taxon 5 uses structure *b*. The scenario depicted in Figure 4.1a implies (using parsimony) transference of function directly from using *a* to *b* and thus satisfies the criterion of phylogenetic continuity. The scenario depicted in Figure 4.1b implies progressive transference of function from using *a* to using *a* + *b* to using just *b* and thus also satisfies the criterion of phylogenetic continuity. The scenario depicted in Figure 4.1c implies (using parsimony) the existence of ancestors that used neither *a* nor *b* to fulfil the function and thus contradicts the criterion of phylogenetic continuity. The scenario depicted in Figure 4.1d implies (using parsimony) an ancestor that used both *a* and *b* to fulfil the function with independent contraction to using either *a* or *b* and, thus, fails the criterion of phylogenetic continuity.

All species in this clade, except those in *Anacardium*, have a fleshy pericarp, suggesting that a fleshy pericarp is plesiomorphic. However, *Semecarpus* also has a swollen hypocarp resembling that seen in *Anacardium* (but less juicy and colorful). As a result, it is plausible that initially fleshiness was expressed in both the pericarp and hypocarp and that later cashews and mangoes *lost* this property from the pericarp and hypocarp respectively. This result, if confirmed, would contradict Corner's hypothesis of transference of function.

As shown above, one does have the ability to reject a hypothesis of transference of function based on phylogenetic data. Nonetheless, it should be noted that in some cases one might be tempted to rescue a hypothesis by proposing the existence of a further structure that has acted as a repository of the function. For example, one

might look at the strawberry/raspberry case and suggest that some other part of the plant, perhaps the stem, was the source of the fleshiness that was transferred independently to the receptacle and pericarp. However, this would not so much rescue the original hypothesis as replace it with a new hypothesis, subject also to a test of phylogenetic continuity.

#### 4.3.2 Functional equivalence

The second, testable implication of a hypothesis of transference of function is that the structures should be fulfilling the same ecological function. This could be explored by standard ecological/functional studies. To clarify the content of such tests we will use an example that may well pass the test of phylogenetic continuity. Most banisterioid Malpighiaceae have wings that develop from the carpel wall during fruit maturation and are assumed to aid in fruit dispersal. The genus *Dicella*, however, lacks carpel wings but its five calyx lobes are expanded and adopt a wing-like form in fruit (Chase, 1981). The hypothesis one might posit is that this represents transference of fruit dispersal function from the gynoecium to the calyx. Based on a recent phylogenetic analysis (Davis *et al.*, 2001), *Dicella* is embedded in a large clade of wing-fruited taxa. The sister to *Dicella*, *Tricomaria*, has membranous outgrowth of the pericarp, but instead of forming wings these have been modified into bristles, which are unlikely to play a role in wind dispersal due to their small size compared to the mass of the fruit. While the Davis *et al.* tree is consistent with phylogenetic continuity between wind dispersal via carpel and calyx wings, one cannot entirely rule out a loss of wind dispersal in the common ancestor of *Dicella* and *Tricomaria*, followed by its re-evolution (via calyx wings) in *Dicella*.

If we assume that *Dicella* does indeed pass the test of phylogenetic continuity, it would be appropriate to consider tests of the ecological function of these traits. Tests of ecological equivalence would involve showing that both the carpel and sepal wings function as aids to dispersal. For example, in both *Dicella* and species with carpel wings one could determine whether the dispersal shadow obtained when wings are removed is skewed towards short dispersal distances relative to those of intact fruit. Such experiments have not, to our knowledge, been carried out in Malpighiaceae but have been used to study other taxa with winged diaspores (Augspurger, 1986; Augspurger and Franson, 1987; Matlack, 1987; Sipe and Linne-rooth, 1995). If one did not find evidence for a role of wings in seed dispersal alternative hypotheses, such as function in water dispersal (Chase, 1981), might then be considered.

One might suppose that there would be an evolutionary shift in the structure performing a function only if the derived structure fulfilled the ecological role better than the original structure. Thus, in the *Dicella* example, one might predict that sepal wings would be more effective at wind dispersal than carpel wings. However, derived characters are not always selectively better because natural selection is not always involved. And, even if selection was responsible for the transition, the functional transfer could have been driven by other components of fitness (Baum and Larson, 1991). For example, wings could shift location due to impacts on predator evasion, seed germination, or desiccation avoidance.



#### 4.4 Genetic identity of organismic structures

Transference of function implies the movement of properties between the structural elements that make up an organism. Therefore, before initiating a discussion of the mechanisms underlying transference of function, it is important to clarify the notion of the genetic identity of organismic structures. This is problematic because of uncertainty as to whether the parts of organisms ("characters") can be viewed as individuals and, if so, what underlying phenomena serve to individuate them (e.g. Wagner, 1989). We will skirt these issues and assume that characters are somehow individuated and that they may be grouped into classes that exist in multiple organisms in a population and/or many times in a single organism (e.g. epidermal cells, petals, cotyledons, root hairs).

Considering a particular class of characters (say, those organs we call petals), there will be a particular combination of genes that is characteristic of that kind of structure in a species under study. If we consider this combination of genes to give the structure its current genetic identity, then expansion or movement of the expression of those genes to a different location would result in a transfer of genetic identity. Note that genetic identity is here understood to be a local property of a particular species at a particular time, rather than a global property of a "type" (in the classic sense) of structure. Because the genes that characterize categories such as "petal" or "leaf" will constantly evolve, it is very unlikely that there exists a set of genes that characterize every organ conventionally assigned to these typological classes. Thus, gene expression data may be of little help in assigning structures to such categories.

Under our view of genetic identity, when a structure expresses new genes, its genetic identity changes. If those newly expressed genes were formerly part of the genetic identity of another structure, then genetic identity has, in a sense, been transferred from the donor to the recipient character. For example, if all the genes expressed in the petal of an ancestor came to be expressed in a position that was previously occupied by a sepal (and sepal-specific genes were turned off), the resulting structure would share genetic identity with a petal while showing positional homology to a sepal. Alternatively, some but not all of the genes could show modified expression such that a subset of the petal-specific genes came to be expressed in the calyx whorl and a subset of the sepal genes were turned off (or were not turned on) in that whorl. In this case one can interpret the resultant structure as having a mixture of petal and sepal properties. The implications of this view of genetic identity are discussed further in Section 4.6.2. Here, the key point is that the identity of a structure is in some way linked to the developmental regulatory genes that are expressed in that structure relative to those that were expressed in ancestral organisms.

#### 4.5 Developmental causes of transference of function

##### 4.5.1 Homologous versus non-homologous transfer of function

Given our modern understanding of developmental and evolutionary mechanisms it is useful to distinguish two broad explanations for the pattern of transference of

function. The first explanation is independent evolution or non-homology. This was illustrated in Section 4.2 with a hypothetical example of the transfer of dispersal function between hairs and wings. In this case none of the properties that permit the new structure to fulfill the function evolved by activating the expression of those genes that allowed the old structure to complete that function. Alternatively transference of function could involve the transfer of genetic identity between structures. Given that we believe there is a close link between homology and genetic identity, we think it is appropriate to refer to the latter pattern as "homologous transference of function." However, even in cases of homologous transference of function, there could be some properties that facilitate completion of the ecological function but that evolved *de novo* in the derived structure rather than being transferred from the ancestral structure. We would consider these to be valid cases of homologous transference of function so long as *some* genetic properties arose by transfer from the donor structure.

Homologous transference of function was the basis of Corner's (1949b, 1958) claim that superficially similar structures that are traditionally interpreted as being non-homologous may, in terms of genetic identity, show some degree of "hidden" homology (see also Sattler, 1988). For example, consider the superficial similarity of pinnate leaves and branch systems, despite the supposed homology of pinnate leaves and simple leaves (as indicated traditionally by determinate growth and the lack of axillary meristems). Corner's (1958: 37) suggestion that this similarity could reflect the sharing of genetic mechanisms has since been supported by morphological developmental work (Sattler and Rutishauser, 1992). Additionally, molecular studies have found that genes that act in shoot meristems and are absent from simple leaves may be expressed in compound leaves (e.g. Sinha *et al.*, 1993; Hareven *et al.*, 1996; Chen *et al.*, 1997). If this interpretation is correct, the transfer of shoot properties and associated ecological functions to leaves would be an example of homologous transference of function.

##### 4.5.2 A definitional scheme for heterotopy

Homologous transference of function implies that developmental events come to take place in different parts of the organism. Hence, it must entail heterotopy: evolutionary change in the spatial location of a developmental program (Bateman, 1994; Zelditch and Fink, 1996). Heterotopy is a concept that has achieved little attention relative to the reams of literature on heterochrony: evolutionary change in the relative timing of developmental processes (e.g. Alberch *et al.*, 1979; Guarrant, 1988; Raff and Wray, 1989; Bateman, 1994). Nonetheless, it would seem to be an important mechanism in plant developmental evolution (Kellogg, 2000). It has been claimed that plant evolution may often entail changes to the promoter/enhancer elements that cause changes in the expression patterns of regulatory genes (e.g. Doebley and Lukens, 1998). Such changes in the expression of developmental regulatory genes will usually result in changes in the spatial location of downstream developmental phenomena and, thus, would frequently result in heterotopy.

We think it is valuable to distinguish two kinds of heterotopy. *Neoheterotopy* refers to cases in which a structure is generated in a novel location. For example, *Phyllonoma* is usually interpreted as having an inflorescence that has been transferred to the surface of a leaf (Dickinson and Sattler, 1974). *Homeoheterotopy*, in

contrast, refers to cases in which genetic identity is transferred from a donor structure to another, pre-existing recipient structure. For example, the transfer of wing-like properties from the carpels to the sepals in the ancestor of *Dicella* could have entailed homeoheterotopy. *Homeosis* is here defined as a special case of homeoheterotopy in which all aspects of genetic identity are conferred upon the recipient structure.

Our definitional scheme is summarized in Figure 4.2. It is important to note that, notwithstanding our admiration for his contributions to developmental botany, we have chosen not to use the definitions proposed by Sattler (1988). His broader use of the term "homeosis" is virtually synonymous with our homeoheterotopy. We prefer to maintain a narrow definition of homeosis as complete homeoheterotopy because this terminology accords with current usage in molecular developmental biology. Additionally, Sattler (1988) took a narrow view of "heterotopy" that closely resembles our neoheterotopy. We prefer a broader notion because it frees up "homeosis" for the more restricted usage and because under Sattler's (1988) scheme there is no term for the combination of homeoheterotopy and neoheterotopy.

The definitional scheme proposed here suggests that homologous transference of function must entail homeoheterotopy (including homeosis). This follows because transference of function involves the transfer of properties among pre-existing structures. However, homeoheterotopy and homologous transference of function are not synonymous because heterotopy can occur without any ecological function being translocated.

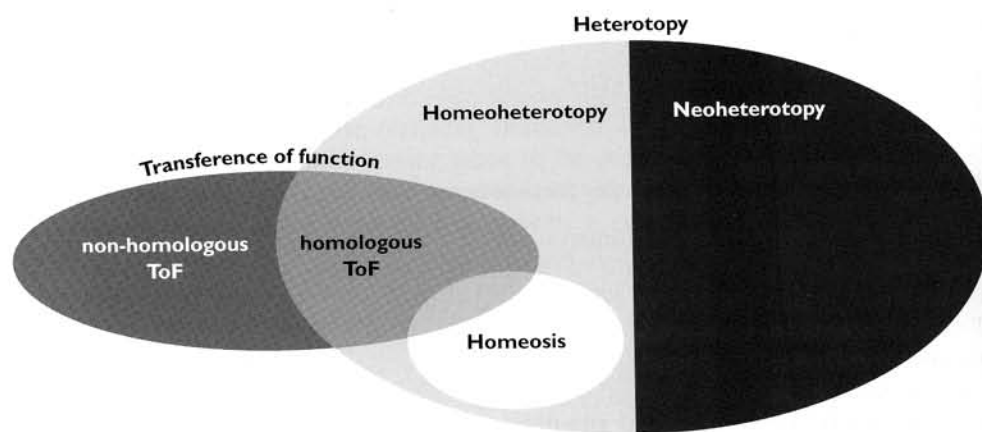


Figure 4.2 Schematic showing the relationship between some key developmental concepts. The large oval represents heterotopy: evolution via a change in the spatial location of developmental phenomena. This is divided into two halves based on whether (a) the developmental program is shifted to a pre-existing structural module (homeoheterotopy) or (b) a new structural module arises (neoheterotopy). Homeosis is here understood as complete homeoheterotopy, wherein all elements of the genetic identity of one structure come to replace those in another structure. Transference of function (ToF) refers to cases in which an ecological function performed by one structure comes to be carried out by another structure. This can involve the transfer of genetic properties from the old to the new structure (homologous ToF: a subset of homeoheterotopy) or it might not involve any genetic transfer (non-homologous ToF).

#### 4.5.3 Fuzzy boundaries between categories

Definitional schemes for biological concepts may have heuristic value even when the boundaries between concepts are not always absolute or objective. We hope this is the case here because many of the boundaries depicted with solid lines in Figure 4.2 are, in fact, fuzzy.

The distinction between homeo- and neoheterotopy is a case in point. Consider the hypothetical transfer of the property of redness from an aril to the testa (as suggested within *Pithecellobium* by Corner, 1958), which could be considered as homeoheterotopy via the expression of pigment biosynthetic genes in the testa. If instead the property transferred was the production of glandular trichomes, then one might lean towards an interpretation of neoheterotopy in which trichome production came to be ectopically activated in a new location. This may seem curious since indumentum and pigmentation are both properties of epidermal tissues. The distinction between homeoheterotopy and neoheterotopy thus depends on whether one considers the property transferred to be a property of a character or an individuated character in its own right. Pigmentation is hard to see as anything but a property of cells and tissues, whereas multicellular trichomes may be viewed as individuated structures. However, as intimated earlier, the notion of the individuation of structural modules is challenging. Therefore, the distinction between neo- and homeoheterotopy is somewhat subjective, depending on how one delimits characters and how one defines homology (see also Sattler, 1988).

The issue of whether one considers a structure to be an individuated character is often influenced by how one interprets evolutionary history and, thus, the decision to treat a case as homeo- versus neoheterotopy can turn on historical inferences. For example, the case used in Section 4.5.2 to illustrate neoheterotopy – epiphyllous inflorescences – is subject to an alternative homeoheterotopic interpretation in which a leaf genetic program comes to be expressed in an inflorescence peduncle. This latter interpretation seems less plausible, however, because although a stem segment (peduncle) and a leaf are both developmental modules, they are generally considered to be different kinds of modules. As a result, it seems unlikely that the peduncle should be converted so perfectly to a leaf while at the same time maintaining the property of bearing flowers that was "inherited" from the peduncle. It seems, instead, much easier to imagine the ectopic formation of shoot meristems on leaves, as can occur in tissue culture or when shoot meristem identity genes are overexpressed (e.g. Chuck *et al.*, 1996). Thus, the claim that epiphyllous flowering represents neoheterotopy implies that an inflorescence is an individuated module and that it evolved by the ectopic initiation of shoot meristems on the surface of a leaf.

Just as the foregoing paragraphs have highlighted some blurriness in the distinction between homeoheterotopy and neoheterotopy, a similar fuzziness can be recognized between heterotopy and heterochrony. Since different structural modules develop at different times in ontogeny, heterotopy can perhaps always be reinterpreted as heterochrony, and vice versa (Sattler, 1988). For example, imagine the transition from a simple to a compound umbel in which the function of positioning flowers for pollinator visits has been transferred from the primary peduncle to the secondary peduncles by converting the floral meristems into inflorescence meristems. This can be interpreted as heterochrony, in that the onset of floral meristem identity



has been delayed. However, it can also be viewed as heterotopy because the part of the plant producing the floral organs has changed. In this particular case it seems equally accurate to invoke heterochrony or heterotopy. Other cases may be shifted to one end of the spectrum or another. For example, if one envisages transfer of the petal genetic program to a sepal, then heterotopy is a more natural explanation, despite the fact that sepals usually develop earlier than petals. Conversely, the cases in which floral form is modified by changes in the timing of anthesis relative to floral development (Guerrant, 1982, 1988) are easier to interpret in terms of heterochrony.

#### 4.6 Evolutionary implications of transference of function and homeoheterotopy

We have suggested that the concept of transference of function provides a useful prism for interpreting certain patterns of plant evolution and for suggesting fruitful avenues for further research. To justify this claim we now explore an assortment of topics that emerge from a consideration of this phenomenon.

##### 4.6.1 Spatial propinquity

Corner (1958) suggested that most instances of transference of function occur between structures in close spatial proximity, for example, between petals and sepals. There are, doubtless, exceptions to this "rule." For example, in *Salvia*, petals or bracts may be showy but never, so far as we know, sepals. Nonetheless, based on our subjective assessment, the hypothesis that spatial propinquity influences the likelihood of transference of function is plausible.

We can suggest two classes of explanation that would account for an increased tendency for transference of function between closely-spaced or adjacent structures. First, this could reflect underlying developmental mechanisms. For example, the commonest cause of transference of function could be via expansion and then contraction of the expression of regulatory genes. The second possible explanation is that structures in close proximity are better situated to take up a similar function. For example, it is plausible that only floral organs or bracts closely associated with flowers could serve the role of attracting pollinators or dispersers. On the other hand, although ecological function may favor physical proximity between donor and recipient organs, it may sometimes prevent transfer between adjacent organs. For example, in *Dicella* we hypothesized transference of the function of seed dispersal from the carpels to the calyx. While it is likely that a structure associated with dispersal would have to develop within the flower/inflorescence, it is unlikely to involve the adjacent structures to the carpels, namely the stamens, because those structures fulfill other important ecological functions related to sexual reproduction.

It would take a broad-scale comparative phylogenetic study to rigorously evaluate whether there is some truth to Corner's intuition and, if so, to evaluate whether the explanation for the pattern is developmental or functional. To determine whether spatial propinquity dominates, one might use a randomization procedure to ask whether transfers more commonly involve adjacent structures than one would expect by chance. In order to distinguish the developmental and functional explana-

tions one could exploit the fact that the developmental explanation could apply only in cases of homologous transfers of function, whereas the functional explanation would apply to both homologous and non-homologous cases. Consequently, finding that the proportion of adjacent transfers was higher in homologous than non-homologous transfers would serve to support the developmental explanation. That being said, we are a long way from possessing the kind of empirical data needed to conduct such a comparative meta-analysis.

##### 4.6.2 Mixed homology

Homologous transference of function involves the movement of genetic identity from one spatial location to another. In cases of complete homeosis it might be said that there has simply been a movement in the spatial location of a particular structure or, if the structure persists in the original location, a module duplication. In other cases of homeoheterotopy some, but not all, of the genetic properties are transferred, resulting in a structure with mixed homology. This notion can be illustrated by "inflorescence-flowers."

Inflorescence-flowers are compact inflorescences where the whole structure functions as a single blossom (see Faegri and van der Pijl, 196: 21–23). In many cases these inflorescences are also organized much like a flower, with enlarged petal-like bracts or sterile florets around the periphery and, sometimes, a subdivision into concentric zones of differing sexual identity. The most obvious example is the capitulum of Asteraceae, but flower-inflorescences with sterile marginal structures are abundant in other angiosperm groups, including *Cornus*, *Euphorbia*, *Eryngium*, *Hydrangea*, *Parkia*, *Protea*, *Psychotria* and *Viburnum*.

Corner (1958) hypothesized that flower-inflorescences arise through partial transfer of a floral genetic program to the whole inflorescence (see also Albert *et al.*, 1998). This hypothesis would be explicable, given current developmental knowledge, if compact inflorescences showed broad expression of floral meristem identity genes such as *LEAFY* (*LFY*). This in turn could activate floral organ identity genes in a manner that is partially floral. For example, one could hypothesize that enhanced expression of C-class floral organ identity genes in florets situated towards the center of the inflorescence is the explanation for fertile flowers being produced centrally and sterile flowers marginally. Likewise, the increased activation of B-class genes peripherally could serve to enhance the petaloid quality of the marginal florets. This hypothesis has not yet been tested (but see Albert *et al.*, 1998).

Coincidentally, an experiment conducted in one of our labs (DAB) using wildtype *Arabidopsis* plants containing a 35S::*LFY:GR* transgene (see Wagner *et al.*, 1999) bears on this issue. After inflorescence meristems were initiated, *LFY* was activated by application of dexamethasone. This should result in the production of physiologically active *LFY* in all parts of the plant, including the inflorescence meristems, which normally lack *LFY* activity (Weigel *et al.*, 1992). Interestingly, in almost all treated plants (but no control plants) inflorescence apices became converted into condensed multiflowered structures that lack internode elongation and, thus, resemble capitula (H.-S. Yoon and D. A. Baum, unpubl. obs.). One interpretation of this result is that the flower meristem identity gene *LEAFY* is conferring some floral properties, specifically the lack of internode elongation, upon the inflorescence

meristem. This evidence is circumstantial, but it provides support for the notion that the identity of flowers and inflorescences can become mixed.

Another case of mixed homology which is gaining experimental support relates to the claim that compound leaves (e.g. Corner, 1958; Sattler, 1988; Sattler and Rutishauser, 1992; Rutishauser, 1995; Goliber *et al.*, 1999) and gesneriad phylomorphs (Corner, 1958; Jong and Burt, 1975) have mixed shoot-leaf identity. This inference has gained support from evidence that shoot meristem identity genes may be expressed in developing compound leaves, but not in simple leaves, and that these genes influence the degree of compounding in tomatoes (Sinha *et al.*, 1993; Hareven *et al.*, 1996; Chen *et al.*, 1997).

The notion of mixed homology bears obvious similarities to the concept of partial homology, promoted especially by Rolf Sattler (e.g. Sattler, 1984, 1988, 1991; see also Roth, 1991; Minelli, 1998). Both are based upon the idea that developmental processes can be transferred piecemeal from one structure to another such that characters in different species need not have 1:1 relationships with each other. Thus, Sattler suggested that a character could show a defined degree of partial homology to each of several structures in its ancestor. Thus, a petal could be imagined to be 70 percent homologous to a stamen and 30 percent to a sepal.

"Partial" and "mixed" homology may differ subtly, however, in orientation. In Sattler's approach the challenge seems to be to devise a semi-quantitative index of the proportion of whole structures that have different identities. In contrast, we wish to focus our efforts on decomposing structures into their genetic elements. Thus, our notion of "mixed" homology is more historical in outlook and suggests that we strive to reconstruct how and why different genetic modules come to co-exist in particular structures.

Mixed and partial homology both call into question much evolutionary developmental research whose primary aim seems to be identifying a single correct homology statement for highly derived structures. For example, some have hoped to use the expression of B-group MADS-box genes to determine whether petals are derived from sepals/bracts or stamens (Albert *et al.*, 1998; Kramer and Irish, 1999). However, if, as we suspect, petals represent a mixture of sepal and stamen developmental programs, B-gene expression will not provide a complete answer (Baum and Whitlock, 1999; Kramer and Irish, 2000).

Not only does mixed homology influence evolutionary developmental genetics, it can also complicate the phylogenetic analysis of morphological data. The first step in morphological phylogenetics is to construct a data matrix in which the columns represent inferred homologies at one level in the hierarchy and shared character-states within a column represent hypothesized homologies at a lower hierarchical level (Hawkins, 2002). This matrix therefore assumes hierarchically nested homology relationships between organismic characters. However, if a compound leaf is both a leaf *and* a shoot, then the homology relationships become reticulate (see also Minelli, 1998). The leaf of a closely related simple-leaved species could be simultaneously homologous with the leaflet *and* the leaf of the compound-leaved species. Thus, if one scored a "leaf" property such as petiole length one might not know whether to score the petiole of the compound leaf as a whole or the petioles of the leaflets (Hawkins, 2002). This situation is analogous to phylogenetic analysis using a duplicated gene wherein one species has a "hybrid" gene arising by partial gene con-

version between paralogs. In that case there is no meaningful way to include that species without first breaking it up into the regions that are derived from each of the two paralogs. The same is true of morphological structures with mixed homology except that, deprived of the linearity of gene sequences, it is much more difficult to identify the source of developmental modules.

#### 4.6.3 Variation in the propensity to show homologous transference of function

As discussed in Section 4.5.2, homologous transference of function requires homeoheterotopy. In order to manifest homeoheterotopy a developmental program needs to be composed of distinct modules and it needs to be possible, in the sense of not being massively deleterious, for genetic subroutines that are "adapted" for one module to be activated elsewhere. (A genetic subroutine is an integrated piece of a developmental program analogous to a subroutine in a computer program.) In this section we consider the possibility that angiosperms may be especially prone to transference of function because their developmental systems are highly modular and have evolved to tolerate shifts of genetic subroutines from module to module.

There is little hard data comparing the number of structural modules in different eukaryotic lineages. However, while there is a risk that we are being biased by human perception, we are fairly confident that, among land plants, angiosperms show, on average, the greatest degree of modular proliferation (a possible exception being the rhizomorphic lycopsids: Bateman, 1994). This can be seen by considering the numerous determinate, leaf-like modules that are found in the typical angiosperm, including cotyledons, juvenile leaves, vegetative leaves, reproductive leaves, bracts, sepals, petals, stamens and carpels. The diversity of leaf modules may be further enhanced by specializations (e.g. anisophylly, involucre bracts), additional developmental phases (spring versus summer leaves), or variants exposed to different environmental conditions and therefore expressing different suites of genes (e.g. sun versus shade; under insect attack versus intact). In contrast, even a relatively complex moss is unlikely to have more than a handful of structural modules.

Although angiosperms might tend to be more highly modular than other land plants, one would have a hard time arguing that they are more modular than animals. After all, animals such as mammals have innumerable distinct anatomical modules (e.g. eyes, femurs, finger nails, hearts and kidneys). The presence of multiple modules is, however, insufficient to predict extensive homeoheterotopy. It is also necessary that the genetic program be composed of genetic subroutines that are specialized for particular modules but that can become activated in a new module without having massively detrimental effects.

It has frequently been claimed, based on anecdotal evidence, that plants can tolerate more massive genetic alterations than animals (Van Steenis, 1969, 1977, 1978; Gottlieb, 1984). Although this claim is in need of empirical verification, a theoretical consideration of the structure of plant and animal developmental programs provides some justification for the idea that plants are more tolerant than animals of the mis-expression of genetic subroutines.

It is generally agreed that animals and plants differ in their developmental architecture. Animal (especially vertebrate) development is "closed" in the sense that it is



largely buffered against environmental variability such that final form is for the most part explicable in terms of the underlying genotype. In contrast, plants have more open developmental systems consisting of a limited number of modular units whose deployment is highly responsive to local environmental cues. Why should these two developmental styles differ in the expected degree of disruption caused by a homeo-heterotopic mutation?

The essence of an open developmental system is that structural modules, such as leaves, are deployed repeatedly at times and in positions governed by the environment. Consequently, a structural module will find itself in different settings (e.g. leaves in shade versus full sun), making it necessary that structural modules show some plasticity, turning on or off developmental subroutines as needed. Furthermore, since the environmental cues to which a plant responds are varied (e.g. light, temperature, pathogen attack), it seems necessary that a subroutine activated in response to one cue should function in all modules, regardless of which combination of other subroutines are active. As a result, one might expect the evolution of multiple subroutines, each of which is an integrated unit that can function in different modules that vary somewhat in their genetic identity. The properties of a given structural module would then be determined in a combinatorial manner by the set of subroutines that are activated. As a consequence, generalized subroutines may be easily activated in a novel structural module without severe detrimental consequences (see Gottlieb, 1984).

Vertebrates produce many structural modules at various hierarchical levels (e.g. heart, kidney, glomeruli, femurs). However, most modules are reiterated only once or twice. For example, a vertebrate produces only one heart, and that heart experiences basically the same "environment" from organism to organism. As a result, there is less need for plasticity when a module develops, and greater potential for functional specialization. Thus, we expect that genetic subroutines expressed in the heart will tend to be specialized for the heart and will depend upon that specific "environment" for proper deployment.

Based on the reasoning presented above, we suspect that plant developmental subroutines, unlike in most animals, are robust to the cellular environment in which they are activated. Consequently, it is likely that homeoheterotopy may be more important in angiosperm evolution than in animal evolution. On the other hand, it is important to note that there are many animals that have a more open, plant-like developmental system (e.g. bryozoa, colonial cnidarians), there are some aspects of animals that more closely resemble plant modular development (e.g. vertebrae, feathers, scales, arthropod appendages), and there are some aspects of plant development that are more animal-like (e.g. embryogenesis). Nonetheless, as a working hypothesis aimed at promoting further work, we suggest that plants (especially angiosperms) are likely to show more homeoheterotopy than animals.

#### 4.6.4 Future prospects

Corner built his notion of transference of function upon a foundation of careful observations of plant morphology. This bedrock of botanical knowledge is perhaps the main reason why his idea still has relevance fifty years later, despite massive changes in evolutionary theory, systematics and developmental biology. His intuit-

ions resonate remarkably well with modern perspectives, such as recent claims for the importance of changes in the enhancer/promoter domains of developmental regulatory genes (Doebley and Lukens, 1998). Furthermore, Corner (1958) is rich in novel interpretations and creative hypotheses that warrant rigorous exploration. Our hope is that this chapter will bring the concept of transference of function to the attention of a wider audience and will promote additional studies of its mechanisms, distribution and consequences.

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