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Heterochrony in Plant Evolutionary Studies through the Twentieth Century

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I. Abstract

The evolution of plant morphology is the result of changes in developmental processes. Heterochrony, the evolutionary change in developmental rate or timing, is a major cause of ontogenetic modification during evolution. It is responsible for both interspecific and intraspecific morphological differences. Other causes include heterotopy, the change of structural position, and homeosis, the replacement of a structure by another. This paper discusses and reviews the role of heterochrony in plant evolution at the organismal, organ, tissue, cellular, and molecular levels, as well as the relationships among heterochrony, heterotopy, and homeosis. An attempt has been made to include all published studies through late 1999. It is likely that most heterochronic change involves more than one of the six classic pure heterochronic processes. Of these processes, we found neoteny (decreased developmental rate in descendant), progenesis (earlier offset), and acceleration (increased rate) to be more commonly reported than hypermorphosis (delayed offset) or predisplacement (earlier onset). We found no reports of postdisplacement (delayed onset). Therefore, although rate changes are common (both neoteny and acceleration), shifts in timing most commonly involve earlier termination in the descendant (progenesis). These relative frequencies may change as more kinds of structures are analyzed. Phenotypic effects of evolutionary changes in onset or offset timing can be exaggerated, suppressed, or reversed by changes in rate. Because not all developmental changes responsible for evolution result from heterochrony, however, we propose that plant evolution be studied from a viewpoint that integrates these different developmental mechanisms.

II. Introduction

Heterochrony, a change in the relative timing and/or rate of developmental processes in a descendant relative to its ancestor, has become one of the most popular developmental and evolutionary topics in recent years. The symbol of this trend may be seen in recent book titles, such as *Heterochrony in Evolution* (McKinney, ed., 1988), *Heterochrony: The Evolution of Ontogeny* (McKinney & McNamara, 1991), and *Evolutionary Change and Heterochrony* (McNamara, 1995), and in reviews on heterochrony and development (Carlson, 1991; Conway & Poethig, 1993; Fink, 1988; Gould, 1992; Hall, 1990, 1992, 1998; Hall & Miyake, 1995; Hill, 1996; Klingenberg, 1996; Raff & Raff, 1987; Raff & Wray, 1989; Richardson, 1995), heterochrony and evolution (Alberch & Blanco, 1996; Gould, 1988; Hill & Lord, 1990; Lord & Hill, 1987; McKinney, 1988b; McKinney & McNamara, 1991; Mosbrugger, 1995; Parichy et al., 1992; Zelditch & Fink, 1996), heterochrony and genetics (Ambros, 1997; Atchley, 1987, 1990; Slatkin, 1987; Wiltshire et al., 1994), and some other perspectives on heterochrony (Fiorello & German, 1997; Guerrant, 1988; Klingenberg, 1998; Klingenberg & Spence, 1994; Reilly, 1997; Rice, 1997; Richardson, 1995).

Heterochrony, as a term, has been defined and redefined many times since Haeckel (1875, 1905) first formally used it. After a thorough review and analysis of the history and meaning of heterochrony proposed by previous authors, Gould (1977: 2) redefined heterochrony as "changes in the relative time of appearance and rate of development for characters already present in ancestors." Heterochrony is thus a "phyletic change in the timing of development, such that features of ancestors shift to earlier or later stages in the ontogeny of descendants" (Gould, 1992). Based on this concept, Alberch et al. (1979) and McKinney (1988a) further classified various heterochronic possibilities, which have become widely accepted (see Fig. 1). More recently, Reilly (1997) modified the current model of heterochrony, replacing some of the terminology with new nomenclature. Despite the recent attempts at clarification

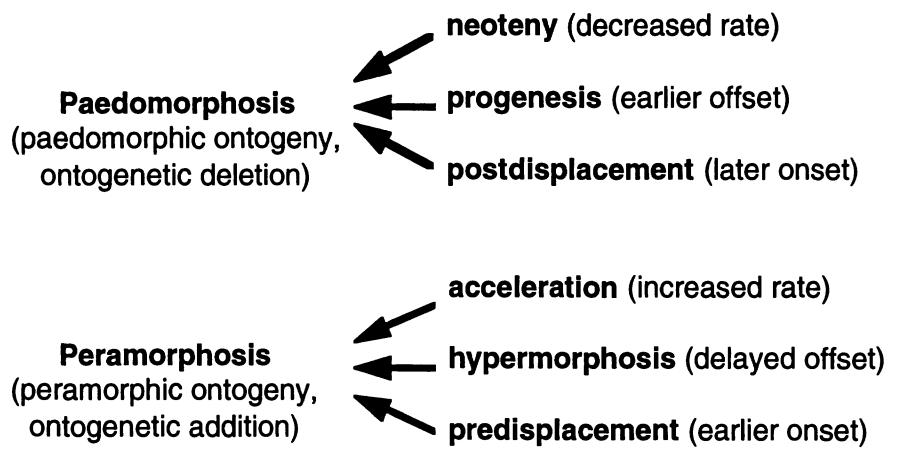

Fig. 1. Two types of heterochrony and their developmental causes. (After Alberch et al., 1979)

and consensus, controversy and confusion persist (McKinney, 1999). The debates will probably continue as data on more taxa accumulate and as heterochrony is further examined in relation to other developmental and evolutionary mechanisms.

Although predominantly studied in animals, heterochrony has been increasingly studied in plants during the past ten years. Here we briefly review some perspectives on heterochrony and its role in evolutionary changes of plant morphology. The main focus is on the evidence and progress that have been made in the study of heterochrony in plants, especially in the flower. We have attempted to include all studies appearing in print through late 1999. Results are summarized in Appendix 1, which includes only those studies having adequate phylogenies and time-based developmental data (as well as some fossils). We will also discuss some of the limitations of heterochrony and suggest an integrative approach incorporating heterochrony, homeosis and heterotopy in plant ontogenetic and phylogenetic studies.

III. Heterochrony, Evolution, and Development

Heterochrony has a special significance because it can produce dramatic novelties simply by changing the timing of developmental events and/or the rate of developmental processes. Heterochrony has both developmental and evolutionary components. Development is often studied by quantitative comparisons, which lead to the identification of particular developmental differences (timing, rate) that result in divergent phenotypes. The evolutionary component can be easily linked to the developmental results if one knows the probable phylogenetic relationships of the concerned groups. Thus, it is possible to draw a conclusion about the direction and type of developmental change associated with morphological evolution by integrating developmental information with phylogenetic hypotheses (Diggle, 1992).

"Ontogeny" usually refers to the sequence of events or stages occurring during development from a zygote to a sexually mature organism (Gould, 1977; Hall, 1992). In plants, especially in perennials, new leaves and flowers are produced on the mature plant body. Therefore, the development of a leaf or a flower starts from its primordium insertion on a mature plant to a fully expanded mature leaf or a fully opened flower and may be regarded as leaf or flower

ontogeny. Ontogeny in any organism can also be the development of tissues or cells from their initiation to maturity (Gifford & Foster, 1989: 8).

IV. Types of Heterochrony

Heterochronic processes, or heterochronic changes of developmental processes, are the direct causes of morphological changes. The changes of development may involve onset time, offset time, and rate (Alberch et al., 1979; Fink, 1982, 1988; Reilly, 1997). Based on the final effect of such perturbations, two basic heterochronic processes underlying organismal development can be identified: paedomorphosis and peramorphosis (Fig. 1). Paedomorphosis refers to a truncated developmental process, which can result from a descendant having a shorter developmental duration or a lower developmental rate than that of its ancestor. Peramorphosis refers to an extended developmental process, which can result from a longer developmental duration or a higher developmental rate (Alberch et al., 1979; Kluge, 1988; McKinney, 1988a; McKinney & McNamara, 1991). Paedomorphosis results in the descendant having an adult size and shape similar to the juvenile condition in the ancestor, whereas peramorphosis leads to the descendant having a larger adult size with a shape beyond that in the ancestor. The six heterochronic processes proposed by Alberch et al. (1979) were recently further illustrated by Wiltshire et al. (1994) in the garden pea, *Pisum sativum* (Leguminosae), using both real (mutant) and imagined developmental changes. Recently, Niklas (1994) proposed a third type of heterochronic process, akratomorphosis, which results in the descendant having an adult shape similar to that of its ancestor but with a difference in size, either larger ("gigas") or smaller ("dwarfism"). More recently, Reilly (1997) rejected the terms "neoteny" and "progenesis" and proposed to use "deceleration" and "hypomorphosis," instead, in an effort to reduce confusion about the actual meanings of these terms. For continuity and standardization, however, we will use the original terms here. Based on the fact not only that the initiation or termination timing of developmental processes can be identical, earlier, or later but also that the developmental rate can be identical, faster, or slower in descendants than in ancestors, Niklas (1994: 262–274) proposed a $3 \times 3 \times 3$ matrix containing 27 possible heterochronic processes and suggested that the same descendant phenotype can be achieved through different combinations of developmental processes (combinations of different onset timing, offset timing, and growth rate).

Recently, Rice (1997) proposed a narrowed definition of heterochrony and stated that heterochrony is "a uniform change in the rate or timing of some ontogenetic process, with no change in the nature of the biological interactions going on within that process." In other words, heterochrony explains the developmental changes as a simple speedup, slowdown, or change of timing. Development, however, is a multidimensional process that is hardly uniform over time, and several studies have shown that both paedomorphosis and peramorphosis can be caused by either single or multiple developmental changes (Klingenberg & Spence, 1994; Kluge, 1985; Reilly, 1997). For example, the ontogenies of both the calyx and the corolla lobes in *Veronica chamaedrys* (Scrophulariaceae), a species with putatively derived floral forms, show a slower early growth but an accelerated later development, compared with *Veronicastrum virginicum* (Scrophulariaceae), having putatively ancestral floral forms (Kampny et al., 1993). In addition, the derivation of a number of cleistogamous flower traits from the presumed ancestral chasmogamous flower in *Collomia grandiflora* (Polemoniaceae) results from two types of peramorphosis; namely, acceleration and predisplacement (Minter & Lord, 1983). It is probable that most observed morphological changes are the joint effect of several types of heterochronic processes (Alberch et al., 1979; McNa-

mara, 1993). In addition, some characters may have one kind of heterochrony, but other characters on the same organism may have no heterochrony or a different type of heterochrony. A good example is the derivation of the flowers of hummingbird-pollinated *Delphinium nudicaule* (Ranunculaceae) from those of bumblebee-pollinated *D. decorum* by a combination of paedomorphic and peramorphic ontogenies (Guerrant, 1982). Paedomorphic development (neoteny) of sepals and petals in *D. nudicaule* results in the mature flowers resembling the buds ("juveniles") of *D. decorum,* whereas peramorphic development (both acceleration and hypermorphosis) causes larger nectariferous petals in *D. nudicaule* than in *D. decorum*.

The evolution of any one character may sometimes also be the result of both paedomorphosis and peramorphosis. For example, the evolution of both male and female gametophytes in angiosperms from those of their gymnosperm ancestors results from both paedomorphosis (progenesis) and peramorphosis (acceleration) (Friedman & Carmichael, 1998; Takhtajan, 1976, 1991). The progenesis and acceleration of gametogenesis in flowering plants resulted in the loss of gametangia (antheridia and archegonia) on their gametophytes. The gametangium, in which the gametes are produced, is part of the sexual reproductive organ in most gymnosperms and all lower vascular plants. The loss of gametangia makes the gametophytes in flowering plants the most simplified among the higher plants. In general, reductions are regarded as an advanced feature in evolution and probably usually result from paedomorphosis (Stebbins, 1992; Takhtajan, 1954, 1976, 1991). Our studies (Li & Johnston, unpubl.) on the development of various floral morphs in *Amsinckia spectabilis* (Boraginaceae) also indicate that both paedomorphic and peramorphic ontogenies are involved in the derivation of small homostylous flowers from their putative ancestor; namely, populations having large distylous flowers (see section IX.B). Another example of both paedomorphosis and peramorphosis shaping the evolution of a single character is the derivation of larger sepals of *Veronica chamaedrys* by a slower development (neoteny) and a delayed offset (hypermorphosis) from the smaller sepals of *Veronicastrum virginicum* (Kampny et al., 1993).

Heterochrony may also cause intraspecific morphological differences in plants, such as variations in leaf morphology among individuals in *Begonia dregei* (Begoniaceae) (McLellan, 1990, 1993; McLellan & Dengler, 1995). We too found this in our study (Li & Johnston, unpubl.) of the evolution of small homostylous flowers in *A. spectabilis* in terms of changes in floral ontogenies (see section IX.B). Heterochrony is usually responsible for variations in the shape and size of organs of the same type on a plant. It occurs in almost all plant organs, but especially in leaves.

Just as different developmental changes can lead to different morphologies, the same or similar morphology can also arise from a variety of developmental pathways. There are several examples of similar adult leaf morphology being produced by a variety of developmental patterns and processes (Jones, 1988; Kaplan, 1970, 1973b; McLellan, 1990). For example, the degree of incision of leaf margins varies among individuals in *B. dregei*; mature leaves from three least-incised varieties are very similar in shape (McLellan, 1990). Development of these varieties differs in size and shape of leaf primordium at initiation, in the timing of leaf incision, and in growth rate. McLellan (1990) concluded that two different developmental pathways are involved in the formation of the similar leaf morphs among the three varieties. There are also floral examples. Different developmental pathways have been found to result in similar mature carpels in *Persoonia falcata* and *Placospermun coriaceum* (Proteaceae, Douglas & Tucker, 1996) and, similarly, of long corolla tubes in *Pseudolysimachion* and *Veronicastrum* (Scrophulariaceae) and of long corolla lobes in *Pseudolysimachion* and *Veronica* (Scrophulariaceae, Kampny et al., 1994).

Caution must be taken while analyzing developmental and morphological changes in terms of heterochrony. The possible phenotypic effect caused by changes of developmental timing may be exaggerated or suppressed by changes of developmental rate, and vice versa. In other words, early onset (predisplacement) does not guarantee that the descendant final size or shape will be larger than or different from that of the ancestor because of a possible slower developmental rate (neoteny) and/or earlier offset (progenesis) in the descendant, in spite of the fact that it probably does happen at most times. Similarly, delayed onset may not necessarily result in a smaller or different adult size or form. Zygomorphic (bilaterally symmetrical) flowers are believed to be more specialized and advanced compared with actinomorphic (radially symmetrical) flowers (Carlquist, 1969; Stebbins, 1992). The zygomorphic character in a flower may be initiated at earlier floral developmental stages (predisplacement) (Stebbins, 1992; Tucker, 1987). The degree of zygomorphy, however, can be exaggerated or suppressed later in development. For example, flowers in *Cadia* and *Gleditsia* (Leguminosae) start to show their zygomorphic character at the sepal- and petal-initiation stages, but at anthesis they are no longer strongly zygomorphic because they were modified during later development by a lack of petal differentiation (Tucker, 1984, 1987), possibly caused by a slower growth rate. A change in offset timing can enhance, reduce, or eliminate the effects of a change in early developmental rate. This interaction between timing and rate is certainly important to morphogenesis, yet it seems often to be ignored in developmental and evolutionary studies, as well as in the discussion of the heterochronic models.

V. Problems and Solutions

A. ATOMIZING DEVELOPMENT

The use of heterochronic models such as the one proposed by Alberch et al. (1979) has as a shortcoming that the whole developmental process is conceptually divided into discrete stages. Sattler (1992, 1994) therefore advocated the use of process morphology, a dynamic approach to morphology based on the idea that structure is process. In his view, development is the combination of morphogenetic processes, and evolution occurs when these process combinations change. Process morphology gives a more integrated and more dynamic picture of development and evolution. Because process morphology uses process combinations that contain all kinds of parameters, however, it becomes more complicated and possibly difficult to use in analyzing developmental changes, compared with the heterochronic model. It may be difficult to use this outlook in practice, and it is probably not a very practical analytic tool for the study of development and evolution.

Heterochrony is seen as both a developmental process and an evolutionary pattern, causing confusion at times. Because of this, Alberch and Blanco (1996) recently proposed that we "reduce the dependence of current thinking about heterochrony on the concept of 'timing' and instead focus on the organization of sequences of developmental events in ontogeny." Their new perspective on heterochrony searches for regularities in the developmental sequences, such as dissociation events (substitution/alteration of events in developmental sequence) and the nonterminal conservancy (insertion, addition, or deletion of developmental events in the sequence), especially the terminal modification of developmental sequences. Examples of this type of study have shown its distinct value in understanding organismal morphological evolution (Alberch & Blanco, 1996; O'Grady, 1985).

B. HOMOLOGY

Although heterochrony is considered insufficient as a mechanism responsible for the integration of development and evolution (Gilbert et al., 1996; Raff, 1996; Raff & Kaufman, 1983), studying homology, including homologous genes and homologous developmental pathways, can help us understand the mechanisms underlying development and the relationships between development and evolution. Homology occurs at every level of organismal organization, development, and evolution. It is regarded as the hierarchical basis of comparative biology and the core concept in interpreting the logical relationships between ontogeny and phylogeny (Bolker & Raff, 1996; Goodwin, 1989; Hall, 1994). The role of homology in plant development and evolution is far less studied than that in animals (for reviews, see Donoghue & Sanderson, 1994; Kaplan, 1984; Sattler, 1994). After reevaluating the relationships among homology, developmental genetics, and evolution, Gilbert et al. (1996) recently reproposed the morphogenetic field, a discrete unit of embryonic development, as a major developmental unit. In such a view, genes and gene products create morphogenetic fields, and changes in these fields will modify organismal developmental pathways and thus lead to evolutionary changes.

C. DEVELOPMENTAL REFERENCE POINTS

The most frequently used developmental termination reference in animals is sexual maturity. However, one must be cautious about using sexual maturity as an offset reference (Guerrant, 1982), because it is possible that some small changes in earlier developmental events may not be detected if sexual maturity occurs very late during development (Niklas, 1994; Raff & Wray, 1989). This is especially true in plants with indeterminate development. Different temporal references are often used in plant developmental studies. For example, the most frequently used onset and offset points in floral studies are the initiation of primordium, meiosis, tetrad formation, anthesis, and fertilization.

D. ABSOLUTE VERSUS RELATIVE TIMING

Consider the timing of two reference points, R_1 and R_2, and that of the developmental event in the descendant, E_d. If the R_2–R_1 period changes in the descendant, then heterochronies interpreted on relative scales can give results different from those on absolute scales. For example, if development of an organ commences earlier in the descendant (lower E_d), then evolution has occurred by predisplacement. If, however, the total developmental time, R_2–R_1, is also shorter in the descendant, then heterochrony can be predisplacement, none, or postdisplacement, according to the proportional change in E_d compared with that in R_2–R_1. The problem of absolute versus relative scales generally does not apply to neoteny or acceleration, because these two rate-based heterochronies automatically incorporate the time separating the reference points R_2–R_1. In short, the type of heterochrony can depend on whether absolute or relative scales are used when the proportional change in reference points differs from the proportional change in event timing (see also Raff & Wray, 1989).

E. PHYLOGENIES

Heterochrony is often used in plant developmental and morphological studies even when phylogenetic information is absent. It is usually applied to explain the developmental differ-

ences between morphologically and/or functionally different organs. For example, the heteromorphic inflorescence in *Neptunia pubescens* (Leguminosae) produces three types of flowers. The perfect, male, and neuter flowers are formed from the upper, middle, and basal sections of the inflorescence, respectively. Comparative developmental studies among the three types of flowers indicate that the most significant developmental divergence responsible for the flower type is the delay of floral organs' initiation in the male and neuter flowers, which was interpreted as heterochrony, a change of onset timing during development (Tucker, 1988). Because of the lack of phylogenetic information, it is difficult to know the direction of evolutionary change. Furthermore, strictly speaking, without a known phylogeny this is not a heterochrony. Therefore, it is a necessary challenge for biologists interested in heterochrony to obtain phylogenetic information or some knowledge of an organ's evolutionary history.

Ontogeny does not always provide a clear indication of phylogeny, and some organisms, such as prokaryotes and single-celled eukaryotes, may even lack ontogeny (Kluge, 1985). Therefore, heterochrony may not always be a responsible force in evolution, at least in some groups of organisms. In order to understand the phylogenetic relationships and evolution among different organisms, researchers will often find it useful to employ other methods, such as comparisons with outgroups, multiple-character congruence, and parsimony (Kluge, 1985).

VI. Allometry, a Tool Complementary to Heterochronic Study

Allometric study, "the study of size and its consequences" (Gould, 1966) or "the study of the consequences of size for shape" (Bookstein et al., 1985), can provide important developmental information even when age information is absent (McKinney, 1988a). It can further often illuminate the evolutionary adaptations of size or shape changes (Gould, 1966). Allometry has been extensively used by botanists (Niklas, 1994), for example, in the comparative development of floral forms and size (Greyson, 1972; Jones, 1992; Kellogg, 1990; Kirchoff, 1983, 1988; Lord, 1982; Mayers & Lord, 1983a; Minter & Lord, 1983; Smith-Huerta, 1984).

During development, size, shape, timing, and rate are functionally interrelated. A change in one of these four variables may affect another, and such changes are subject to selection. Because a change in size or shape detected by allometry is not a function of time, allometry is not heterochrony. Results from allometric study reveal only the growth relationships between different parts of the organism or between a part of an organism in relation to the whole organism. To qualify as heterochrony, and for one to be able to distinguish the types of developmental processes and patterns, one must have developmental age information, and development must be studied over time. Unfortunately, there often is a practical difficulty with the identification of the types of heterochrony when organismal developmental data are examined over time instead of size. This is because the developmental rate is often constantly changing during organismal development. As Fiorello and German (1997) stated, "nonlinear growth data do not vary in simple factors like rate, timing, and starting size."

However, because allometry has its distinctive function in interpreting the relationships between size and shape, it is a useful tool in assisting heterochronic study (Blackstone, 1987a, 1987b; Fiorello & German, 1997; McKinney, 1988a). Klingenberg (1998) recently commented that "there are close connections between heterochrony and changes in allometric growth trajectories, although there is no one-to-one correspondence." Therefore, a complementary use of both size and timescales would give us a better understanding of the relationships between developmental process and evolution. To make use of allometry in developmental and evolution-

ary study, McKinney (1988a) proposed an allometry-heterochrony scheme, which not only is a useful tool for allometric analysis but also distinguishes itself from heterochronic timing and/or rate effects.

VII. Applicability of Heterochrony to Plant Studies

Heterochrony has been extensively studied as a source of animal variation and evolution. There are far fewer studies on the role of heterochrony in plant evolution. Most plant ontogenetic or morphogenetic studies focus on developmental processes, the sequence or description of the morphological changes in a plant or its organs during its development. Many studies lack data on either event timing or growth rate, mainly because of the difficulty in obtaining them, especially during the earliest developmental stages. This means that plant biologists are often unable to identify the heterochronic changes underlying plant or plant organ's development. Another main cause limiting the application of heterochrony in plant evolutionary study is indeterminate development. This is especially true for embryos and seedlings. Some plants or organs even have a period of dormancy during their normal development. The lack of distinction between the somatic "juvenile" phase and the sexually mature "adult" phase in many plants is certainly one of the reasons why heterochrony has not been well studied in this kingdom.

Some plant organs, such as flowers, fruits, and leaves, are determinate in their development. Their normal development, however, is easily affected by both their internal and external growth environments. For example, the final sizes and shapes of leaves can depend on the age of the plant and/or environmental conditions. A good example is heterophylly in aquatic plants, such as in *Ranunculus flabellaris* (Ranunculaceae) (Young et al., 1995). Among organs with determinate development, the flower shows the least plasticity. For this reason, most heterochronic studies in plants focus on flowers. Of course, from the paleobotanic point of view, heterochrony was also involved in the evolution of land plants. There have been some discussions about heterochrony in relation to the evolution of plant life cycles, telome theory, stelar evolution, and other aspects related to the evolution of land plants (Mosbrugger, 1995; Takhtajan, 1991; Zimmermann, 1959); these will not be discussed here.

VIII. Heterochrony in Fossil Plants

Heterochrony must have played an important role in plant evolution, although fossils cannot provide direct evidence. For instance, the fossil crown-branched pseudoherb *Hizemodendron* is believed to be derived from a possibly crown-branched tree, *Lepidodendron,* by earlier cessation of stem elongation (progenesis) (Bateman, 1994; Bateman & DiMichele, 1991). These two genera had very similar reproductive characters, but their vegetative architectures were very different. *Hizemodendron* was only about 0.1–0.5 m tall, with simplicity in its anatomy, whereas *Lepidodendron* was about 30 m tall, with relative complexity of anatomy. In another example, it is postulated that the fossil *Chaloneria* (Isoetales) evolved from its putative ancestor *Sigillaria* (Lepidodendrales) by neoteny and progenesis (Bateman, 1994). The two genera differed not only in size but also in shape and in time of reproduction. *Sigillaria* was a tree about 15 m tall, with both terminal and cauline lateral branches, and *Chaloneria* was a small-bodied shrub about 0.1–2 m tall, with no branches. Bateman (1994) suggested that a reduced developmental rate caused the smaller size of descendant and that terminal and nonterminal deletions during stem development resulted in the loss of all

branches. The paedomorphic development also shortened *Chaloneria*'s life history and caused earlier reproduction.

As discussed earlier, a heterochronic approach is valid only when a developmental analysis is based on a time or age scale. Considering that it is almost impossible to reconstruct the timing of development in a fossil plant, the heterochrony-like analysis of putative ancestral and descendant fossil plants is meaningful only as a hypothesis.

IX. Heterochrony in Flowering Plants

A. HETEROCHRONY AND TIMING OF FLOWERING

Most heterochronic studies in plants are focused on plant organs, and only a few heterochronic studies have been conducted at the whole-plant level for the reasons and difficulties mentioned above. One such study (Jones, 1992) was conducted on shoot development and flowering timing in two subspecies of *Cucurbita argyrosperma* (Cucurbitaceae), a cultivar (*C. argyrosperma* var. *argyrosperma*), and its wild progenitor (*C. argyrosperma,* subsp. *sororia*). Jones found that the nodal position—that is, the timing—of flower production differed significantly in the two subspecies. In *C. sororia* the earliest fertile male flower was produced at node 19, and the first fertile female flower was produced at node 39. In *C. argyrosperma,* however, the earliest fertile male and female flowers were produced at node 12 and node 30, respectively. Jones concluded that the shift to earlier flower production in the cultivar was a result of paedomorphic development by progenesis.

The phenomenon of heterochrony is most often seen when the timing of a developmental change is related to the onset of organismal sexual maturity or to the time when the vegetative phase switches to the reproductive phase. The latter may occur when the shoot meristem or axillary bud, instead of producing leaves, starts to differentiate as a flower, a flower-producing branch, or an inflorescence. The switch from vegetative to reproductive development is under both genetic and environmental controls. In several species, heterochronic mutations are known to change the phase length and/or the timing of the switch. For example, the *Tp2* mutation in maize increases leaf production, thus extending the vegetative phase and delaying the transition from vegetative to reproductive growth (Poethig, 1988). In contrast, the *leafy calyx* mutation in *Primula sinensis* (Primulaceae) (Anderson & DeWinton, 1985) and *leafy* (*lfy*) mutation in *Arabidopsis thaliana* (Brassicaceae) (Schultz & Haughn, 1991, 1993; Weigel & Nilsson, 1995; Weigel et al., 1992) can prolong the vegetative phase without delaying the onset of the reproductive phase. In these mutations the flower (in *P. sinensis*) or inflorescence (in *A. thaliana*) is subtended by leaves, leaflike bracts, or even bractlike or sepal-like floral organs (in *A. thaliana*).

It is also true that the vegetative growth phase often overlaps the reproductive growth phase in plants, which is evidenced by the production of new leaves and even new vegetative shoots while the plant is in the flowering phase. In such cases it will be difficult to conclude that the precocious flowering is a result of earlier offset of the vegetative growth phase.

By altering the onset of flowering, heterochrony can cause changes in life history (McKinney, 1999; Zopfi, 1995). Zopfi (1995) studied patterns of life-history variation, morphology, ecology, and phylogeny in seven different habitat types of *Rhinanthus glacialis* (Scrophulariaceae). It was found that the onset of vegetative growth is about two weeks earlier in populations of subalpine hay meadows, postulated descendants, than in populations of alpine grassland, postulated ancestors. In addition, flowering time is about six to ten weeks later in populations of subalpine limestone grassland, postulated descendants, than in populations of

alpine grassland, postulated ancestors, mainly due to later offset of vegetative growth of the main axis in plants. Plants from descendant populations have more internodes, taller stems, and more branches. Thus, it was suggested that populations of subalpine hay meadows are the peramorphic variants derived from populations of alpine grassland by predisplacement in vegetative growth and that populations of subalpine limestone grassland are peramorphic variants derived from populations of alpine grassland by hypermorphosis in vegetative growth. Similarly, populations from grassland on rocks, the postulated descendants, have a later offset of vegetative growth compared with that of populations from dry continental meadows, the postulated ancestors; therefore, the former are proposed also to have arisen from the latter through hypermorphosis in vegetative growth. In contrast, Zopfi (1995) also found that populations in litter meadows, postulated descendants, have earlier offset in vegetative growth than populations from grassland on rocks, postulated ancestors. Plants from the postulated descendant populations have fewer internodes and branches, as well as shorter stems, than their ancestors. Thus, the populations in litter meadows are suggested to be the paedomorphic variants derived through progenesis.

B. HETEROCHRONY AND FLORAL MORPHOLOGY

In general, the flower was derived from a primitive reproductive shoot of a seed fern and most probably resulted from developmental deletion and subsequent modifications, as well as specializations (Takhtajan, 1976). There are many examples demonstrating that not only the flower as a whole but also floral organs, such as sepals, petals, stamens, and carpels, were all derived by progenesis and modified from some laminar structures (for details, see Takhtajan, 1976, 1991). Changes in the timing, rate, and/or location of developmental events must have played important roles in the diversification and evolution of floral morphology. Kampny and Harris (1998) suggested that heterochrony is "the basis of floral shape evolution." Here our discussion on heterochrony will be mostly centered on the evolution of mating systems.

Within angiosperms, the evolution of the cleistogamous (CL) flower from the ancestral chasmogamous (CH) flower is generally believed to be the result of heterochrony (Gallardo et al., 1993; Lord & Hill, 1987). The mature CL flower looks like the young bud of the CH flower. Self-pollination occurs within the CL flower without opening. The mature CH flower is a typical open flower, and there is a temporal difference in sexual maturity between stamen and pistil, causing some degree of outcrossing. CL flowers occur in many angiosperm species, usually on the same plant and often on the same inflorescence as CH flowers. The CL flower is often regarded as a progenetic dwarf derived from the CH flower (Gould, 1988; Guerrant, 1988; Lord & Hill, 1987), but various developmental pathways can result in the production of CL flowers. For example, in *Viola odorata* (Violaceae), the smaller size of the floral primordium at its inception and the faster floral developmental rate (acceleration) caused earlier maturation, producing a CL flower (Mayers & Lord, 1983a, 1983b). The CL flower reached its sexual maturity 15 days earlier than did the CH flower (Mayers & Lord, 1983a). In a study of flower development in *Lamium amplexicaule* (Labiatae), Lord (1979, 1982) found that the accelerated floral development after pollen–mother-cell meiosis resulted in the precocious maturation of the CL flower (about 10 days earlier than the CH flower). A similar developmental pattern was also seen in *Astragalus cymbicarpos* (Fabaceae) (Gallardo et al., 1993). In *Collomia grandiflora* (Polemoniaceae), accelerated development at early floral developmental stages (before pollen–mother-cell meiosis) and the earlier onset of pollen–mother-cell meiosis were responsible for the shorter development time of CL flowers (two days earlier than CH flowers) (Minter & Lord, 1983). It was also reported that the small CL

corolla form in *Salpiglossis sinuata* (Solanaceae) resulted from the arrest of cell expansion (progenesis) (Lee et al., 1979). From the examples above, it is clear that CL flower production involves not only progenesis but also the acceleration of sexual maturity and, therefore, an increase in developmental rate. In other words, CL flowers can evolve not only through paedomorphic development by progenesis but also through peramorphic development by acceleration and/or predisplacement. It is probable that more than one type of heterochronic process is involved in the origin of cleistogamous flowers in most species.

Flowers of highly self-fertilizing species are often smaller than those of their outbreeding ancestors (Diggle, 1992; Guerrant, 1984, 1988, 1989; Solbrig & Rollons, 1977; Wyatt, 1983). Comparative floral developmental studies between *Limnanthes floccosa* (Limnanthaceae) and *L. alba* by Guerrant (1984, 1988) showed that *L. floccosa* had its reproductive developmental stages (microsporocyte meiosis and tetrad formation) and maturity (anthesis) earlier than did those in its putative ancestor, *L. alba,* although the two species had similar size-shape growth trajectories. *L. floccosa* produces small selfing flowers, whereas *L. alba* produces large outcrossing flowers. Early developmental offset (progenesis) was the primary cause of the precocious maturity of *L. floccosa* flower, although an increased floral developmental rate (acceleration) may also be involved (Guerrant, 1984, 1988).

Runions and Geber (1998) recently found that progenetic vegetative growth and accelerated sexual development lead to the derivation of self-pollinating *Clarkia xantiana ssp. parviflora* (Onagraceae) from cross-pollinating *C. xantiana ssp. xantiana.* The selfers of *C. xantiana* are smaller in plant size, flower earlier, and produce smaller flowers. Runions and Geber's studies (1998) showed that the selfers possess shorter leaf and internode growth duration, flower 2.6 nodes earlier than do the crossers, and have faster ovary elongation and ovule development rate compared to the crossers. It is reasonable to suggest that progenesis (early offset of vegetative growth leading to early flowering) and acceleration (relatively rapid maturation of ovaries and ovules) played an important role in the evolution of self-pollinating from cross-pollinating in *C. xantiana.*

We (Li & Johnston, unpubl.) compared flower ontogenies between distylous and homostylous species in three separate evolutionary lineages of *Amsinckia* (Boraginaceae) and found that neoteny is primarily responsible for the derivation of highly self-fertilizing species from their outcrossing ancestors. The homostylous, small-flowered *A. vernicosa* evolved from distylous, larger-flowered *A. furcata,* and the tetraploid, smaller-flowered, homostylous *A. gloriosa* evolved from distylous, diploid, larger-flowered *A. douglasiana* (Ray & Chisaki, 1957a, 1957b; Schoen et al., 1997). Individuals of distylous species bear either pin or thrum flowers. In pins, the stigma is exserted above the open corolla, and the anthers are located at the lower portion of the corolla tube. In thrums, the stigma is positioned at the lower portion of the corolla tube, and the anthers are at the entrance of the open corolla. In homostylous species the stigma and anthers in a flower are positioned almost at the same level. The larger distylous flowers are predominantly outcross-pollinated, whereas homostylous flowers are smaller and predominantly self-pollinated (Ganders, 1975, 1976, 1979; Johnston & Schoen, 1996; Schoen et al., 1997). Our study finds that the developmental duration from the initiation of floral primordium to flower opening is the same for distylous and homostylous flowers in both lineages. The developmental rate for most floral traits, such as floral bud length and width, pistil length, stamen filament length, and so forth, in homostylous flower is highly significantly lower than in distylous flowers (neoteny).

A change in developmental rate is not only responsible for floral evolution differentiating species but also plays an important role in the derivation of different floral morphs and mating systems within a species. *Arenaria uniflora* (Caryophyllaceae) shows intraspecific variation

in floral size and mating types. Plants in selfing populations produce small flowers, whereas those in outcrossing populations produce large flowers. Detailed morphological and growth-rate studies of the two types of flowers indicate that the selfing flowers evolved from the outcrossing ones by a reduced developmental rate (neoteny) and longer growth duration (Hill et al., 1992). A similar result was also seen in our studies of the flower development and evolution of homostylous selfing flowers from distylous outcrossing ones within *Amsinckia spectabilis* (Li & Johnston, unpubl.). In this third evolutionary lineage of *Amsinckia* there are three types of population: distylous, large homostylous (sometimes including pins and thrums), and small homostylous. Outcrossing rates are approximately 50–70 percent, 25 percent, and <1 percent, respectively (Johnston & Schoen, 1996; Schoen et al., 1997). The large homostylous flower is similar to the distylous flowers in floral developmental duration (18, 17, and 15 days for pin, thrum, and large homostylous flowers, respectively); the duration for the small homostylous flower is much longer (23 days). There is thus a later developmental offset (hypermorphosis) in small homostylous flowers. Our study also shows that, compared with the two distylous morphs, the small homostylous flower has a significantly lower developmental rate (neoteny) and a later onset of pollen–mother-cell meiosis (postdisplacement). Therefore, a joint effect of hypermorphosis, neoteny, and postdisplacement has resulted in the evolution of small homostylous flowers in *A. spectabilis*.

As discussed in section V.D, different heterochronies can be obtained with relative and absolute timescales. In all three *Amsinckia* lineages studied, the timing of pollen–mother-cell meiosis shows no heterochrony when measured on a relative rather than absolute scale (Li & Johnston, 1999). On such a relative scale, the period of flower development from primordium initiation to flower opening represents one unit. Thus the fraction of floral development preceding (and following) pollen–mother-cell meiosis has remained invariant during extensive floral evolution.

It seems clear that the developmental processes responsible for the evolution of smaller, selfing flowers from larger, outcrossing progenitors vary among and within species. Early anther differentiation and precocious anther or floral maturation (all examples of progenesis) are the major causes of many evolutionary processes; changes in developmental rate (particularly neoteny) and growth duration are also involved in some cases.

In addition to organismal and organ levels, heterochrony can also be observed at smaller levels, such as floral parts, tissues, and cells. Heterochrony has played a major role in the origin of the smaller size of anthers in self-pollinated flowers from the large anthers in outcross-pollinated flowers (Hill, 1996; Lord et al., 1989). The size and shape of stamen primordia for both types of flowers are almost the same, and the first noticeable difference during their development usually occurs at the archesporial cell stage (Hill & Lord, 1990; Lord, 1982; Minter & Lord, 1983). In *Collomia grandiflora* (Polemoniaceae), an earlier onset of CL anther differentiation (predisplacement) (Hill & Lord, 1990; Lord et al., 1989), or a slower developmental rate (neoteny) and a shorter developmental duration (progenesis) between archesporial cell differentiation and microsporocyte meiosis in CL anthers (Lord et al., 1989; Minter & Lord, 1983) are responsible in CL flowers for the precocious anther maturation and smaller mature anther size (about half the size of CH flowers) with fewer pollen grains (only 1/10th the number of CH flowers). A slower developmental rate (neoteny) and earlier anther dehiscence (progenesis) may be the causes of small anthers of CL flowers in *Bromus unioloides* (Gramineae) (Langer & Wilson, 1965). The archesporial cells in the anthers of selfing flowers start to divide while the anthers are still small, compared with the anthers of outcrossing flowers in *Arenaria uniflora* (Caryophyllaceae). This causes the anthers in selfing flowers to reach maturity while they are still small (Hill, 1996; Hill & Lord, 1990) and indicates that

the timing of archesporial cell division relative to the size of the developing anther has played a role in shaping anther and floral morphologies. Because no time information was available in the study of *A. uniflora,* however, we are unable to detect the type of heterochronic process responsible for the morphological changes. A short meiotic duration (progenesis) in CL anthers was reported to be responsible for the precocious maturation of anthers and flowers in *Bromus carinatus* (Gramineae) (Harlan, 1945).

C. HETEROCHRONY AND LEAF MORPHOLOGY

Leaves show greater plasticity than do flowers. It is believed that leaves of flowering plants were derived from frondlike leaves of primitive ferns or seed ferns by early offset of development (progenesis) and structural modifications (Asama, 1960; Axelrod, 1960; Takhtajan, 1954, 1976, 1991). For example, the leaves of the primitive flowering plants, such as Magnoliales, are simple and entire, with pinnate venation, and they could have evolved from primitive gymnosperm leaves, such as those of Lyginopteridopsida, resulting from developmental arrest at an earlier stage of leaf development (Takhtajan, 1976). Early developmental offset was formerly called neoteny (Asama, 1960; Axelrod, 1960; Takhtajan, 1954, 1976), based on the idea that neoteny is "the terminal abbreviation of development (the loss of late stages) and a premature completion of development of the whole organism (total neoteny) or of parts of it (partial neoteny)" (Takhtajan, 1976). However, according to the modern heterochronic scheme, it should be called progenesis.

Variation of leaf morphology in angiosperms has been shown to be closely related to leaf ontogenetic differences (Gleissberg & Kadereit, 1999). In Hawaiian Lobelioideae (Campanulaceae), Lammers (1990) found that mature leaves in some species were similar to juvenile leaves of their ancestral species. It was concluded that paedomorphosis not only was responsible for the reiteration of ancestral juvenile leaves in descendants but also had occurred several times in Lobelioideae. Timing data, unfortunately, are lacking.

Leaf shape often differs, even between subspecies, as a result of heterochronic development. Comparative studies of two subspecies of *Cucurbita* (Cucurbitaceae) indicated that the shape of leaves along the main shoot in *C. argyrosperma* subsp. *sororia* (wild) changes as the shoot grows, from hardly lobed, earlier-produced leaves to more highly lobed, later leaves (Jones, 1992). In contrast, leaf shape in *C. argyrosperma* var. *argyrosperma* (a cultivar) does not change with shoot growth, all leaves being similar to the earlier-produced, less-lobed leaves of the wild subspecies. Jones (1992) proposed that the less-lobed leaves of *C. argyrosperma* var. *argyrosperma* resulted from paedomorphosis by which the juvenile leaf form was retained from its progenitor. Nonetheless, from further developmental studies she noticed that the formation of the juvenile-looking leaf in *C. argyrosperma* was not simply the result of paedomorphosis but was, instead, a combination of evolutionarily conserved early development and later allometric growth (Jones, 1993).

Although evolutionary changes in leaf morphology have often resulted from paedomorphosis, peramorphosis is also common in leaf evolution. In *Viola odorata* (Violaceae), both leaves and petioles of CL plants are much larger than are those of the ancestral CH plants, probably as a result of increased growth rate (acceleration) (Mayers & Lord, 1983a). Similar results have been found in *Pseudopanax crassifolius* (Araliaceae), a heteroblastic tree, in which leaf size and shape differ greatly between juvenile and mature shoots. Leaves from a juvenile plant are narrow, linear, sharply toothed, about 25–100 cm long and 0.5–1.5 cm wide, whereas leaves from an adult tree are about 10–20 cm long and 1.5–3.0 cm wide (Clearwater & Gould, 1993). The adult leaves are regarded as ancestral because they are similar to

leaves of homoblastic *Pseudopanax* species in both form and development (Clearwater & Gould, 1993; Philipson, 1971). Comparative leaf developmental studies showed that the two leaf types differed soon after their inception and that accelerated (length) development in the "juvenile" leaf primordium was probably responsible for its derivation from the "adult" type of leaf (Clearwater & Gould, 1993). The differences in relative growth rates of lobes and sinus during leaf development and cell size in the mature leaves are possibly responsible for the variation in leaf morphology within *Tropaeolum* (Tropaeolaceae), from acutely lobed, to roundly lobed, to orbicular (Whaley & Whaley, 1942).

The type of leaf architecture, simple versus compound, can also be related to heterochronic development. Merrill (1979) studied leaf ontogenies in three species of *Sorbus* (Rosaceae), each with a distinct leaf form. The relative timing of initiation of the primordial lamina (leaflet) differed among the three types of leaf. The earliest was in compound-leaved *S. decora,* then in half-compound-leaved *S. hybrida,* and finally in simple-leaved *S. alnifolia.* Similar results of leaflet-initiation timing were also obtained by Dengler (1984) in three tomato genotypes with compound, half-compound, or simple leaves. According to Cronquist's theory, compound-leaved species in general originated from simple-leaved ancestors (Cronquist, 1988). It is reasonable to assume that predisplacement is involved in the derivation of the compound leaf types.

X. Heterochrony at the Cellular and Tissue Levels

The timing and pattern of cell division and differentiation in plants determine the type of organ, tissue, or cell formed (Esau, 1977). For example, the timing, rate, and duration of cell division, as well as differentiation during anther development, are believed to have a direct impact on the final size of the anther and the amount of pollen produced (Hill, 1996; Minter & Lord, 1983). Changes of timing and rate of cell division during leaf development are the major developmental causes that lead to the formation of heteroblastic leaves on the same stem in some plants (Dengler, 1992; Kaplan, 1973a, 1980; Richards, 1983).

Heterochrony also exists in single-celled organisms, such as yeast. Mitosis in yeast is an indication of sexual maturity. Compared with normal yeast, the heterochronic mutants of yeast undergo mitosis at an unusual time, either earlier (progenesis, mitosis occurs at smaller size) or later (hypermorphosis, mitosis occurs when it is oversized) (Lee, 1988).

Heterochrony is not so well studied at cellular and tissue levels in plants. Nevertheless, heterochrony must exist at these levels because of the hierarchical nature of development. For example, the type of leaf produced by the shoot apical meristem not only depends on whether and when leaflets are formed but also relates to the timing of the offset of cell division or the onset of cell enlargement during leaf development (Dengler, 1984; Sinha et al., 1993). Comparative leaf developmental studies among three tomato genotypes showed that cell division precociously ceased and cells began to enlarge at a much earlier time in the development of simple entire leaf compared with those in half-compound and compound leaves (Dengler, 1984). Therefore, it can be inferred that the delayed offset of cell division and thus a later onset of cell enlargement during the expansion of leaf lamina were at least partially responsible for the formation of a large and/or compound leaf.

XI. Heterochrony at the Molecular Level

Morphological evolution can arise not only from structural changes but also from development-related gene regulation (Ambros, 1997; Atchley, 1990; Niklas, 1997). The com-

position, functional sequence, and timing of the activities of genes responsible for development determine both the duration of the developmental process and the timing of specific events. The underlying cause of developmental modification must include changes in temporal and/or spatial gene-expression patterns. Any morphological changes we observe, including the underlying changes in both rate and timing of physiological processes, are caused mostly by changes of gene combinations and/or their activities. From this point of view, any alteration of the temporal patterns of gene expression during development can be regarded as a heterochronic change at the molecular level. If we follow Alberch and Blanco's (1996) recent idea that heterochrony should focus on the changes of sequences of developmental events, which is also supported by Raff (1996), then alteration of the gene-expression sequence during development is also a molecular heterochrony. In any case, comparative molecular data within and among taxa can provide insights into the variation of development and, therefore, into the evolution of development.

It is clear that even a minor alteration of a plant developmental pathway could cause dramatic changes in phenotype (Wiltshire et al., 1994). A mutation that changed developmental rate or the timing of developmental events, such as meiosis, flower opening, or the transition from vegetative growth to reproductive growth, is often termed a heterochronic mutant (Wiltshire et al., 1994). Examples include *Hairy-sheath-frayed1–O* (*Hsf1–O*) in maize (Bertrand-Garcia & Freeling, 1991; Freeling et al., 1992) and *early-flowering* (*elf*) in *Arabidopsis* (Zagotta et al., 1992). In *Pisum sativum* (Leguminosae) alone, nine heterochronic mutants have been found (Wiltshire et al., 1994). These mutants cause dramatic morphological changes by different types of heterochronic processes, including neoteny, progenesis, acceleration, and hypermorphosis. For example, plants with the recessive mutant allele *sn,* under short-day conditions, begin to flower in the axil of first four-leaflet leaf and produce a total of only four leaves, all with four leaflets. Growth stops before the adult vegetative phase (no six-leaflet leaf is formed). Individuals with dominant allele *Sn,* on the other hand, begin flowering in the axil of first four-leaflet leaf, produce a total of seven four-leaflet leaves, and grow until 17 six-leaflet leaves are formed. Thus, the earlier offset of vegetative development, subsequent earlier flowering, and earlier senescence in *sn* mutants are examples of progenesis (Wiltshire et al., 1994).

Recent experimental studies have found that the overexpression of some genes can change flowering time. For example, under the control of the CaMV 35S promoter, the overexpression of *LEAFY* can convert the inflorescence meristem into a flower meristem and cause early flowering in *Arabidopsis*. *LEAFY* can also induce transformed shoots to flower precociously in a hybrid aspen (*Populus tremulax* X *tremuloides,* Salicaceae), a plant that normally requires 8–20 years to flower (Weigel & Nilsson, 1995). It is also found that the overexpression of the *APETALA1* (*AP1*) gene alone can cause early flowering in *Arabidopsis,* by converting inflorescence shoot meristems into floral meristems and thus dramatically reducing the time to flowering (Mandel & Yanofsky, 1995). Early flowering can be caused by additional heterochronic genes. For example, early flowering in *A. thaliana* can result from those genes mentioned above, as well as *terminal flower* 1 (*thl1*), *early-flowering* (*elf*) 1, 2, and 3 (Zagotta et al., 1992), *embryonic flower* (*emf*) (Sung et al., 1992), and *early short days* (*esd*) (Coupland et al., 1993). Mutations of some other genes can cause late flowering (Colasanti & Sundaresan, 1996; Koornneef et al., 1991). In *Arabidopsis* examples include mutants of *LD, FRI, CO,* and *FCA* (Colasanti & Sundaresan, 1996; Coupland, 1995; Lee et al., 1994).

Although changes in the expression of some genes can cause earlier or later flowering, mutations can also affect transitions between developmental stages, often leading to a retention of early developmental stages. It has been found that *Tp1, Tp2, Cg,* and *Hsf1-O* in maize can slow stage transitions during shoot development and can cause some juvenile stages to be

prolonged, a result that could also be called paedomorphosis (Bertrand-Garcia & Freeling, 1991; Freeling et al., 1992). It has also been found that *EMBRYONIC FLOWER* (*EMF*), *EARLY-FLOWERING* (*ELF*), *CONSTANS* (*CO*), and some other genes play important roles in controlling and regulating the transition time from vegetative to reproductive phase in *A. thaliana* (Haughn et al., 1995; Yang et al., 1995). The activity of the *EMF* genes gradually declines as vegetative growth proceeds during normal plant development. When *EMF* activity falls to a critical threshold, the plant or its shoot initiates a transition from vegetative to reproductive growth. The decline in *EMF* activity during vegetative growth in turn is regulated by *ELF* and *CO* genes, which can lead to promoting or delaying the transition time from vegetative to reproductive growth, thus changing the offset time of vegetative growth or onset time of reproductive growth.

In addition to flowering time and floral morphology, heterochronic genes may change inflorescence architecture. Coen et al. (1990, 1994) found that changes in the *floricaula* (*flo*) gene expression timing or site will lead to a change of inflorescence types in *Antirrhinum majus* (Scrophulariaceae). For example, when activation of the *flo* gene was delayed, a compound cyme (thyrse) was produced instead of the normal single flower.

As Stebbins (1992), Purugganan (1996), and Purugganan et al. (1995) all noted, any evolutionary change has a molecular basis, and in order to understand fully morphological evolution it is necessary to know the molecular basis of morphology. Molecular evolution of flower development has been the main focus in investigating plant evolution at the molecular level during recent years, and it has greatly advanced our knowledge of genetic control of flower development. Most results have been from homeotic mutants, the importance of which to floral evolution remains unknown.

XII. Homeosis

There is no doubt that heterochrony is one of the most important developmental mechanisms responsible for morphological evolution. Heterochrony, however, is not the only mechanism that can account for phenotypic evolution. Other developmental mechanisms include homeosis, heterotopy, and homology.

Homeosis refers to a structure, "A," or part of "A," developing at the site of structure "B" (Sattler, 1988, 1994). In terms of "process morphology," homeosis occurs when "a process combination or process(es) of that combination are expressed at the site of another process combination (of the same organism)" (Sattler, 1992). According to this view, homeosis is the replacement of one developmental pathway by another, or of one part by another. A homeotic mutant, then, refers to a mutation that alters the normal developmental pattern and leads to organ "A" developing at the site of "B," and "B" could be partially or wholly replaced by "A."

Many homeotic mutants have been identified in plants, primarily in the flower (An, 1994; Bowman et al., 1989, 1992, 1993; Coen, 1991; Crone & Lord, 1994; Drews et al., 1991; Flanagan & Ma, 1994; Jack et al., 1992, 1993; Jordan & Anthony, 1993; Krol & Chua, 1993; Lord et al., 1994; Saedler & Huijser, 1993; Veit et al., 1993; Weigel & Meyerowitz, 1994) and leaf (Freeling et al., 1992; Marx, 1987; Murfet & Reid, 1993; Schneeberger et al., 1995). The best-known example of homeosis in plants is the replacement of one kind of floral organ by another. For example, both single- and double-flowered varieties exist in *Hibiscus rosa-sinensis* (Malvaceae). The single flower has about 60–70 stamens inside a pentamerous whorl of petals, whereas the double flower has many more modified petals and petalodia but fewer stamens. Floral developmental studies indicate that homeosis played a role in the replacement of stamens by petals or petalodia in the double flowers (MacIntyre & Lacroix, 1996).

A good example of partial homeosis is the development of male flowers on the heteromorphic inflorescences in *Neptunia pubescens* (Leguminosae). The flower usually produces petal-like stamens, called "staminodia" (Tucker, 1987, 1988). Staminodia develop from normal stamen primordia, but with altered developmental processes and patterns. Extended cell enlargement and large intercellular spaces lead to the formation of staminodial lamina. This is also different from the petal developmental process in which large amount of marginal meristem activities (cell divisions) are the main cause of petal lamina expansion (Tucker, 1987, 1988).

Takahashi (1994) proposed the term "serial homeosis" for a homeotic phenomenon occurring in flowers of *Trillium apetalon* (Liliaceae). *T. apetalon* is the only apetalous species in its genus. The whorl of three petals was replaced by three stamens, and this replacement triggered a serial floral-organ replacement in the inner whorls: the inner stamens replaced outer ones, and carpels replaced inner stamens.

Although most studies of homeosis in plants focus on its role in floral morphological evolutionary changes (e.g., Coen, 1991; Kirchoff, 1991; Lehmann & Sattler, 1996; Posluszny et al., 1990), homeosis in other plant organs has also been studied. For example, in a published discussion (Posluszny et al., 1990) Gerrath used homeosis to explain the origin of tendrils in Vitaceae, *Pisum sativum* (Leguminosae), and *Passiflora guadrangularis* (Passifloraceae). Some of the pea (*P. sativum*) leaf mutants, such as *afila* (*af*) and *tendrilless* (*tl*), have been regarded as examples of homeosis in leaf ontogeny: the *af* mutant causes leaflets to be replaced by tendrils, and *tl* causes the opposite (Demason & Villani, 1998). Developmental study of double mutants and heterozygotes, however, shows that these genes interact to influence many aspects of leaf development, including timing, and that the conversion from one organ type to the other may actually be an example of heterochrony rather than homeosis (Demason & Villani, 1998).

In many cases, the developmental changes explained with heterochrony can also be interpreted by homeosis (Jordan & Anthony, 1993). The best examples in plants are the changes of floral morphogenesis caused by floral homeotic genes. Many homeotic genes have been identified and characterized, and most belong to the plant MADS-box regulatory gene family (Purugganan et al., 1995). Their expression can cause dramatic changes in flower morphology and thus possibly result in the evolution of flower development. For example, both *apetala3* (*ap3*) in *Arabidopsis* and *deficiens* (*def*) in *Antirrhinum* can cause homeotic transformations from petals to sepals and from stamens to carpels (Bowman et al., 1989; Jack et al., 1992, 1994; Schwarz-Sommer et al., 1990; Weigel, 1995; Weigel & Meyerowitz, 1993). The developmental switch from petal to sepal possibly happens after the petal primordium is initiated (Hill & Lord, 1989). The expression of *Agamous* gene from *Arabidopsis* in tobacco flowers converts sepals to carpels and petals to stamens (Mandel et al., 1992; Martin, 1996). These facts demonstrate that a change at the gene level can lead to the production of a totally different morphology, a replacement of parts in an organism. Therefore, homeotic genes may be responsible for at least some of morphological divergence during evolution.

XIII. Heterotopy

Heterotopy in plants usually refers to the formation of an organ at the "wrong place." A typical example might be epiphylly, the formation on angiosperm leaves of inflorescences, shoots, buds, or leaves. For instance, flowers or inflorescences may form on the surface of leaf lamina, such as in *Callopsis volkensii* (Araceae) (Dickinson, 1978), *Helwingia* (Cornaceae) (personal observations), and *Tilia* (Tiliaceae) (Dickinson, 1978), or in the sinus of leaf tips, such as in

Polycardia phyllanthoides (Celastraceae) (Dickinson, 1978; Perrier de la Bathie, 1946). In the genus *Begonia* (Begoniaceae), some species form inflorescences at the junction of petiole and leaf lamina (e.g., *B. paleacea* and *B. prolifera*), other species produce shoots/branches on the leaf lamina (e.g., *B. sinuata*), and still others may form leaflike structures on the leaves (e.g., *B. manicata* and *B. phyllomaniaca*) (Dickinson, 1978). In a well-known example of plant vegetative reproduction, the "maternity plant," *Kalanchoe daigremontaina* (Crassulaceae), produces many buds with roots ("plantlets") in the notches along its leaf margins.

Developmental studies of the epiphyllous inflorescences of *Phyllonoma integerrima* (Dulongiaceae) (Dickinson & Sattler, 1974) and "hooded" barley (Gupta & Stebbins, 1969) have indicated that the inflorescence primordia are initiated on the leaf and bract primordia, rather than from the shoot apex. Similarly, epiphyllous leaflike structures are initiated from leaf primordia or young leaves in *Begonia hispida* var. *cucullifera* (Lieu & Sattler, 1976; Maier & Sattler, 1977; Sattler & Maier, 1977), and epiphyllous branches/shoots are initiated from leaf primordia in *Chrysolidocarpus lutescens* (Fisher, 1973). The shifting of these developmental onset positions from their normal place on the stem constitutes heterotopy. The development of these epiphyllous structures may involve other developmental processes as well (for details, see Dickinson, 1978).

Heterotopy also occurs on a smaller scale in plant morphogenesis, as, for instance, in the shifting of the onset position of a floral organ's primordia during flower development. The position of petal primordium inception is usually on the floral apex, in most species. The primordium, however, can also be initiated on the stamen primordia (Duchartre, 1844; Sattler, 1962), on the calyx tube (Cheung & Sattler, 1967), or on the common petal-stamen primordia (Sundberg, 1982).

In a broad sense, heterotopy is the positional displacement or translocation of an organ or structure. Thus, the homeotic replacement or transformation of floral organs, such as from petal to sepal, stamen to petal, petal to stamen, sepal to carpel, or stamen to carpel, may also be described as a displacement or translocation of an organ's development; that is, as heterotopy. Homeosis and heterotopy are therefore overlapping concepts: complete homeosis is simply heterotopy. Heterotopy is probably often involved in homeosis by initial changes to the developmental patterns.

Heterochrony changes developmental timing and/or rate, thereby altering only the size and/or shape of an ancestral character. Heterotopy, in contrast, creates a character in a novel position by altering the ontogenetic trajectory. Therefore, the evolutionary effects of heterotopy are more profound than are those of heterochrony. Hall (1998: 388) stated that "heterochrony tinkers, but heterotopy creates." In actual morphological evolution, however, heterotopy may not be as common as heterochrony, because of the greater extent of developmental changes with heterotopy (Hall, 1998: 357). On the other hand, heterotopy is little studied, especially in plants. In fact, the term "heterotopy" is usually not found in books dealing with botany or plant science. There is no doubt that both heterochrony and heterotopy play important roles in evolution. As Zelditch and Fink (1996) recently emphasized, "most ontogenies evolve by changes of spatiotemporal pattern." Heterochrony and heterotopy are probably the two basic mechanisms underlying development and jointly responsible for evolution. It is time for developmental biologists to pay more attention to the role of heterotopy in evolution, and it is important to keep in mind that heterotopy has a distinct and complementary role to heterochrony in evolution. Heterochrony changes developmental timing and rate without changing the developmental trajectory; heterotopy changes the trajectory but not the timing or rate. The simple quantitative changes involved in heterochrony may be more readily available in evolution than the more qualitative changes involved in heterotopy.

XIV. Conclusions

Heterochrony leads to both interspecific and intraspecific morphological changes in plants. Both paedomorphosis and peramorphosis can be caused by either single or multiple developmental changes. In fact, it seems likely that most heterochronic change involves more than one of the six pure heterochronic processes defined by Alberch et al. (1979), so that an observed morphological change is often caused by the joint effect of several types of heterochronic processes representing paedomorphosis, peramorphosis, or both. Heterochrony occurs at various organization levels within an organism and varies among organs or characters. Just as different developmental changes can lead to divergent morphologies, identical or similar morphologies can arise from different developmental pathways. The phenotypic effect caused by changes in developmental timing may be exaggerated or suppressed by changes in developmental rate, and vice versa. This timing and rate interaction determines final phenotype. To date, most studies simply list one type of heterochrony, probably from the lack of information about the complete developmental trajectory rather than from the true lack of several types of heterochrony. Whether morphological evolution typically involves more than one of the six pure types will be resolved only with more time-based studies of complete developmental trajectories. This will often require measuring morphologies from the time of primordium initiation.

Heterochrony appears to be responsible for much morphological evolution, particularly in floral morphology. Heterochrony has clearly played an important role in the evolution of plant mating systems, where progenesis and neoteny are the major causes of the evolution of small selfing flowers from large outcrossing flowers. Heterochrony is also often responsible for changes of flowering time and for the extent of vegetative-reproductive developmental overlap.

Other development-related mechanisms, such as homeosis and heterotopy, are important causes of evolutionary morphological change. The importance of heterochrony relative to other processes, and the levels at which it most commonly acts, are unresolved. It will be preferable to study plant evolution from an approach that integrates the different developmental mechanisms at various organizational levels.

Heterochrony has been the subject much more of discussion than of actual quantification. The somewhat small number of studies we found in the literature (Appendix 1) is almost certainly due to a lack of good phylogenic information at the species level. Of the six pure classic heterochronic processes, we found neoteny (decreased developmental rate in descendant), progenesis (earlier offset), and acceleration (increased rate) to be more commonly reported than hypermorphosis (delayed offset) or predisplacement (earlier onset). Understanding the full importance of heterochrony to plant evolution requires additional studies employing sound phylogenies and time-based developmental trajectories. Only then will the true relative frequency of each process be known.

XV. Acknowledgments

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XVI. Literature Cited

Alberch, P. & M. J. Blanco. 1996. Evolutionary patterns in ontogenetic transformation: From laws to regularities. Int. J. Developm. Biol. 40: 845–858.

———, **S. J. Gould, G. F. Oster & D. B. Wake.** 1979. Size and shape in ontogeny and phylogeny. Paleobiology 5: 296–317.

Ambros, V. 1997. Heterochronic genes. Pp. 501–518 *in* D. L. Riddle, T. Blumenthal, B. J. Meyer & J. R. Priess (eds.), *C. elegans* II. Cold Spring Harbor Laboratory Press, New York.

An, G. 1994. Regulatory genes controlling flowering time or floral organ development. Pl. Molec. Biol. 25: 335–337.

Anderson, E. & D. DeWinton. 1985. The genetics of *Primula sinensis*. IV. Indications as to the ontogenetic relationship of leaf and inflorescence. Ann. Bot. 49: 671–687.

Asama, K. 1960. Evolution of the leaf forms through the ages explained by the successive retardation and neoteny. Sci. Rep. Tôhoku Imp. Univ., ser. 2, Special vol. 4: 252–280.

Atchley, W. R. 1987. Developmental quantitative genetics and the evolution of ontogenies. Evolution 41: 316–330.

———. 1990. Heterochrony and morphological change: A quantitative genetic perspective. Semin. Developm. Biol. 1: 289–297.

Axelrod, D. I. 1960. The evolution of flowering plants. Pp. 227–305 *in* S. Tax (ed.), Evolution after Darwin, vol. 1. University of Chicago Press, Chicago.

Bateman, R. M. 1994. Evolutionary-developmental change in the growth architecture of fossil rhizomorphic lycopsids: Scenarios constructed on cladistic foundations. Biol. Rev. 69: 527–597.

——— **& W. A. DiMichele.** 1991. *Hizemodendron,* gen. nov., a pseudoherbaceous segregate of *Lepidodendron* (Pennsylvanian): Phylogenetic context for evolutionary changes in lycopsid growth architecture. Syst. Bot. 16: 195–205.

Bertrand-Garcia, R. & M. Freeling. 1991. Hairy-sheath-frayed1–O: a systemic, heterochronic mutant of maize that specifies slow developmental stage transitions. Amer. J. Bot. 78: 747–765.

Blackstone, N. W. 1987a. Allometry and relative growth: Pattern and process in evolutionary studies. Syst. Zool. 36: 76–78.

———. 1987b. Size and time. Syst. Zool. 36: 211–215.

Bolker, J. A. & R. A. Raff. 1996. Developmental genetics and traditional homology. BioEssays 18: 489–494.

Bookstein, F. L., B. C. Chernoff, R. L. Elder, J. M. Humphries, G. R. Smith & R. E. Strauss. 1985. Morphometrics in evolutionary biology. Academy of Natural Sciences of Philadelphia, Philadelphia, PA.

Bowman, J. L., D. R. Smyth & E. M. Meyerowitz. 1989. Genes directing flower development in *Arabidopsis*. Pl. Cell 1: 37–52.

———, **H. Sakai, T. Jack, D. Weigel, U. Mayer & E. M. Meyerowitz.** 1992. *SUPERMAN,* a regulator of floral homeotic genes in *Arabidopsis*. Development 114: 599–615.

———, **J. Alvarez, D. Weigel, E. M. Meyerowitz & D. R. Smyth.** 1993. Control of flower development in *Arabidopsis thaliana* by *APETALA1* and interacting genes. Development 119: 721– 743.

Carlquist, S. 1969. Toward acceptable evolutionary interpretations of floral anatomy. Phytomorphology: 332–362.

Carlson, S. J. 1991. Development as an evolutionary force. Evolution 45: 1534–1535.

Cheung, M. & R. Sattler. 1967. Early floral development of *Lythrum salicaria*. Canad. J. Bot. 45: 1609–1618.

Clearwater, M. J. & K. S. Gould. 1993. Comparative leaf development of juvenile and adult *Pseudopanax crassifolius*. Canad. J. Bot. 72: 658–670.

Coen, E. S. 1991. The role of homeotic genes in flower development and evolution. Ann. Rev. Pl. Physiol. & Pl. Molec. Biol. 42: 241–279.

——— **& J. M. Nugent.** 1994. Evolution of flowers and inflorescences. Development Supplement: 107–116.

———, **J. M. Romero, S. Doyle, R. Elliott, G. Murphy & R. Carpenter.** 1990. *Floricaula*: A homeotic gene required for flower development in *Antirrhinum majus*. Cell 63: 1311–1322.

Colasanti, J. & V. Sundaresan. 1996. Control of the transition to flowering. Current Opin. Biotechnol. 7: 145–149.

Conway, L. J. & R. S. Poethig. 1993. Heterochrony in plant development. Semin. Developm. Biol. 4: 65–72.

Coupland, G. 1995. Regulation of flowering time: *Arabidopsis* as a model system to study genes that promote or delay flowering. Philos. Trans. 350: 27–34.

———, **S. Dash, J. Goodrich, K. Lee, D. Long, M. Martin, P. Puangsomlee, J. Putterill, F. Robson, E. Sundberg & K. Wilson.** 1993. Molecular and genetic analysis of the control of flowering time in response to day length in *Arabidopsis thaliana.* Flowering Newsletter 16: 27–32.

Crone, W. & E. M. Lord. 1994. Floral organ initiation and development in wild-type *Arabidopsis thaliana* (Brassicaceae) and in the organ identity mutants *apetala2–1* and *agamous–1.* Canad. J. Bot. 72: 384–401.

Cronquist, A. 1988. The evolution and classification of flowering plants. Ed. 2. The New York Botanical Garden, New York.

Demason, D. A. & P. J. Villani. 1998. Roles of the *Af* and *Tl* genes in pea leaf development: Homeosis or heterochrony? Amer. J. Bot. Supplement: 3.

Dengler, N. G. 1984. Comparison of leaf development in normal (+/+), entire (e/e), and lanceolate (La/+) plants of tomato, *Lycopersicon esculentum* 'Ailsa Craig.' Bot. Gaz. 145: 66–77.

———. 1992. Patterns of leaf development in anisophyllous shoots. Canad. J. Bot. 70: 676–691.

Dickinson, T. A. 1978. Epiphylly in angiosperms. Bot. Rev. (Lancaster) 44: 181–232.

——— **& R. Sattler.** 1974. Development of the epiphyllous inflorescence of *Phyllonoma integerrima* (Turcz.) Loes.: Implications for comparative morphology. J. Linn. Soc., Bot. 69: 1–13.

Diggle, P. K. 1992. Development and the evolution of plant reproductive characters. Pp. 326–355 *in* R. Wyatt (ed.), Ecology and evolution of plant reproduction: New approaches. Chapman & Hall, New York.

Donoghue, M. J. & M. J. Sanderson. 1994. Complexity and homology in plants. Pp. 393–421 *in* B. K. Hall (ed.), Homology: The hierarchical basis of comparative biology. Academic Press, San Diego, CA.

Douglas, A. W. & S. C. Tucker. 1996. Comparative floral ontogenies among Persoonioideae including *Bellendena* (Proteaceae). Amer. J. Bot. 83: 1528–1555.

Drews, G. N., D. Weigel & E. M. Meyerowitz. 1991. Floral patterning. Current Opin. Gen. Developm. 1: 174–178.

Duchartre, P. 1844. Observations sur l'organogénie de la fleur et en particulier de l'ovaire chez les plantes à placenta central libre. Ann. Sci. Nat. Paris III 2: 279–297.

Esau, K. 1977. Anatomy of seed plants. John Wiley, New York.

Fink, W. L. 1982. The conceptual relationship between ontogeny and phylogeny. Paleobiology 8: 254–264.

———. 1988. Phylogenetic analysis and the detection of ontogenetic patterns. Pp. 71–91 *in* M. L. McKinney (ed.), Heterochrony in evolution: A multidisciplinary approach. Plenum Press, New York.

Fiorello, C. V. & R. Z. German. 1997. Heterochrony within species: Craniofacial growth in giant, standard, and dwarf rabbits. Evolution 51: 250–261.

Fisher, J. B. 1973. Unusual branch development in the palm *Chrysalidocarpus.* J. Linn. Soc., Bot. 66: 83–95.

Flanagan, C. A. & H. Ma. 1994. Spatially and temporally regulated expression of the MADS-box gene *AGL2* in wild-type and mutant *Arabidopsis* flowers. Pl. Molec. Biol. 26: 581–595.

Freeling, M., R. Bertrand-Garcia & N. Sinha. 1992. Maize mutants and variants altering developmental time and their heterochronic interactions. BioEssays 14: 227–236.

Friedman, W. E. & J. S. Carmichael. 1998. Heterochrony and developmental innovation of female gametophyte ontogeny in *Gnetum,* a highly apomorphic seed plant. Evolution 52: 1016–1030.

Gallardo, R., E. Dominguez & J. M. Muñoz. 1993. The heterochronic origin of the cleistogamous flower in *Astragalus cymbicarpos* (Fabaceae). Amer. J. Bot. 80: 814–823.

Ganders, F. R. 1975. Mating patterns in self-compatible distylous populations of *Amsinckia* (Boraginaceae). Canad. J. Bot. 53: 773–779.

———. 1976. Pollen flow in distylous populations of *Amsinckia* (Boraginaceae). Canad. J. Bot. 54: 2530–2535.

———. 1979. The biology of heterostyly. New Zealand J. Bot. 17: 607–635.

Gifford, E. M. & A. S. Foster. 1989. Morphology and evolution of vascular plants. Ed. 3. W. H. Freeman, New York.

Gilbert, S. F., J. M. Opitz & R. A. Raff. 1996. Resynthesizing evolutionary and developmental biology. Developm. Biol. 173: 357–372.

Gleissberg, S. & J. W. Kadereit. 1999. Evolution of leaf morphogenesis: Evidence from developmental and phylogenetic data in Papaveraceae. Int. J. Pl. Sci. 160: 787–794.

Goodwin, B. 1989. Morphogenesis, evolution and organic stability. Pp. 187–192 *in* B. David, J. L. Dommergues, J. Chaline & B. Laurin (eds.), Ontogenèse et évolution, Vol. Geobios, mémoire spécial no. 12. Édition de L'Université Claude-Bernard, Lyon.

Gould, S. J. 1966. Allometry and size in ontogeny and phylogeny. Biol. Rev. 41: 587–640.

———. 1977. Ontogeny and phylogeny. Harvard University Press, Cambridge, MA.

———. 1988. The uses of heterochrony. Pp. 1–13 *in* M. L. McKinney (ed.), Heterochrony in evolution: A multidisciplinary approach. Plenum Press, New York.

———. 1992. Ontogeny and phylogeny: Revisited and reunited. BioEssays 14: 275–279.

Greyson, R. I. 1972. Initiation and early growth of flower organs of *Nigella* and *Lycopersicon*: Insights from allometry. Bot. Gaz. 133: 184–190.

Guerrant, E. O. 1982. Neotenic evolution of *Delphinium nudicaule* (Ranunculaceae): A hummingbird-pollinated larkspur. Evolution 36: 699–712.

———. 1984. The role of ontogeny in the evolution and ecology of selected species of *Delphinium* and *Limnanthes*. Ph.D. diss., University of California.

———. 1988. Heterochrony in plants: The intersection of evolution, ecology, and ontogeny. Pp. 111–133 *in* M. L. McKinney (ed.), Heterochrony in evolution: A multidisciplinary approch. Plenum Press, New York.

———. 1989. Early maturity, small flowers and autogamy: A developmental connection? Pp. 61–84 *in* J. H. Bock & Y. B. Linhart (eds.), The evolutionary ecology of plants. Westview Press, Boulder, CO.

Gupta, V. K. & G. L. Stebbins. 1969. Peroxidase activity in hooded and awned barley at successive stages of development. Biochem. Gen. 3: 15–24.

Haeckel, E. 1875. Die Gastrula and die Eifurchung der Thiere. Jena Z. Naturwiss 9: 402–508.

———. 1905. The evolution of man. Watts, London.

Hall, B. K. 1990. Heterochrony in vertebrate development. Developm. Biol. 1: 237–243.

———. 1992. Evolutionary developmental biology. Chapman & Hall, New York.

———. 1998. Evolutionary developmental biology. Ed. 2. Chapman & Hall, New York.

———, **ed.** 1994. Homology: The hierarchical basis of comparative biology. Academic Press, San Diego, CA.

——— **& T. Miyake.** 1995. How do embryos measure time? Pp. 3–19 *in* K. J. McNamara (ed.), Evolutionary change and heterochrony. John Wiley, New York.

Harlan, J. R. 1945. Cleistogamy and chasmogamy in *Bromus carinatus* Hook. & Arn. Amer. J. Bot. 32: 66–72.

Haugh, G. W., E. A. Schultz & J. M. Martinez-Zapater. 1995. The regulation of flowering in *Arabidopsis thaliana*: Meristems, morphogenesis, and mutants. Canad. J. Bot. 73: 959–981.

Hill, J. P. 1996. Heterochrony in the anther. Pp. 118–135 *in* W. G. D'Arcy & R. C. Keating (eds.), The anther: Form, function and phylogeny. Cambridge University Press. Cambridge, England.

——— **& E. M. Lord.** 1989. Floral development in *Arabidopsis thaliana*: A comparison of the wild type and the homeotic pistillata mutant. Canad. J. Bot. 67: 2922–2936.

——— & ———. 1990. The role of developmental timing in the evolution of floral form. Semin. Developm. Biol. 1: 281–287.

———, ——— **& R. G. Shaw.** 1992. Morphological and growth rate differences among outcrossing and self-pollinating races of *Arenaria uniflora* (Caryophyllaceae). J. Evol. Biol. 5: 559–573.

Jack, T., L. L. Brockman & E. M. Meyerowitz. 1992. The homeotic gene *APETALA3* of *Arabidopsis thaliana* encodes a MADS box and is expressed in petals and stamens. Cell 68: 683–697.

———, **L. E. Sieburth & E. M. Meyerowitz.** 1993. Genes that control flower development in *Arabidopsis*. Semin. Developm. Biol. 4: 51–63.

———, **G. L. Fox & E. M. Meyerowitz.** 1994. *Arabidopsis* homeotic gene *APETALA3* ectopic expression: Transcriptional and posttranscriptional regulation determine floral organ identity. Cell 76: 703–716.

Johnston, M. O. & D. J. Schoen. 1996. Correlated evolution of self-fertilization and inbreeding depression: An experimental study of nine populations of *Amsinckia* (Boraginaceae). Evolution 50: 1478–1491.

Jones, C. S. 1988. Positional influences on leaf development in a wild and cultivated *Cucurbita* species. Amer. J. Bot. 75: 33.

———. 1992. Comparative ontogeny of a wild cucurbit and its derived cultivar. Evolution 46: 1827–1847.

———. 1993. Heterochrony and heteroblastic leaf development in two subspecies of *Cucurbita argyrosperma* (Cucurbitaceae). Amer. J. Bot. 80: 778–795.

Jordan, B. R. & R. G. Anthony. 1993. Floral homeotic genes: Isolation, characterization and expression during floral development. Pp. 93–116 *in* B. R. Jordan (ed.), The molecular biology of flowering. CAB International, Wallingford, England.

Kampny, C. M. & E. M. Harris. 1998. Heterochrony: The basis of floral shape evolution. Amer. J. Bot. Supplement: 4.

———, **T. A. Dickinson & N. G. Dengler.** 1993. Quantitative comparison of floral development in *Veronica chamaedrys* and *Veronicastrum virginicum* (Scrophulariaceae). Amer. J. Bot. 80: 449–460.

———, ——— & ———. 1994. Quantitative floral development in *Pseudolysimachion* (Scrophulariaceae): Intraspecific variation and comparison with *Veronica* and *Veronicastrum*. Amer. J. Bot. 81: 1343–1353.

Kaplan, D. R. 1970. Comparative foliar histogenesis in *Acorus calamus* and its bearing on the phyllode theory of monocotyledonous leaves. Amer. J. Bot. 57: 331–361.

———. 1973a. Comparative developmental analysis of the heteroblastic leaf series of axillary shoots of *Acorus calamus* L. (Araceae). Cellule 69: 253–290.

———. 1973b. The monocotyledons: Their evolution and comparative biology. VII. The problem of leaf morphology and evolution in the monocotyledons. Quart. Rev. Biol. 48: 437–457.

———. 1980. Heteroblastic leaf development in *Acacia*: Morphological and morphogenetic implications. Cellule 73: 135–203.

———. 1984. The concept of homology and its central role in the elucidation of plant systematic relation. Pp. 51–70 *in* T. Duncan & T. F. Stuessy (eds.), Cladistics: Perspectives on the reconstruction of evolutionary history. Columbia University Press, New York.

Kellogg, E. A. 1990. Ontogenetic studies of florets in *Poa* (Gramineae): Allometry and heterochrony. Evolution 44: 1978–1989.

Kirchoff, B. K. 1983. Allometric growth of the flowers in five genera of the Marantaceae and in *Canna* (Cannaceae). Bot. Gaz. 144: 110–118.

———. 1988. Floral ontogeny and evolution in the ginger group of the Zingiberales. Pp. 45–56 *in* P. Leins, S. C. Tucker & P. K. Endress (eds.), Aspects of floral development. J. Cramer, Berlin.

———. 1991. Homeosis in the flowers of the Zingiberales. Amer. J. Bot. 78: 833–837.

Klingenberg, C. P. 1996. Individual variation of ontogenies: A longitudinal study of growth and timing. Evolution 50: 2412–2428.

———. 1998. Heterochrony and allometry: The analysis of evolutionary change in ontogeny. Biol. Rev. 73: 79–123.

——— **& J. R. Spence.** 1994. Heterochrony and allometry: Lessons from the water strider genus *Limnoporus*. Evolution 47: 1834–1853.

Kluge, A. G. 1985. Ontogeny and phylogenetic systematics. Cladistics 1: 13–27.

———. 1988. The characterization of ontogeny. Pp. 57–81 *in* C. J. Humphries (ed.), Ontogeny and systematics. Columbia University Press, New York.

Koornneef, M., C. J. Hanhart & J. H. Van der Veen. 1991. A genetic and physiological analysis of late flowering mutants in *Arabidopsis thaliana*. Molec. Gen. Genet. 229: 57–66.

Krol, A. R. v. d. & N.-H. Chua. 1993. Flower development in *Petunia*. Pl. Cell 5: 1195–1203.

Lammers, T. G. 1990. Sequential paedomorphosis among the endemic Hawaiian Lobelioideae (Campanulaceae). Taxon 39: 206–211.

Langer, R. H. M. & D. Wilson. 1965. Environmental control of cleistogamy in prairie grass (*Bromus unioloides* HBK). New Phytol. 65: 80–85.

Lee, C. W., H. T. Erickson & J. Janick. 1979. Cleistogamy in *Salpiglossis sinuata*. Amer. J. Bot. 66: 626–632.

Lee, I., M. J. Aukerman, S. L. Gore, K. N. Lohman, S. D. Michaels, L. M. Weaver, M. C. John, K. A. Feldmann & R. M. Amasino. 1994. Isolation of *LUMINIDEPENDENS*: A gene involved in the control of flowering time in *Arabidopsis*. Pl. Cell 6: 75–83.

Lee, M. P. N. 1988. Cell cycle control genes in fission yeast and mammalian cells. Trends Genet. 4: 287–290.

Lehmann, N. L. & R. Sattler. 1996. Staminate floral development in *Begonia cucullata* var. *hookeri* and three double-flowering begonia cultivars, examples of homeosis. Canad. J. Bot. 74: 1729–1741.

Li, P. & M. O. Johnston. 1999. Evolution of meiosis timing during floral development. Proc. Roy. Soc. Lond. B 266: 185–190.

Lieu, S. M. & R. Sattler. 1976. Leaf development in *Begonia hispida* Schott var. *cucullifera* Irmsch. with special reference to vascular organization. Canad. J. Bot. 54: 2108–2121.

Lord, E. M. 1979. The development of cleistogamous and chasmogamous flowers in *Lamium amplexicaule* (Labiatae): An example of heteroblastic inflorescence development. Bot. Gaz. 140: 39–50.

———. 1982. Floral morphogenesis in *Lamium amplexicaule* L. (Labiatae) with a model for the evolution of the cleistogamous flower. Bot. Gaz. 143: 63–72.

——— **& J. P. Hill.** 1987. Evidence for heterochrony in the evolution of plant form. Pp. 47–70 *in* R. A. Raff & E. C. Raff (eds.), Development as an evolutionary process. Alan R. Liss, New York.

———, **K. J. Eckard & W. Crone.** 1989. Development of the dimorphic anthers in *Collomia grandiflora:* Evidence for heterochrony in the evolution of the cleistogamous anther. J. Evol. Biol. 2: 81–93.

———, **W. Crone & J. P. Hill.** 1994. Timing of events during flower organogenesis: *Arabidopsis* as a model system. Curr. Topics Developm. Biol. 29: 325–356.

MacIntyre, J. P. & C. R. Lacroix. 1996. Comparative development of perianth and androecial primordia of the single flower and the homeotic double-flowered mutant in *Hibiscus rosa-sinensis* (Makvaceae). Canad. J. Bot. 74: 1871–1882.

Maier, U. & R. Sattler. 1977. The structure of the epiphyllous appendages of *Begonia hispida* Schott var. *cucullifera* Irmsch. Canad. J. Bot. 55: 264–280.

Mandel, M. A. & M. F. Yanofsky. 1995. A gene triggering flower formation in *Arabidopsis*. Nature 377: 522–524.

———, **J. L. Bowman, S. A. Kempin, H. Ma, E. M. Meyerowitz & M. F. Yanofsky.** 1992. Manipulation of flower structure in transgenic tobacco. Cell 71: 133–143.

Martin, C. 1996. Transcription factors and the manipulation of plant traits. Curr. Opin. Biotechnol. 7: 130–138.

Marx, G. A. 1987. A suit of mutants that modify pattern formation in pea leaves. Pl. Mol. Biol. Rep. 5: 311–335.

Mayers, A. M. & E. M. Lord. 1983a. Comparative flower development in the cleistogamous species *Viola odorata*. I. A growth rate study. Amer. J. Bot. 70: 1548–1555.

——— **&** ———. 1983b. Comparative flower development in the cleistogamous species *Viola odorata*. II. An organographic study. Amer. J. Bot. 70: 1556–1563.

McKinney, M. L. 1988a. Classifying heterochrony: Allometry, size, and time. Pp. 17–34 *in* M. L. McKinney (ed.), Heterochrony in evolution: A multidisciplinary approach. Plenum Press, New York.

———. 1988b. Heterochrony in evolution: An overview. Pp. 327–340 *in* M. L. McKinney (ed.), Heterochrony in evolution: A multidisciplinary approach. Plenum Press, New York.

———. 1999. Heterochrony: Beyond words. Paleobiology 25: 149–153.

———, **ed.** 1988. Heterochrony in evolution: A multidisciplinary approach. Plenum Press, New York.

———. **& K. J. McNamara.** 1991. Heterochrony: The evolution of ontogeny. Plenum Press, New York.

McLellan, T. 1990. Development of differences in leaf shape in *Begonia dregei* (Begoniaceae). Amer. J. Bot. 77: 323–337.

———. 1993. The roles of heterochrony and heteroblasty in the diversification of leaf shapes in *Begonia dregei* (Begoniaceae). Amer. J. Bot. 80: 796–804.

——— **& N. G. Dengler.** 1995. Pattern and form in repeated elements in the development of simple leaves of *Begonia dregei*. Int. J. Pl. Sci. 156: 581–589.

McNamara, K. J. 1993. Inside evolution: 1992 presidential address. J. Roy. Soc. W. Australia. 76: 3–12.

———, **ed.** 1995. Evolutionary change and heterochrony. John Wiley, New York.

Merrill, E. K. 1979. Comparison of ontogeny of three types of leaf architecture in *Sorbus* L. (Rosaceae). Bot. Gaz. 140: 328–337.

Minter, T. C. & E. M. Lord. 1983. A comparison of cleistogamous and chasmogamous floral development in *Collomia grandiflora* Dougl. ex Lindl. (Polemoniaceae). Amer. J. Bot. 70: 1499–1508.

Mosbrugger, V. 1995. Heterochrony and the evolution of land plants. Pp. 93–105 *in* K. J. McNamara (ed.), Evolutionary change and heterochrony. John Wiley, New York.

Murfet, I. C. & J. B. Reid. 1993. Developmental mutants. Pp. 165–216 *in* R. Casey & D. R. Davies (eds.), Peas: Genetics, molecular biology, and biotechnology. CAB International, Wallingford, England.

Niklas, K. J. 1994. Plant allometry: The scaling of form and process. University of Chicago Press, Chicago.

———. 1997. The evolutionary biology of plants. University of Chicago Press, Chicago.

O'Grady, R. T. 1985. Ontogenetic sequences and the phylogenetics of flatworms. Cladistics 1: 159–170.

Parichy, D. M., H. B. Shaffer & M. Mangel. 1992. Heterochrony as a unifying theme in evolution and development. Evolution 46: 1252–1254.

Perrier de la Bathie, H. 1946. Celastracées. *In* H. Humbert (ed.), Flore de Madagascar et des Comores. Impr. Officielle, Tananarive, Madagascar.

Philipson, W. R. 1971. Shoot differentiation in the Araliaceae of New Zealand. J. Indian Bot. Soc. 50A: 188–195.

Poethig, R. S. 1988. Heterochronic mutations affecting shoot development in maize. Genetics 119: 959–973.

Posluszny, U., R. Sattler, J. P. Hill, M. K. Komaki, J. M. Gerrath, N. Lehmann & B. K. Kirchoff. 1990. Homeosis and the evolution of plants. Pp. 447–454 *in* E. C. Dudley (ed.), Proceedings of the Fourth International Congress of Systematic and Evolutionary Biology, vol. 1. Dioscorides Press, University of Maryland, College Park.

Purugganan, M. D. 1996. Evolution of development: Molecules, mechanisms and phylogenetics. TREE 11: 5–7.

———, **S. D. Rounsley, R. J. Schmidt & M. F. Yanofsky.** 1995. Molecular evolution of flower development: Diversification of the plant MADS-box regulatory gene family. Genetics 140: 345–356.

Raff, R. A. 1996. The shape of life: Genes, development, and the evolution of animal form. University of Chicago Press, Chicago.

——— **& T. C. Kaufman.** 1983. Embryos, genes, and evolution. Macmillan, New York.

——— **& G. A. Wray.** 1989. Heterochrony: Developmental mechanisms and evolutionary results. J. Evol. Biol. 2: 409–434.

——— **& E. C. Raff, eds.** 1987. Development as an evolutionary process. Alan R. Liss, New York.

Ray, P. M. & H. F. Chisaki. 1957a. Studies on *Amsinckia*. II. Relationships among the primitive species. Amer. J. Bot. 44: 537–544.

——— **&** ———. 1957b. Studies on *Amsinckia*. I. A synopsis of the genus, with a study of heterostyly in it. Amer. J. Bot. 44: 529–536.

Reilly, S. M. 1997. An integrative approach to heterochrony: The distinction between interspecific and intraspecific phenomena. Biol. J. Linn. Soc. 60: 119–143.

Rice, S. H. 1997. The analysis of ontogenetic trajectories: When a change in size or shape is not heterochrony. Proc. Natl. Acad. Sci. USA 94: 907–912.

Richards, J. H. 1983. Heteroblastic development in the water hyacinth *Eichhornia crassipes* Solms. Bot. Gaz. 144: 247–259.

Richardson, M. K. 1995. Heterochrony and the phylotypic period. Developm. Biol. 172: 412–421.

Runions, C. J. & M. A. Geber. 1998. A heterochronic shift leading to self-pollination in *Clarkia xantiana ssp. parviflora* (Onagraceae). Amer. J. Bot. Supplement: 18.

Saedler, H. & P. Huijser. 1993. Molecular biology of flower development in *Antirrhinum majus* (snapdragon). Gene 135: 239–243.

Sattler, R. 1962. Zur frühen Infloreszenz-und Blütenentwicklung der Primulales sensu lato mit besonderer Berücksichtigung der Stamen-Petalum Entwicklung. Botan. Jahrb. 81: 358–396.

———. 1988. Homeosis in plants. Amer. J. Bot. 75: 1606–1617.

———. 1992. Process morphology: Structural dynamics in development and evolution. Canad. J. Bot. 70: 708–714.

———. 1994. Homology, homeosis, and process morphology in plants. Pp. 423–475 *in* B. K. Hall (ed.), Homology: The hierarchical basis of comparative biology. Academic Press, San Diego, CA.

——— **& U. Maier.** 1977. Development of the epiphyllous appendages of *Begonia hispida* Schott var. *cucullifera* Irmsch.: Implications for comparative morphology. Canad. J. Bot. 55: 411–425.

Schneeberger, R. G., P. W. Becraft, S. Hake & M. Freeling. 1995. Ectopic expression of the knox homeo box gene rough sheath1 alters cell fate in the maize leaf. Genes Developm. 9: 2292–2304.

Schoen, D. J., M. O. Johnston, A. M. L'Heureux & J. V. Marsolais. 1997. Evolutionary history of the mating system in *Amsinckia* (Boraginaceae). Evolution 51: 1090–1099.

Schultz, E. A. & G. W. Haughn. 1991. *LEAFY,* a homeotic gene that regulates inflorescence development in *Arabidopsis*. Pl. Cell 3: 771–781.

——— & ———. 1993. Genetic analysis of the floral initiation process (FLIP) in *Arabidopsis*. Development 119: 745–765.

Schwarz-Sommer, Z., P. Huijser, W. Nacken, H. Saedler & H. Sommer. 1990. Genetic control of flower development by homeotic genes in *Antirrhinum majus*. Science 250: 931–936.

Sinha, N., S. Hake & M. Freeling. 1993. Genetic and molecular analysis of leaf development. Curr. Topics Developm. Biol. 28: 47–80.

Slatkin, M. 1987. Quantitative genetics of heterochrony. Evolution 41: 799–811.

Smith-Huerta, N. L. 1984. Development of flower form in an allotetraploid *Clarkia* and its parental diploid species. Amer. J. Bot. 71: 720–726.

Solbrig, O. T. & R. C. Rollons. 1977. The evolution of autogamy in species of the mustard genus *Leavenworthia*. Evolution 31: 265–281.

Stebbins, G. L. 1992. Comparative aspects of plant morphogenesis: A cellular, molecular, and evolutionary approach. Amer. J. Bot. 79: 589–598.

Sundberg, M. D. 1982. Petal-stamen initiation in the genus *Cyclamen* (Primulaceae). Amer. J. Bot. 69: 1707–1709.

Sung, Z. R., A. Belachew, S. Bai & R. Bertrand-Garcia. 1992. *EMF,* an *Arabidopsis* gene required for vegetative shoot development. Science 258: 1645–1647.

Takahashi, H. 1994. A comparative study of floral development in *Trillium apetalon* and *T. kamtschaticum* (Liliaceae). J. Pl. Res. 107: 237–243.

Takhtajan, A. 1954. Voprosy Evolyutsionnoy Morfologii Rasteniy. Leningrad University, Leningrad.

———. 1976. Neoteny and the origin of flowering plants. Pp. 207–219 *in* C. B. Beck (ed.), Origin and early evolution of angiosperms. Columbia University Press, New York.

———. 1991. Evolutionary trends in flowering plants. Columbia University, New York.

Tucker, S. C. 1984. Origin of symmetry in flowers. Pp. 351–394 *in* R. A. White & W. C. Dickison (eds.), Contemporary problems in plant anatomy. Academic Press, London.

———. 1987. Floral initiation and development in legumes. Pp. 183–239 *in* C. H. Stirtion (ed.), Advances in legume systematics, part 3. Royal Botanic Gardens, Kew.

———. 1988. Heteromorphic flower development in *Neptunia pubescens,* a mimosoid legume. Amer. J. Bot. 75: 205–224.

Veit, B., R. J. Schmidt, S. Hake & M. F. Yanofsky. 1993. Maize floral development: New genes and old mutants. Pl. Cell 5: 1205–1215.

Weigel, D. 1995. The genetics of flower development: From floral induction to ovule morphogenesis. Annual Rev. Genet. 29: 19–39.

——— **& E. M. Meyerowitz.** 1993. Genetic hierarchy controlling flower development. Pp. 93–107 *in* M. Bernfeld (ed.), Molecular basis of morphogenesis. Wiley-Liss, New York.

——— & ———. 1994. The ABCs of floral homeotic genes. Cell 78: 203–209.

——— **& O. Nilsson.** 1995. A developmental switch sufficient for flower initiation in diverse plants. Nature 377: 495–500.

———, **J. Alvarez, D. R. Smyth, M. F. Yanofsky & E. M. Meyerowitz.** 1992. *LEAFY* controls floral meristem identity in *Arabidopsis*. Cell 69: 843–859.

Whaley, W. G. & C. Y. Whaley. 1942. A developmental analysis of inherited leaf patterns in *Tropaeolum*. Amer. J. Bot. 29: 195–200.

Wiltshire, R. J. E., I. C. Murfet & J. B. Reid. 1994. The genetic control of heterochrony: Evidence from developmental mutants of *Pisum sativum* L. J. Evol. Biol. 7: 447–465.

Wyatt, R. 1983. Pollinator-plant interactions and the evolution of breeding systems. Pp. 51–95 *in* L. Real (ed.), Pollination biology. Academic Press, New York.

Yang, C.-H., L.-J. Chen & Z. R. Sung. 1995. Genetic regulation of shoot development in *Arabidopsis*L role of the EMF genes. Dev. Biol. 169: 421–435.

Young, J. P., T. A. Dickinson & N. G. Dengler. 1995. A morphometric analysis of heterophyllous leaf development in *Ranunculus flabellaris*. Int. J. Pl. Sci. 156: 590–602.

Zagotta, M. T., S. Shannon & C. Jacobs. 1992. Early-flowering mutants of *Arabidopsis thaliana*. Aust. J. Pl. Physiol. 19: 411–418.

Zelditch, M. L. & W. L. Fink. 1996. Heterochrony and heterotopy: stability and innovation in the evolution of form. Paleobiology 22: 241–254.

Zimmermann, W. 1959. Die Phylogenie der Pflanzen. Ed. 2. G. Fischer, Stuttgart.

Zopfi, H.-J. 1995. Life history variation and infraspecific heterochrony in *Rhinanthus glacialis* (Scrophulariaceae). Pl. Syst. Evol. 198: 209–233.

XVII. Appendix 1: Heterochrony in plants.
Entries are restricted to cases of reasonably certain phylogeny, plus some fossils. See text for further explanation.

Ancestor, descendant	Structure or event	Derived morphology	Paedomorphosis[a]			Peramorphosis[b]			References; notes
			Neot.	Progen.	Postdisp.	Accel.	Hypermor.	Predisp.	
			Reproductive traits						
Gymnosperms, Angiosperms	Flower generally	Flower (from ancestral reproductive shoot)		×					Takhtajan, 1976, 1991
Gymnosperms, Angiosperms	Gametophyte	Reduced size, reduced complexity, loss of gametangia		×		×			Takhtajan, 1976, 1991; Friedman & Carmichael, 1998
Angiosperms generally	Whole flower	Zygomorphic (from actinomorphic)						×	Tucker, 1987; Stebbins, 1992
Amsinckia douglasiana (distylous), *A. gloriosa* (homostylous)	Whole flower	Reduced size	×						Li & Johnston, unpubl.
Amsinckia furcata (distylous), *A. vernicosa* (homostylous)	Whole flower	Reduced size	×						Li & Johnston, unpubl.
Amsinckia spectabilis (distylous), *A. s.* (homostylous)	Whole flower	Reduced size	×		×		×		Li & Johnston, unpubl.
Arenaria uniflora outcrossing flower, Selfing flower	Whole flower	Reduced size	×				×		Hill et al., 1992
Astragalus cymbicarpos CH flowers, CL flowers	Whole flower	Reduced size		×		×			Lord, 1979, 1982 Acceleration occurred after PMC meiosis
Bromus carinatus CH flowers, CL flowers	Anther and flower maturation	Earlier		×					Harlan, 1945

Ancestor, descendant	Structure or event	Derived morphology	Paedomorphosis[a]			Peramorphosis[b]			References; notes
			Neot.	Progen.	Postdisp.	Accel.	Hypermor.	Predisp.	
Reproductive traits									
Bromus unioloides CH flowers, CL flowers	Anther	Reduced size	×	×					Langer & Wilson, 1965
Clarkia xantiana ssp. Xantiana, *C. x. ssp. parviflora*	Plant/flowering time/pollination type	Smaller/earlier/selfing		×		×			Runions & Geber, 1998
Collomia grandiflora CH flowers, CL flowers	Anther	Reduced size						×	Lord et al., 1989; Hill & Lord, 1990; Minter & Lord, 1983
Collomia grandiflora CH flowers, CL flowers	Pollen	Reduced number						×	Lord et al., 1989; Hill & Lord, 1990; Minter & Lord, 1983
Collomia grandiflora CH flowers, CL flowers	Whole flower	Reduced size				×			Minter & Lord, 1983 Acceleration occurred before PMC meiosis PMC meiosis earlier onset
Cucurbita argyrosperma sororia, *C. a. argyrosperma*	Timing (nodal position) of first flower	Earlier (lower nodal position)		×					Jones, 1992, 1993
Delphinium decorum, *D. nudicaule*	Sepals and nonnectariferous petals	Resemble buds of ancestral form	×						Guerrant, 1982 Applies to whole flower externally viewed
Delphinium decorum, *D. nudicaule*	Nectariferous petal	Increased size				×	×		Guerrant, 1982
Ephedra, *Gentum gnemon*	Female gametophyte matures sexually (fertilized)	Earlier		×		×			Friedman & Carmichael, 1998

Lamium amplexicaule CH flowers, CL flowers	Whole flower	Reduced size		×		×		Gallardo et al., 1993 Acceleration occurred after PMC meiosis
Limnanthes alba, *L. floccosa*	Whole flower	Reduced size		×				Guerrant, 1984, 1988
Limnanthes alba, *L. floccosa*	Flower maturation	Earlier		×		×		Guerrant, 1984, 1988
Salpiglossis sinuata CH flowers, CL flowers	Corolla	Reduced size		×				Lee et al., 1979
Sigillaria, *Chaloneria* (both fossils)	Time of reproduction	Earlier	×	×				Bateman, 1994
Veroniocastrum virginicum, *Veronica chamaedrys*	Sepals	Increased size	×			×	×	Kampny et al., 1993 Neoteny in early stages; acceleration later
Viola odorata CH flowers, CL flowers	Maturation time	Earlier				×		Mayers, 1983a, 1983b
Viola odorata CH flowers, CL flowers	Whole flower	Reduced size				×		Mayers, 1983a, 1983b CL floral primordium is smaller
				Vegetative traits				
Cucurbita argyrosperma sororia, *C. a. argyrosperma*	Leaf	Reduced lobing	?	?	?			Jones, 1992, 1993 Paedomorphosis plus allometric growth
Lepidodendron, *Hizemodendron* (both fossils)	Stem	Reduced height		×				Bateman & DiMichele, 1991; Bateman, 1994
Lyginopteridopsida, Magnoliales	Leaf	Simple, entire		×				Takhtajan, 1976, 1991
Pseudopanax crassifolius mature leaves, Juvenile leaves	Leaf	Increased length, decreased width				×		Clearwater & Gould, 1993

Ancestor, descendant	Structure or event	Derived morphology	Paedomorphosis[a]			Peramorphosis[b]			References; notes
			Neot.	Progen.	Postdisp.	Accel.	Hypermor.	Predisp.	
Vegetative traits									
Rhinanthus glacialis populations from alpine grassland, Populations from subalpine hay meadows	Onset of vegetative growth	Earlier						×	Zopfi, 1995
Rhinanthus glacialis populations from alpine grassland, Populations from subalpine limestone grassland	Offset of vegetative growth	Later					×		Zopfi, 1995
Rhinanthus glacialis population from grassland on rocks, Population from litter meadows	Offset of vegetative growth			×					Zopf, 1995
Sigillaria, Chaloneria (both fossils)	Whole plant	Shorter, lacking branches	×	×					Bateman, 1994
Viola odorata CH plants, CL plants	Leaf, petiole	Increased size				×			Mayers, 1983a

[a] Neot. = Neoteny; Progen. = Progenesis; Postdisp. = Postdisplacement.

[b] Accel. = Acceleration; Hypermor. = Hypermorphosis; Predisp. = Predisplacement.