# 1 Introduction: How to Understand Development?

One way to understand organisms is through their embryonic development. How have they become what they are, starting from the egg? The answer to this question that is common: it's all in the genes. This is not only a layperson's answer, it is also the answer given by many biologists. The embryologist Lewis Wolpert states it clearly: "DNA provides the programme which controls the development of the embryo" (Wolpert 1991, 5). Development is pictured as a hierarchical process of differentiation in which the decisions are made by control genes. Though the picture is not known in all its complicated detail, the overall message could hardly be simpler. As the historian Garland Allen writes, embryology and genetics have been integrated on the basis of the idea that all biological phenomena can be described in terms largely derived from genetics (Allen 1978, 144).

But consider the following phenomena. In 1912, the marine echiurid *Bonellia viridis* was the first organism for which environmental sex determination was described; that is, environmental factors determine whether the animal becomes male or female. Larvae are planktonic and sex develops after settling. If a larva lands on a rock, it develops into a female with a body of about 10 centimeters and a long proboscis, which can become more than a meter in length. This proboscis has a function in feeding, but also in sex determination. If a larva lands on the proboscis of a female, it migrates into the female and develops into a tiny (1- to 3-mm) parasitic male. The male stays inside the female throughout its life and fertilizes her eggs (Bull 1983, 110; Gilbert 1994, 783). See Figure 1.1.

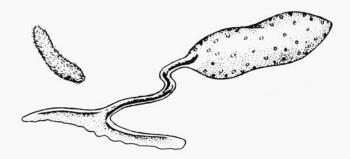


Figure 1.1

Bonellia viridis. Right: female. Left: male, greatly magnified compared with the female

Environmental sex determination is not the dominant form of sex determination among animals, but neither is it rare. It takes many forms: temperature, food, density, or the sex of nearby conspecifics may be crucial. In many reptiles, for example, temperature is the factor. This was discovered for a lizard in 1966, and subsequently it has been found that in many other lizards, in many turtles, too, and in all crocodiles, the sex of the animal is determined in this way. The details are species-specific. In some species, females are produced at high temperature and males when it is colder. In other species it is the other way around, while females can also result at high and low temperatures with males in between (Bull and Vogt 1979; Bull 1980; Bull 1983; Deeming and Ferguson 1988; Lang et al. 1989; Janzen and Paukstis 1991). See Figure 1.2.



Figure 1.2 A crocodile embryo

Other traits can also be under environmental influence. Many butterflies show seasonal polyphenism; that is, animals which develop in one part of the year, notably the wet season or spring, are phenotypically different from those developing in the dry season or in summer. One of the cases that has been known for a long time concerns the map butterfly or European map, Araschnia levana. Its two phenotypes differ so strikingly that Linnaeus classified them as different species (Bink 1992). The spring form is orange, with black spots, while the summer morph is black with a white band. Day length and temperature during the larval period are simultaneously influential (Shapiro 1976). Under experimental conditions with constant temperature, daylength makes the difference. It influences the release of the hormone ecdysone that initiates adult development. Larvae reared under short-day conditions become diapausing pupae and emerge as spring morphs. Long-day larvae become nondiapausing pupae, emerging as the black and white summer morph (Koch and Bückmann 1987).

Other mechanisms are also found. For some butterflies, photoperiod makes the difference, for others, temperature, while sometimes both factors are operative.

DDT and PCBs influence the development of gulls and terns. These chemicals are broken down in the body of the mother into products with estrogen-like effects, which interfere with the normal development of the reproductive organs in male birds. Sterile intersex animals are the result (Fry and Toone 1981; Fox 1994). This example is different from the two earlier ones, in that it involves abnormal development caused by pollutants.

The next and final example is again different, because it does not refer to phenotypic differences resulting from environmental differences, but to the complex specificity of the environment that an animal may need for its development. See Figure 1.3.

Larvae of the insect *Mantispa uhleri* (which resembles a mantid but belongs to the Neuroptera) feed on spider eggs. First instar larvae board immature spiderlings and spend most of their time in the book lungs. They feed on spider hemolymph, and overwinter in the spider. When they happen to find themselves on a male spider, they die, but when their host is female they enter the egg sac when it is produced and resume development there, feeding on the contents of the spider's eggs. The mature third instar spins a cocoon within the spider egg sac,

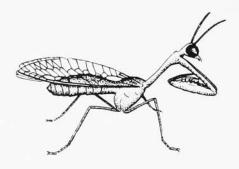


Figure 1.3 Mantispa uhleri

from which the adult animal later emerges. Spider eggs are the obligate larval food for this species (Redborg and Macleod 1983).

#### Choices

In books that approach developmental biology genetically, for example Lawrence (1992), phenomena such as that discussed earlier get no attention. Gilbert's broader oriented textbook *Developmental Biology* (fourth edition, 1994) does briefly mention various environmental influences. But it is remarkable that they find their place in notes, in special sections called "sidelights and speculations" or, in passing, in discussions that are meant to clarify other aspects of development. Environmental influences evidently have no clear place in developmental biology, and have to be dealt with in the margins.

My aim is to question this situation. First: why are environmental influences almost absent from recent accounts of development, or present only in the margins? Second: could and should something be done about that from a scientific point of view? Third: should something be done about it from a moral point of view?

In the next few paragraphs, I will introduce the various roads traveled in this book to answer these questions. But first, let me sketch the philosophical spirit of the undertaking.

My approach to scientific analysis is a pragmatic one that focuses on the inevitability of choices. I like Stephen Pepper's (1942)

characterization of pragmatism, in his book *World Hypotheses*. He distinguishes four "world views," each characterized by a root metaphor. Pragmatism, or contextualism, has the historic event as its root metaphor. It is a "horizontal" world view in that there is no absolute top or bottom of analysis; there are many potentially revealing ways to analyze something. This is its principal difference from the other views, where analysis must be done in prescribed ways. Contextualism rejects analysis for analysis' sake; it is always directly or indirectly practical. As I see it, this holds for scientific, philosophical, as well as any other kind of analysis.

A focus on scientific choices—associated with purposes and with consequences—is the core of my pragmatic approach. Nothing more is involved; I am not defending all the characteristics of the philosophical position termed "pragmatism." In particular, the notion of truth is not central (as it is, for example, in Rorty 1982; see also Murphy 1990); I do not defend a pragmatic theory of truth. Nor do I defend any other theory of truth, for that matter. The concept of truth, in the present book, is taken for granted. Given a vocabulary and given a subject of study, some things are true and other things are not. Scientists try to say things that are true, and this leads to many unproblematically accepted truths as well as many problematic, uncertain, or contested cases. In the context of science, some intersubjective criterion of "that which is agreed upon" suffices to make the notion of truth operational.

Scientists have to choose and define subjects about which they want to find truth, and they have to choose vocabularies and methods. The all-purpose all-encompassing approach does not and cannot exist; the adequacy of a particular approach depends on its purpose. I regard this need for choices as uncontroversial, and therefore the kind of pragmatism that I emphasize is not special or surprising. I just think it deserves more emphasis, in philosophy as well as in science.

### Three Approaches to Development

Dressed in this pragmatic "suit," let me sketch how I will address the questions concerning the place of environmental influences in developmental biology.

The first question is: Why are environmental influences almost absent from textbooks on developmental biology? I will answer this question by concentrating on the conceptual situation, not on how this situation has grown. The dominant approach to development is genetic. Within this approach, genes are the primary objects of study, and they are also at the center of the causal picture. Given that picture, attention is not easily drawn to environmental influences; if these are acknowledged at all, they are considered to be relatively unimportant. In Chapter 2, I argue that the mechanisms that exclude the environment are at least partly conceptual.

Though I will not go into the reasons and background of genetic dominance, at least one potentially good reason for it does not hold, which is that a genetic analysis of development might be the only approach that is experimentally feasible. This is not true; other approaches to development are possible, as will be emphasized in later chapters.

The second question is: What could be done about the absence of the environment from explanations of development? A discussion of two different alternatives to the genetic approach provides the background for my answer. The existence of several different alternative approaches is not surprising, for any scientific approach is a complex whole, and there will always be many different potential ways to diverge from it. For the purpose of this book, which is to discuss and highlight the explanatory place of environmental influences in development, I have found it helpful to distinguish three perspectives on development, representing three fundamentally different ways to deal with the environment. The dominant perspective is the genetic one, which is criticized by a structuralist as well as by a constructionist approach. According to both critical positions, the genetic approach concentrates too narrowly on genes. The structuralist approach opposes geneticism by calling attention to the organism as an integrated whole. The constructionist approach takes "organismenvironment systems" to be the important units; the boundaries of the organism are not seen as causally fundamental. Thus, the three positions focus on genes, the organism, and organism-environment systems, respectively, as the fundamental units of development and evolution. Main conceptual differences in biology concerning the role of the environment can be elucidated with the help of these three positions. Evidently, such a classification gets frustrated sooner or later. Not all present work in developmental biology fits in precisely with one of the positions. But the positions are not just constructs for the purpose of the discussion; they are defended in the way I present them.

### Metaphors and Science

Chapters 2 and 3 are devoted to an exploration of the conceptual landscape through a comparison of the three positions. These are compared in two ways. The first focuses on theoretical choices that are involved, particularly choices concerning causation. Since causal explanation is evidently a core goal of science, the relevance of causal issues does not require much introduction. Chapter 2 discusses causal questions concerning development. Chapter 3 adds a philosophical evaluation. I will stress the unavoidability of theoretical choices and the incompleteness of causal explanations.

The second way to compare the approaches, which is interwoven with the first, is through metaphors. The emphasis on metaphors may require a bit more introduction. Metaphors describe something with the help of something else. Arbitrary comparisons may yield metaphors. For instance, life may be called a "telephone," and this image may generate further thoughts, such as on the place of calls in life, though these thoughts do not necessarily lead to anything fruitful. A metaphor that is actually used for life is *journey*. This metaphor with its associated images such as "standing at a crossroads" is helpful for many purposes; it frames questions in terms of "where to go," for example. The metaphor of life as a programmed machine can do different things, such as stimulating questions on parts that fail when someone is ill. The examples illustrate that a pragmatic evaluation of metaphors, associating them with purposes they do or do not suit, is sensible.

Metaphors are not only important in popularized and immature science, as is sometimes assumed, but in theoretically well-developed parts of science as well. Take the well-developed theory

of evolution. Natural selection is and remains a metaphor, however technically the concept may be elaborated. Different metaphorical starting points are feasible, with different technical elaborations. Evelyn Fox Keller rightly notices that "even the most purely technical discourses turn out to depend on metaphor" (Keller 1992, 28). From a pragmatic point of view, the interesting question is if and how different metaphors work out differently.

Metaphors are prominent and irreducible elements in scientific theories; they guide questions, and they guide the integration of data into an overall picture. Donna Haraway's study of organicist developmental biology in the middle part of this century may serve as an illustration. Haraway describes proposals for a nonvitalistic organicism intended to transcend the conceptual devices of the "mechanismvitalism" controversy. Mechanism saw the organism as a machine. This metaphor was considered completely wrong by Driesch, the vitalist, who thought that embryos are radically indeterminate. The controversy was bitter, but in fact vitalism shared the machine image with mechanism; it only added the assumption that the machine needs a vital substance to make it run. This is the background against which Haraway locates various proposals for a nonvitalistic organicism, which rejected the machine image that had held both sides of the old controversy captivated. The newer approaches centred around different, nonmachine, metaphors such as liquid crystals and fields: "For Harrison the limb field is like a liquid crystal and unlike a jigsaw puzzle. For Needham the embryo is like history interpreted from a Marxist viewpoint and unlike an automobile with gear shifts. For Weiss butterfly behaviour is like a random search and selfcorrecting device and unlike a deterministic stimulus-response machine" (Haraway 1976, 205). For all these researchers, metaphors embodied basic views of development.

Metaphors color pictures of development from their general features down to details, and pertain to subject definition as well as to views of causation. For example, within a genetic perspective on development, even when environmental influences make a crucial difference, the search is often for the "underlying genetics." "Underlying" and "basic" are persistent metaphorical images indeed in the description of genetics' theoretical place.

## Environmental Influence: A General Picture Is Not Enough

A comparison of causal strategies and metaphors clarifies how the three approaches understand development and how they determine what is salient in the process. Both structuralism and constructionism claim to be more complete approaches than the genetic one, suggesting that something is wrong with restrictedness. But a main point of the present book is that none of the approaches is complete. Nor can they be; attention is always selective. Though it is true that the structuralist and constructionist approaches propose to include more factors in developmental biology than a purely genetic one, they, too, through their definitions of the subject of interest and through their causal approaches, depend on restricting choices. Nothing is inherently wrong with this, the important thing is to be aware of the restrictions. Overall frameworks have their limitations, and within these frameworks, the choice of research questions involves further restrictions.

Focused attention is not only unavoidable, it is helpful, even necessary, to get to know a subject in detail. Environmental influences can only have a real place in developmental biology when specific research is devoted to them. In other words, a general picture that acknowledges their in-principle importance in the complex interactive processes is not enough. Let me illustrate this.

In developmental psychology, interaction between internal factors and the environment is widely acknowledged, indeed almost a commonplace. Urie Bronfenbrenner has observed that in spite of this universal approval of interactionism, an internal perspective dominates in psychology; the result is the study of "development-out-of-context" (Bronfenbrenner 1979, 17–21). Bronfenbrenner argues for a broadened perspective that takes into account environmental influences on development. For that end, detailed characterizations are needed of what he calls the "ecological environment," namely, the environment as it is relevant for the developing person—rather than as it may exist in "objective" reality. The ecological environment can be seen as a set of nested structures, beginning with the immediate setting of the developing person, the "micro-environment," up to the "macro-environment," which refers to the cultural or subcultural level. An example of

a macroenvironmental characteristic is that crèches look like each other within a culture, but differ considerably between cultures.

The history of developmental biology, too, illustrates that the in-principle recognition of multiple causes does not guarantee that environmental influences receive particular attention. Concerning embryological development, again, nobody will probably deny when explicitly asked that internal factors by themselves are not causally sufficient for the process. There are even those biologists who are very explicit about the insufficiency of internal causes. Oscar Hertwig, who wrote at the end of the nineteenth century, and Gavin de Beer, who wrote in the middle of the twentieth, are among them. Let me quote them, rather than some present-day biologists, in order to give some historical depth to the present discussion. Though both authors assumed that the genetic material contains the potentials of organisms, they warned against a distorted view of causality that sees all other causal factors in development as uninteresting background.

Oscar Hertwig (1894), in his Zeit- und Streitfragen der Biologie I: Präformation oder Epigenese? argued, against Weismann, for an epigenetic picture of development. Weismann assumed that each biological character is represented by a determining factor, a part of the "Keimplasma." This way of thinking, Hertwig maintained, rests on wrong ideas about causality. The developing organism is almost pictured as a perpetual motion machine, while in fact numerous conditions must be fulfilled to give the outcome. In normal development, the embryo depends on material exchanges, gravity, light, temperature and so on; these conditions must always be present in the same way but that is no reason to forget about them: "Deshalb dürfen wir aber noch keinesweges die Rolle der Bedingungen, als ob sie gar nicht existierten, ausser Acht lassen, wenn es sich darum handelt, den organischen Entwicklungsprozess ursächlich zu begreifen" (Hertwig 1894, 81).

In a similar way, Gavin de Beer asked in *Embryos and Ancestors*: "Do the internal factors which are present in the fertilized egg suffice to account for the normal development of an animal?", answering that "it may be definitely stated that they are not sufficient, for if a few pinches of a simple salt (magnesium chloride) are added to the water in which a fish (*Fundulus*) is developing, that fish will

undergo a modified process of development and have not two eyes, but one" (De Beer 1940, 14).

While De Beer thus stresses that internal factors by themselves are not able to "produce" a normal animal, and are only a "partial cause" of development, the tendency to background the external factors is also clear from his writing: "The internal factors (. . .) enable the animal to react in definite ways to the external factors and by this means give rise to structure after structure in the process of development" (p. 15).

Development cannot take place without an environment: the environment is involved in all traits and in all developmental events. Though this cannot be denied, it recedes easily into the background; a recognition of the general importance of environmental conditions has not resulted in a real place for the environment in developmental biology. To create this real place, study of specific environmental influences is also needed. Chapter 5 contains explicit anwers to the second question of this book—what can be done about the absence of the environment—in the form of examples of environmental influences and ways to study them. One concept that is very useful in the investigation of environmental influence in development is the concept of "reaction norm." It refers to the relation, given a certain genotype, between a range of developmental environments and the resulting phenotypes. Studying reaction norms does not generate complete pictures of developmental processes, but it does yield insights into the environmental dependences of developing organisms.

Hertwig wrote at a time when development was thought to be brought about by either preformation or epigenesis, a distinction deriving from Aristotle. What precisely these terms refer to has been subject to historical change, but by and large preformationist theories hold that development is the unfolding of structures already present in the egg, while epigenesis involves the progressive formation of new structures during development. The present fate of these positions is summarized by Gould, who writes that "modern genetics is about as midway as it could be between the extreme formulations of the eighteenth century" (Gould 1977, 18). Hall, too, writes that neither position has "won out." In one sense, epigenesis has

triumphed because embryonic structures are not preformed in the egg. In another sense, preformation is right because the genetic basis for development lies preformed in the DNA of the egg (Hall 1992, 86).

This feeling of synthesis is well expressed by the word "epigenetics." It was coined by Waddington as a better translation of "Entwicklungsmechanik" than "experimental embryology" or "developmental mechanics" (Waddington 1956, 10). In "epigenetics," "epigenesis" and "genetics" are blended. Epigenetics has come to be seen as the causal analysis of development defined as the mechanisms by which genes express their phenotypic effects (Hall 1992, 89).

On the one hand, that "epigenesis" turned into "epigenetics" is illustrative of the central place that genes now have in developmental biology. Though everyone will agree with Hertwig and De Beer that genes are only partial causes of development, they have nevertheless received the far greater part of scientific attention. On the other hand, epigenetics goes beyond pure genetics in that it studies how genes are regulated. The study of gene regulation began with Jacob and Monod's model for the regulation of the lactose-operon in E. coli. Jacob and Monod emphasized the relevance of their results for "the fundamental problem of chemical embryology (which) is to understand why tissue cells do not express, all the time, all the potencies inherent in their genome" (Jacob and Monod 1961). Mechanisms of gene regulation show how cytoplasmatic factors are involved in embryology. Thus, Jan Sapp notes that the most important aspect of the operon model for embryologists is "the allowance it made for substances existing in the cytoplasm which are able to switch on or off, or to regulate the action of genes" (Sapp 1991, 246). Therefore, models of gene regulation could silence old controversies over the relative importance in development of nucleus and cytoplasm.

When epigenetics is the study of the regulation of one gene by (products of) another gene it does not widen the scope very much. But the role of environmental factors in the regulation of gene expression also belongs to epigenetics in principle. This is why epigenetics is a field where a genetic and a constructionist approach of development may meet, depending on how epigenetics develops experimentally and conceptually. The issue will return at several points in this book.

# Morality

Finally, there is the third question asked at the beginning of this chapter, which is whether something should be done about the absence of the environment in developmental biology from a moral point of view. It is the subject of Chapter 6. Let me sketch the approach.

A pragmatic approach to analysis and explanation could be taken to imply the relativistic view that it does not matter how you approach development, as long as what you do is helpful for whatever you happen to be interested in. But I propose to add a moral dimension by looking at consequences of choices. If science took place in complete isolation from any practical affair, scientific choices and the resulting specific kinds of incompleteness would not have moral consequences. Scientific explanation does have a practical impact, though, in direct and indirect ways. In a world full of problems, perpetual questions arise as to what to do, what to blame, what to change. Causal images are guides for what can and should be done, and the causal pictures that science generates are authoritative guides for what to do, what to blame, and what to change. Alan Garfinkel (1981) has argued these points convincingly. Since scientific views of the facts prestructure moral problems as well as solutions, it matters what causal pictures science generates. So I also agree with Robert Proctor (1991) when he argues for a moral/political philosophy of science, which does not make epistemological but practical questions central. More precisely, in fact, my argument is that these questions cannot be separated.

It matters for practical purposes whether we understand development as a process that is completely governed by genes, or by the whole organism, or as essentially taking place in an environment. Seeing development as an essentially genetic or as an essentially ecological phenomenon gives you quite different starting points when you wonder what it means and takes to live and flourish, and what can possibly go wrong in development. Nothing is wrong with questions about genetic diseases and cures. But those are certainly not the only practical problems concerning development. In nature, things go wrong on a massive scale, by the destruction or pollution

of environments. Climate and temperature, too, are relevant. Did the dinosaurs disappear because they had temperature dependent sex determination and temperature changes led to the disappearance of females, for example? And may present-day reptiles be in danger for the same reason?

#### Relationships with Other Discussions

In this book, approaches to development are mainly discussed and evaluated in terms of the pragmatics and ethics of causal explanation. In the meantime, other discussions are going on that concern development or are relevant to it. Let me sketch relations with some of them.

Within biology, there is much debate on the integration of evolution and development. Embryology was not integrated in the synthetic theory of evolution of the 1930s, and it has long been considered to be evolutionary irrelevant by many. This is now changing rapidly; the view that evolution is constrained by development is gaining influence. Since the disciplines to be integrated are themselves subject to controversy, it comes as no surprise that the character of the integration is controversial. Indeed, the three approaches to development that I distinguish are associated with different views on the integration of evolution and development. In Chapter 4, I will connect this issue with the main focus of this book. A central point is that in neo-Darwinian evolutionary theory, the environment is mainly a cause of selection. This association between environment and selection discourages recognition of a direct causal role for the environment in development.

Another discussion surrounding development, particularly in developmental psychology, is the notorious and never ending nature-nurture discussion. I will hardly ever use the words nature and nurture. Since the issue is so evidently relevant, this silence deserves some comment. Oyama's (1985) book *The Ontogeny of Information* deals with the persistence and many guises of the dichotomy of nature and nurture. The dichotomy has often been declared dead while living on quietly in a different guise. All the guises in some

form or other involved the opposition of internal and external causes. A real solution to the controversy, Oyama argues convincingly, requires dropping the internal-external dichotomy. I agree. It is through this internal-external dichotomy, which will show up repeatedly, that my treatment relates to the nature-nurture issue.

A further discussion associated with development is in terms of holism and reductionism. Since the 1920s, when embryology and genetics became separate disciplines, embryology has been associated with holism and genetics with reductionism. What does this distinction involve? In one general sense, reductionism is the claim that wholes can fully be explained in terms of their parts, while holism denies this. This general characterization has different implementations in different contexts. In discussions on development, reductionism often stands for the idea that DNA is or contains a program of development. Embryologists over decades have repeatedly attacked this metaphor, denied the causal sufficiency of the genome, and defended various forms of holism.

In the terms of this discussion, both alternatives to geneticism that I will discuss are holistic: they emphasize the causal insufficiency of the genome. To a certain extent, Chapters 2 and 3 can thus be read as an elucidation of the one reductionistic and two holistic approaches that I have distinguished. The point in these chapters is to explore the approaches and the role they give to the environment. Clearly, the environment can only have a causal role in holistic approaches. But it figures in only one of the holistic perspectives, the constructionist one. Evidently, for the purpose of this book, holism needs further distinction and clarification, and this is one reason to doubt the helpfulness of the term in this context.

Moreover, reductionism and holism have other meanings than the ones just mentioned. In the philosophy of science, for example, from Nagel's analysis (Nagel 1961) onwards, reduction is something that takes place between theories. With respect to biology, the main question has been whether biological theories can be reduced to physical ones.

In other contexts, the terms have been used in still different meanings. Reductionism is often associated with "simplification," for example, and holism with the refusal to simplify, or, less friendly, with

vagueness. Debates on the status of reductionistic simplification then may center on the question whether the simplification is only heuristic or has also ontological meaning.

All in all, I have avoided the terminology of reductionism and holism because it causes confusion. Yet some of the problems associated with reductionism—holism debates play a role and I have discussed them, but in different terms. In particular, the heuristic use of reduction (in the sense: reduction of the complexity of a research situation) shows up here as the issue of asking restricted questions, as mentioned earlier. I have been tempted to call such questions "reduced" questions, and to argue in favor of "multiple reductions instead of only genetic reduction," but given the tendency in biology to associate reductionism with geneticism, this might add to the confusion. The term "restricted question" will hopefully avoid such confusion.

Finally, the distinction of overarching approaches to development may invite associations with an analysis in terms of "paradigms," a notion which I will not try to define but which refers to systems of thought that differ deeply and fundamentally from each other. Donna Haraway, in her analysis of the metaphors of organicism in developmental biology, did make use of this term. As she uses it, it refers to situations in which scientists show "partial incomprehension of one another's views and talk past one another on crucial issues" (Haraway 1976, 203). According to this characterization, organicism was not really a paradigm on its own, because much work in the organicist tradition formed a continuity with existing work. Besides, efforts to create a theoretical framework were "often in vague terms that are hard to relate to actual experimental issues" (p. 204), so that this approach was not really full-grown. Nevertheless, the paradigm model helps to see the role of metaphor and imagination in science, according to Haraway.

It is now twenty years later, and metaphors no longer need the help of the paradigm-notion in order to be visible. In the present situation, talking of paradigms might harm rather than help my undertaking, because it is not my intention to stress that the views presented in this book are incomprehensible to each other. There are important differences, but there are also points of overlap, and shared

questions, and all kinds of interaction and hybridization may and do occur. This will become apparent in the discussion of the three causal approaches to development, to which I now turn.