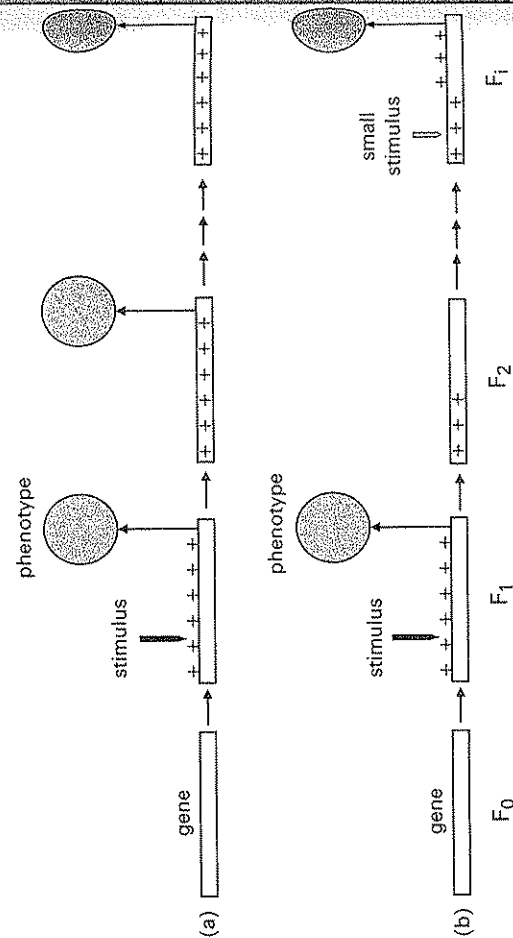


(2009) survey shows that all possibilities—direct germ-line induction, somatically mediated induction with variable effects, and parallel induction of both germ line and soma—have been found.

#### Epigenetic Learning: Expanding the Scope of Studies of Cellular Epigenetics?

In studies of cellular epigenetic inheritance, it is usually assumed that if a mark—say a pattern of six methylated cytosine sites—is induced at a particular locus, it is reconstructed (with a certain error rate) in the descendants, where it has similar phenotypic effects (figure 7.7a). The dynamics of acquiring epigenetic marks (how many generations it takes for an inducer to produce a change that has a phenotypic effect), how quickly it is lost (how many generations are required for a mark to fade), and how the extent of marking relates to the phenotypic response are all issues that have not been addressed and studied systematically.

Ginsburg and Jablonka (2009) have suggested that the problem can best be approached by thinking about it in terms of *cellular epigenetic*



**Figure 7.7** Cell learning through epigenetic inheritance. In (a), a stimulus alters a chromatin mark by adding six methyl groups (+), which leads to a phenotypic change; the mark persists (indicated by + symbols moving into the locus) and produces the same phenotype in subsequent generations. In (b), a stimulus alters a chromatin mark in the same way as previously, and it has a phenotypic effect, but the mark partially fades (only 3 + persist); in the next generation the induced phenotype is not produced, but because traces remain, a smaller stimulus elicits the response in a later generation (F<sub>1</sub>).

learning. Epigenetic learning occurs when an inducing agent elicits a response that leaves a persistent epigenetic trace which later, upon subsequent induction, is the basis of a more effective response. So, for example, an inducing stimulus might cause a gene to become epigenetically marked in a way that affects the phenotype; in the absence of the inducer the mark decays, but when a second stimulus of the same type is applied, because a partial mark is already present, either a smaller stimulus is required to elicit the response or the response is faster (figure 7.7b). Variations on this theme, including the possibility of reactions involving more than a single gene and leading to a kind of “associative” epigenetic learning, have been described and discussed by Ginsburg and Jablonka (2009).

Epigenetic learning is not yet a part of the research program of epigenetics, but there are examples of simple learning in nonneural organisms such as the ciliates *Paramecium* and *Stentor* (Wood 1992; Armus et al. 2006) and the plant *Mimosa pudica* (Appelwhite 1975), which can be interpreted in epigenetic terms. The molecular basis of this is at present unknown, but the ability to learn at this level may be adaptively important. Evolutionary models have shown that in fluctuating environments, epigenetic memory can be an advantage (Lachmann and Jablonka 1996; Balaban et al. 2004; Rando and Verstrepen 2007), but having epigenetic learning, rather than persistent memory, may often be selectively superior. With learning, the cost of a memorized response that is no longer adequate for present conditions (which is incurred when memory is perfect) is reduced, and the cost of development-from-scratch (which is incurred when “forgetting,” or “resetting,” is complete) is also reduced. If the molecular mechanisms that underlie epigenetic learning are the same as those that are the basis of cell memory and the EISs, it is not difficult to see how, through selection, small modulations in the conditions in which these mechanisms operate could lead to complex adaptive plastic responses. The mechanistic simplicity of such learning and the fitness benefits it is likely to confer suggest that a research project that investigates it could be fruitful.

#### Soma-to-Soma Transmission

Although epigenetic inheritance in cell lineages is currently receiving most attention, the soma-to-soma routes of transmission, which by-pass the germ line, are no less important for understanding the hereditary basis of evolution. Soma-to-soma transmission is an umbrella term for the many processes through which phenotypes are inherited because

aspects of the niche in which development takes place are reconstructed in successive generations. It includes transmitting substances that affect development through feces ingestion, through the placenta and milk of mammals, and through the soma-dependent deposition of specific chemicals in the eggs of oviparous animals and plants (Avital and Jablonka 2000). In addition, maternal morphological features can constrain offspring development and lead to heritable and self-perpetuating developmental effects (Jablonka and Lamb 2007a, 2007c), as do socially learned behaviors that do not require the transfer of materials (Avital and Jablonka 2000). Ecological niche construction (Turner 2000; Odling-Smee et al. 2003), which includes developmental interactions among organisms that form coherent and persistent symbiotic communities (Zilber-Rosenberg and Rosenberg 2008), can also contribute to soma-to-soma inheritance.

New somatic phenotypes that are inherited by the following generations can be initiated in more than one way. They may be induced in the soma (figure 7.8a), but it is also possible for soma-to-soma transmission to be initiated by a germ-line mutation or epimutation that has somatic effects that are self-perpetuating after the mutation or epimutation has segregated away (figure 7.8b), or via niche construction (figure 7.8c). The frequency and diversity of soma-to-soma transmission can be seen from the following summary of some of the methods through which phenotypes are reconstructed in successive generations.

#### Maternal Morphological Constraints

Self-perpetuating phenotypes can arise through the effects that maternal morphology (for example, size) have on the development of offspring. This is especially true for viviparous animals, but affects other organisms too. In some insects and oviparous fish, for example, large mothers lay large eggs that develop into large females that will again lay large eggs, and this cycle continues for as long as the environment does not change too drastically (Mousseau and Fox 1998). For humans and rats, there is a positive correlation between environmentally influenced maternal size and offspring size: small mothers have small wombs, with reduced uterine perfusion, and this leads to small offspring. The small daughters of small females will tend to perpetuate the trend (Morton 2006; Gluckman et al. 2007). This means that in the same environment there could be two genetically identical lineages that differ in size because of transient environmental conditions that affected the nutritional state, and hence the size of their maternal ancestors.

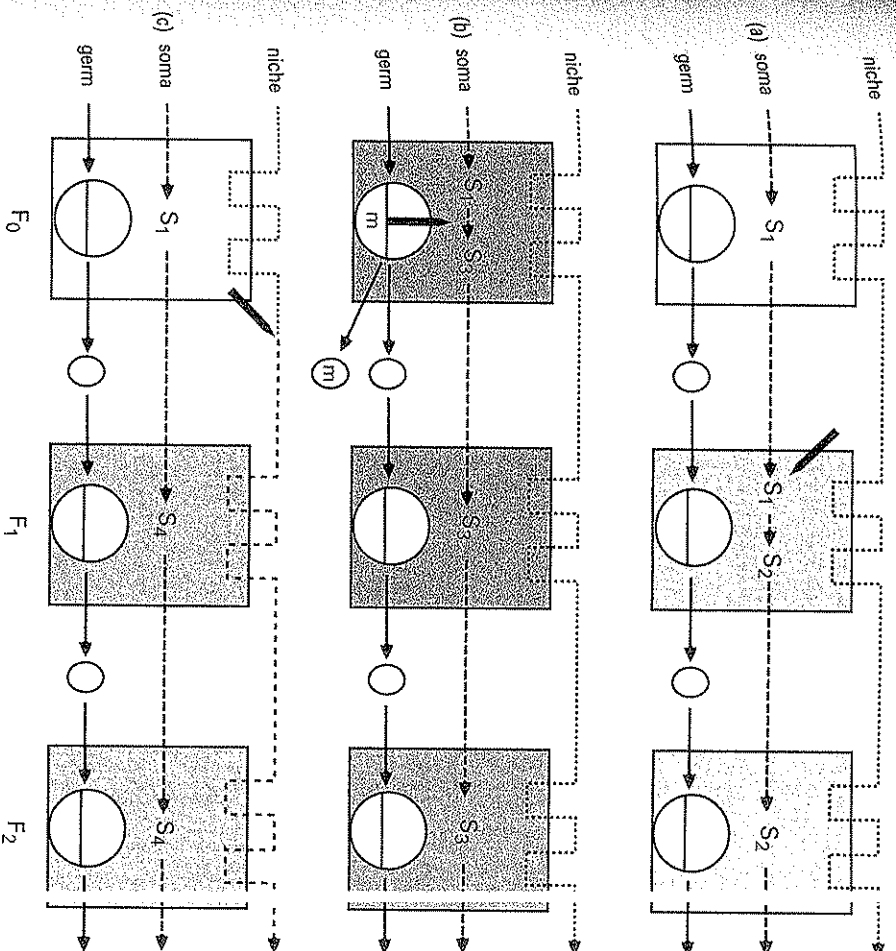


Figure 7.8

Different ways of inducing transmissible somatic changes: (a) an environmental stimulus (heavy arrow) induces a somatic change from  $S_1$  to  $S_2$  in the  $F_0$  generation, and the changed phenotype is developmentally reconstructed in descendants; (b) a mutation (or epimutation) in generation  $F_0$  has somatic effects changing  $S_1$  to  $S_3$ , and this phenotype is developmentally reconstructed in the  $F_1$  and later generations even though the causative mutation is not inherited; (c) because of some new activity, the organism changes its environment in a way that leads to a different organism-environment (niche) relationship and new phenotype, which are then reconstructed in subsequent generations.

### Hormonal and Pheromonal Effects

In 1988 Campbell and Perkins reviewed the evidence for multigenerational effects of hormone treatments and exposure to drugs such as morphine, alcohol, and other chemicals. The work they described suggests soma-to-soma transmission, although germ-line-mediated transmission cannot be ruled out, and possibly both routes were involved. One clear case of soma-to-soma transfer of hormonal effects leading to similarity between parents and offspring is the transgenerational effect of the uterine concentration of testosterone on the sex ratio and behavior of Mongolian gerbils (Clark et al. 1993). In these small rodents, female embryos that develop in a uterus where most of their sibs are male are exposed to high testosterone levels. This has long-term effects: their development is delayed relative to that of females from a uterus with fewer males, they mate later, and their behavior is more territorial. Crucially, when they themselves become pregnant, they produce litters with more males than females, so their daughters are exposed to testosterone in utero, and the cycle is perpetuated.

Locust phase polyphenism, a dramatic example of epigenetic transmission between generations, may involve pheromonal switches. The solitary (nonswarming) and gregarious (swarming) phases differ markedly in morphological, physiological, and behavioral features. The switch from one phase to the other can occur during the lifetime of an individual, or cumulatively over several generations. Simpson and Miller (2007) have argued that gregarious mothers transmit their phenotypic characteristics to offspring by means of a pheromone secreted into the foam plug that protects the egg pods, although Tanaka and Maeno (2008) dispute this, claiming that phase-dependent differences are established in the ovary. In spite of this uncertainty about how transmission occurs, this is a clear case of soma-to-soma inheritance, and one with obvious adaptive significance.

### Transmission through the Placenta, Milk, and Feces

In mammals, useful knowledge about what a mother has been eating can be passed to her offspring through substances present in her placenta, milk, and feces (Avital and Jablonka 2000). European rabbits provide a good example: the food preferences of the young are biased by the food information their mother transmits to them in the uterus, then through her milk, and finally through feces (Bilkó et al. 1994). Immunological information relevant to the current environment is also transmitted across the placenta and through milk. Evidence reviewed by Lemke and

colleagues (2004) shows that transmitted maternal antibodies, which are the outcome of a mother's experiences of microbes and allergens, guide the maturation of the immune system of neonates in ways that enhance its effectiveness in later life; some of the effects can be carried over to grandchildren. Lemke and his colleagues describe this as "Lamarckian inheritance," because the acquired immunological phenotypes of the mother are transmitted to her offspring, and they point out that it has obvious selective advantages.

Information transmission through the placenta, milk, and feces is not always beneficial. Prion diseases and some other amyloidoses can be transmitted by these routes. Amyloidoses are diseases caused by conformational changes in proteins: proteins that are normally soluble form insoluble  $\beta$  sheets which induce further polymerization of  $\beta$  sheets from precursor proteins. Korenaga and his colleagues (2006) found that the milk of female mice with a particular type of amyloidosis transmitted factors that induced the same disease in their biological or fostered offspring. How common such prion-like behavior is with amyloidoses is unknown. Scrapie, a recognized prion disease of sheep, can be transmitted from mothers to offspring through milk, and there is a strong suggestion that it can also be transmitted laterally through saliva, feces, or urine (Konold et al. 2008).

### Behaviorally Mediated Transmission

Soma-to-soma transmission in animals is often the result of their behavior: through social learning, ancestral patterns of feeding, mating, parenting, dispersal, predator avoidance, and other behaviors are actively reconstructed by descendants, leading to similarity between generations. Examples of this are numerous and well known: they range from transmission of local song dialects by songbirds and whales to the cultural differences found in traits such as nut-opening and ant-dipping in populations of chimpanzees (Avital and Jablonka 2000).

A fascinating insight into the kind of cellular epigenetic control mechanisms behind behaviorally mediated transmission is provided by Meaney and his colleagues' studies of maternal care in rats (Meaney 2001; Weaver et al. 2004). They found that some naturally occurring variations in a mother's style of caring not only influence the offspring's responses to stress, they are also transmitted to them. The variations are in the amount of "licking and grooming" (LG) and "arch-back nursing" (ABN) that mothers give their pups during the first week after birth. Pups that receive a lot of licking and grooming are stress-resistant and nonneophobic.

and the daughters that receive this type of care themselves become high LG and ABN mothers. Conversely, the pups of mothers who give their offspring less LG and ABN are more fearful and readily stressed, and, when adult, the females treat their offspring in the same way they were treated. Because the behavior is passed on, genetically identical rat litters in the same environment can display different behaviors, depending on the history of their female ancestors.

Meaney and his team found that changes in gene expression in the hypothalamic-pituitary-adrenal system, which is known to underlie reactions to stress, accompany the behavioral variations. When compared with animals reared by less-caring mothers, offspring of high LG-ABN females have increased expression of the glucocorticoid receptor (GR) gene in the hippocampus. This is correlated with changes in DNA methylation and histone acetylation in the gene's promoter (Weaver et al. 2004). Once established, the state of the GR gene persists throughout life, and is reconstructed in the next generation through maternal behavior. The causal connection between the chromatin marks and the transmitted behavior was established by pharmacologically altering the epigenetic state of the gene in adults, using the methyl donor methionine and inhibitors of histone deacetylation. These treatments reversed the effects of previous maternal care (Weaver et al. 2005).

Maternal care studies in another mammal, the mouse, show how soma-to-soma transmission of a new variant can be initiated by a germline mutation (figure 7.8b). Curley and colleagues (2008) found that mouse mothers having a certain mutant gene gave a low quality of care to their offspring, causing them to be fearful and show decreased exploratory behavior. When these offspring reached adulthood, even though they did not carry the mutant gene, they, too, gave their offspring a low quality of care, with the result that the grandchildren of the original mutant females were also fearful and showed decreased exploratory behavior.

#### Transmission through Symbolic Systems

There is no doubt about the power of language and other symbolic systems to transmit information over many generations, and it is generally recognized that these systems have helped to shape human evolution (Richerson and Boyd 2005). They also provide the best examples of the type of soma-to-soma transmission shown in figure 7.8c. Although great apes seem to have the rudiments of a symbolic system, a capacity that is revealed when they are exposed to human language (Savage-Rumbaugh

et al. 1998), we are not aware of any evidence showing that this is the basis of their various cultural traditions (Whiten et al. 2005). In contrast, human culture is dominated by symbolic systems, which lead to complex, cumulative, cultural evolution, and to far-reaching, rapid changes in the human niche. The invention of the airplane, for example, which depended on symbolic systems, enabled humans to fly, which has had far-reaching consequences for their social and individual lives.

#### Evolutionary Implications

The evidence presented in the previous sections shows that the transgenerational transmission of epigenetic variations through cellular inheritance and through routes that bypass the germ line is not a rarity. Therefore, if we are to understand heredity and evolution, we need to acknowledge these different types of information transfer between generations, and not focus exclusively on genetic transmission. Cellular epigenetic inheritance occurs in all organisms, although the relative importance of the various EISS differs among groups. Soma-to-soma transmission (in the sense that we are using it here) is specific to multicellular organisms, and some types of transmission are limited to certain taxa: obviously there is no neurally based behavioral inheritance in plants, and symbol-mediated inheritance is found almost exclusively in humans. Nevertheless, soft inheritance—the transmission of variations acquired during development—not only exists, it is found in every type of organism and seems to be common. It therefore has to be incorporated into evolutionary thinking.

We have discussed many of the evolutionary implications of epigenetic inheritance in previous publications (Jablonka and Lamb 2005, 2007a, 2007b, 2007c, 2008; Jablonka and Raz 2009), so here we will indicate only briefly how incorporating epigenetic inheritance affects various aspects of evolution.

#### Adaptation

Adaptation can occur through the selection of heritable epigenetic variations; genetic change is not necessary. This may be of particular importance when populations are small and have little genetic variability, such as during periods of intense inbreeding following population fragmentation. The discovery of extensive epigenetic variation in natural populations strengthens the view that it can play an important role in evolution (Bossdorf et al. 2008) and it is not difficult to imagine how some of the

epigenetic variations studied in the lab could be beneficial. For example, the inherited differences in the color and morphology of flowers that are known to be caused by different chromatin marks or RNA-mediated gene silencing might be beneficial if new pollinators or pests were introduced into their habitats. Adam and his colleagues (2008) have made a strong case, based on their experimental data, for epigenetic inheritance of stochastic variations in gene expression, rather than gene mutations, driving the evolution of antibiotic resistance in bacteria, although so far they have not pinpointed the mechanisms involved. Soma-to-soma transmission through social interactions and social learning is also undoubtedly behind some group-specific adaptive behaviors ("traditions") in animals (Avital and Jablonka 2000).

One of the reasons why recognizing epigenetic inheritance is so important for evolutionary thinking is that the dynamics of evolutionary change through inherited epigenetic variants are likely to be very different from those assumed in conventional population genetic models. While the population genetic models assume that mutations are rare events, and only one or very few individuals are likely to have a newly generated mutation, when epigenetic variations are induced, many individuals in a population may independently acquire a similar heritable phenotype at the same time. Moreover, epigenetic variations may be induced almost simultaneously at several different loci and coordinately affect several traits. How incorporating epigenetic inheritance can change an approach to evolutionary problems can be seen from Zuckerkandl and Cavalli's (2007) hypothesis for the origin of complex adaptations. They suggest that heritable epigenetic changes in "junk DNA," which spread across the genome, affecting the regulation of many genes, may be the answer to a problem that is difficult for Modern Synthesis theorists, namely, how in large animals, whose populations are relatively small, all the mutations necessary for a complex adaptation come together.

Another feature of epigenetic inheritance that makes it necessary to think again about the Modern Synthesis view of adaptation is that selection and mutation (epimutation) may not be independent. Epimutations may be induced by the selecting environment, and they sometimes revert if the environmental conditions change again.

#### Genetic Assimilation

Heritable non-DNA variations, even those that last for few generations, may enhance the effectiveness of genetic assimilation and accommodation processes, thereby accelerating adaptive evolution. One way in

which this might happen is evident from True and Lindquist's (2000) study of pairs of yeast strains that differed only in whether or not they carried [PSI<sup>+</sup>], the prion form of a protein necessary for terminating mRNA translation. When present, the prion causes new and different proteins to be produced because translation goes beyond the normal end of the gene and stop-codons in the middle of nonfunctional genes are ignored. In some conditions, this was found to be beneficial: the prion strains grew faster. The presence of prions might therefore enable a lineage to adapt and to maintain the adaptation until such time as genetic changes took over. In this way, a heritable epigenetic variation—the prion conformation—produces phenotypic changes that pave the way for genetic changes. According to the theoretical model developed by Masel and Bergman (2003), the beneficial effects of such an epigenetically based system would lead to its selection even if the response is adaptive only once in a million years. It might be particularly important in asexual lineages, where the accumulation of mutations would be slow.

Soma-to-soma epigenetic inheritance can also facilitate genetic assimilation. Avital and Jablonka (2000) have argued that behaviorally transmitted information that is later partially or fully genetically assimilated is probably a major driver of animal evolution, and Dor and Jablonka (2000) have suggested that the evolution of the language faculty involved similar cultural and genetic processes that were mutually reinforcing. They argued that as language evolved culturally, and as it became an increasingly important element in the social lives of its speakers, the speakers came to be selected on the basis of their linguistic performance. The cultural invention and elaboration of language thus launched a process of genetic accommodation involving the selection of any genetic variants that contributed to linguistic ability, which in turn increased the possibilities of cultural linguistic evolution, and so on.

#### Reproductive Isolation

Heritable epigenetic variations may initiate post-zygotic reproductive isolation. Both the failure of some hybrid offspring to develop normally and hybrid sterility may be caused by incompatibilities in the chromatin marks on the two sets of parental chromosomes (Jablonka and Lamb 1995). These might arise by chance, or be the result of selection in periods when the parent populations were isolated.

Behavioral traditions, whether arising by chance or through selection, might initiate pre-zygotic isolation (Avital and Jablonka 2000). They

could reduce the likelihood of mating between members of two populations if they affected the preferred time or place at which courtship occurs, or the song dialect used, for example. Transmissible differences in food preferences or preferred habitats might also lead to partial prezygotic reproductive isolation.

#### The Evolution of Development

Epigenetic inheritance has constrained the evolution of development. There are several developmental phenomena—such as the difficulty of reversing determined and differentiated cell states, the early segregation and quiescent state of the germ line found in many animal groups, and the massive changes in chromatin structure that occur during meiosis and gamete production—that can be interpreted as indirect outcomes of epigenetic inheritance. All could be the results of selection against transmitting chance epimutations and the parents' epigenetic "memories" to the zygote, which needs to start its development from a totipotent epigenetic state. In some cases, as in the evolution of genomic imprinting, selection may have favored the enhancement of germ-line-transmitted epigenetic memories (Jablonka and Lamb 1995, 2005).

#### Macroevolutionary Change

Epigenetic control mechanisms may play a key role in many macroevolutionary changes, especially those that follow genetic exchanges between species. Speciation through polyploidization and hybridization, which are of central importance in plant evolution, probably depends on them (Jorgensen 2004; Rapp and Wendel 2005; Arnold 2006). Following auto- and allopolyploidization, there is a burst of selectable epigenomic variation, which provides ample opportunities for adaptive change. It seems that, just as McClintock (1984) argued, genomic stress reshapes the genome.

Because regulated genome rearrangements are found during the development of so many different eukaryotes, it has been suggested that the epigenetic control mechanisms that bring them about are very ancient (Zuffall et al. 2005). The role of chromatin marking and RNA-based epigenetic mechanisms in silencing foreign viral genes and experimentally introduced genes in eukaryotes, which is now well established, has also suggested that these are ancient mechanisms, and it has been argued that their evolution was driven by their role in genome defense (Buchon and Vauriy 2006). Whether or not this is so, it increasingly looks as if the

significant role in shaping evolutionary change throughout almost the whole of the history of life. Whenever there was complete or partial genome merging, not only through hybridization but also as a result of symbiogenesis or horizontal gene transfer, then by silencing some of the introduced genes and heritably altering patterns of gene expression, epigenetic control mechanisms allowed the new organism to survive. We therefore suggest that in response to genome disturbance through gene acquisition and damage caused by ecological stresses, the activities of epigenetic control mechanisms produce large-scale epigenetic variations that are inherited and lead to macroevolutionary changes. These epigenetic control mechanisms could underlie the systemic changes (genome repatterning) that Goldschmidt (1940) believed drives macroevolution (Lamm and Jablonka 2008). Certainly, what is already known suggests that a better understanding of macroevolution might come from looking at chromosomal changes and epigenetic systems rather than from studying differences in coding genes.

#### The Major Transitions

We have argued previously (Jablonka and Lamb 2006) that epigenetic inheritance and epigenetic control mechanisms have played a key role in all of the major evolutionary transitions identified by Maynard Smith and Szathmáry (1995). For example, as we indicated earlier in this chapter, structural templating mechanisms were probably important during the crucial periods of symbiogenesis when bacteria became integrated within the ancestors of the modern eukaryotic cell. The evolution of long eukaryotic chromosomes also necessitated the recruitment and evolutionary elaboration of the chromatin-marking epigenetic systems: as DNA sequences were linked together or were added by duplication, there was selection for organizing and packaging these long molecules in ways that protected them, allowed them to be replicated, and made them available for transcription following replication. The later transition to multicellularity is also impossible to understand without taking epigenetic inheritance into account, because for anything other than the simplest levels of organization, cell lineages have to remember their determined state. As we argued previously, the efficiency of cell memory, the stability of the differentiated state, and various features of development enumerated in the section "The Evolution of Development" were all shaped in part by the effects of epigenetic inheritance, and the epigenetic inheritance systems were, in turn, shaped by the evolution of development (Jablonka and Lamb 1995, 2005).

Soma-to-soma epigenetic inheritance in the form of social learning was probably involved in the establishment and evolution of animal social groups, another of Maynard Smith and Szathmáry's (1995) major transitions. Their final transition—to linguistic communities, the hallmark of human culture—involved the co-evolution of symbolic systems and hominid genes, with the former leading the latter. The last two transitions depended on a highly evolved nervous system, and we have suggested that the importance of neural activities in animal evolution means that the origin of neural communication, a new information-transmitting system, should be added to Maynard Smith and Szathmáry's list of major transitions (Jablonka and Lamb 2006).

#### An Extended Evolutionary Synthesis?

At the beginning of this chapter we pointed out that the Modern Synthesis denied the possibility of soft inheritance, and insisted that evolution is usually gradual. However, the mechanisms of epigenetic inheritance that we have discussed are simultaneously involved in the regulation of gene expression and production of phenotypes, as well as in the transmission of information between cells and organisms; they therefore enable soft inheritance. Moreover, probably because some cellular epigenetic control mechanisms have evolved in the context of defenses against genomic parasites, which they silence or eliminate (Bestor 1990; Cerutti and Casas-Mollano 2006), they are recruited and produce genome-wide epigenomic repatterning following the introduction of foreign genes by horizontal gene transfer, symbiogenesis, and hybridization. These are processes leading to reticulate evolution. The same or somewhat modified epigenetic mechanisms may also be recruited under conditions of continuous physiological stress, such as the nutritional stress in flax that causes changes in DNA methylation and in the number of ribosomal genes (Cullis 2005). Hence, both the mechanisms that allow soft inheritance during microevolution, and the epigenetic mechanisms that lead to macrovariations and instances of rapid evolutionary change, need to be incorporated in the emerging extended evolutionary synthesis.

Although the primacy we give to the developmental aspects of variation places our view firmly within the emerging Evo-Devo framework of evolution, our perspective differs from most others because it is focused on inheritance. Evo-Devo biologists often reject the gene-centered view that has dominated evolutionary theory since the 1940s, and argue

convincingly that variations in genes should be regarded as inputs into developmental networks or units. However, the genome should be seen not just as a repository of genes that are inputs into development, but also as a developmental system with its own specific, inducible, variational mechanisms. A broader notion of heredity, based on the mechanisms of epigenetic inheritance at all levels of biological organization, could help to unite the different developmental approaches and transform our understanding of evolution.

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## 8

### Niche Inheritance

John Odling-Smee

The Modern Synthesis has been a highly successful theory of evolution. However, due to some of its underlying assumptions, it is also the source of conceptual barriers that are currently making further progress in some areas stubbornly difficult.

One example is the long-standing inability of the Modern Synthesis to recognize *niche construction* as a co-causal process in evolution (see below). The Modern Synthesis's omission of niche construction not only restricts our understanding of the dynamics of the evolutionary process, it also makes it difficult to integrate evolutionary biology with several neighboring disciplines (Odling-Smee et al. 2003). For instance, it is still not possible to integrate ecosystem-level ecology with evolutionary biology (Jones and Lawton 1995). It is not possible to fully relate evolutionary biology to developmental biology ("evo-devo") correctly, nor to explain some recent data (West-Eberhard 2003; Laland et al. 2008). Nor, in our own species, is it possible to integrate our potent human cultural processes with human genetic evolution without introducing some unacceptable distortions (Odling-Smee et al. 2003).

This chapter seeks to demonstrate how the addition of niche construction to evolutionary theory alleviates or removes many of these problems. Since we have discussed the relationship between evolutionary theory, ecosystem ecology, and the human sciences before (Odling-Smee et al. 2003), I will concentrate primarily on the EvoDevo relationship.

#### Niche Construction Theory

Half a century ago a developmental geneticist, C. H. Waddington (1959), proposed the concept of an "exploitive system" in which animals choose and modify their environments, and by doing so, change some of the natural selection pressures they and their descendants confront. I think