BIOLOGY AND ONTOLOGY:
AN ORGANISM-CENTRED VIEW

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Abstract

In this dissertation I criticize and reconfigure the ontological framework within which discussions of the organization, ontogeny, and evolution of organic form have often been conducted. Explanations of organismal form are frequently given in terms of a force or essence that exists prior to the organism’s life in the world. Traits of organisms are products of the selective environment and the unbroken linear inheritance of genetically coded developmental programs. Homological traits share unbroken vertical inheritance from a single common ancestor. Species are the product of exclusive gene flow between conspecifics and vertical genetic inheritance. And likewise, race is ascribed on the basis of pre-existing essential features.

In place of this underlying preformationism which locates the source of form either in the informational program of inherited genes or within a selecting environment, I suggest form is the product of an organism’s self-construction using diverse resources. This can be understood as a modification of Kant’s view of organisms as self-organizing, set out in his Critique of Judgment (1790). Recast from this perspective the meaning and reference of “trait,” “homology,” “species,” and “race” change.

Firstly, a trait may be the product of the organism’s self-construction utilizing multiple ancestral resources. Given this, homologous traits may correspond in some but not all of their features or may share some but not all of their ancestral sources. Homology may be partial. Species may acquire epigenetic, cellular, behavioural, and ecological resources both vertically and horizontally. As such, they are best conceived of as recurrent successions of self-constructed and reconstructed life cycles of organisms sharing similar resources, a similar habitus, similar capacities for sustaining themselves, and repeated generative processes. Lastly, race identity is not preformed but within the control of human organisms as agents who self-construct, interpret, and ascribe their own race identities utilizing diverse sets of dynamic relationships, lived experiences, and histories.
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CHAPTER ONE

Introduction

There is no denying the impressive achievements of genetics, genomics, and evolutionary biology since the discovery of the structure of DNA and the insights revealed by the many genome sequencing projects. Yet these achievements are often framed using the metaphors of development as the unfolding of a genetic program and of the environment as something that moulds organisms over time. I criticize philosophical commitments that some work on biology imputes to these widely-used metaphors. I do not criticize biological research, only the interpretation of the metaphors employed in describing that research. I introduce a new philosophical perspective employing different metaphors that allows for a clearer understanding of biology. In this introductory chapter I discuss the background against which the thesis is written.

In section one I argue that describing an organism’s ontogeny using the metaphor of an unfolding program and describing evolution using the metaphor of the environment’s moulding organisms over generations involves a commitment to versions of preformationism. In section two I introduce an organism-centred alternative. In section three I summarize the chapters that follow.
1.1 TWO METAPHORS: ONTOGENY AS UNFOLDING AND THE ENVIRONMENT AS MOULDING

Different species exhibit different forms and behaviours. In the *Origin of Species*, Charles Darwin explains these differences as the outcomes of external factors in the environment which cause changes to the form of the organism over many generations which result in its being better fitted to its environment. This explains variation between species in terms of their phylogenetic history: the form of different species is determined by their different selection histories. According to Gregor Mendel, the variation between individual organisms within the same species is the result of internal factors which are passed from one generation to the next. This explains why organisms develop with the characteristics that they do.

One current presentation of evolutionary biology combines elements of these two accounts—Darwin’s theory of variation under natural selection and Mendel’s segregation of inherited factors—with population genetics. There are two different metaphors in play: development as the unfolding of the form contained in the genes and the environment as shaping the form of organisms over time (Lewontin 2001: 59-60). These metaphors pick out kinds of abstract processes: those of unfolding and shaping.

This combined perspective will be referred to as the neo-Darwinian approach. It understands organismal evolution and development to be principally gene-driven. For instance, Richard Dawkins (1989) takes genes to be both ontologically and explanatorily most important with respect to variation and evolutionary change. On his view, genes are “selfish” in their pursuit to replicate themselves. They are “immortal replicators” because they survive the demise of the individual organism, organisms are merely the transient vehicles the genes use for their own replication. Genes are the source of the continuity of form across generations that we see in the biological world.

Another example of this view is that of Ernst Mayr. Mayr (1982) uses the metaphor of a “genetic program” that controls the development and
organization of organisms: “the activity of an orchestra ... is just as much controlled by the score as the development of an organism is controlled by its genetic program” (Mayr 1968: 379).

This gene-centred perspective on organismal ontogeny is based on a dualism which separates the organizational form of the organism from the physical matter of the organism. The metaphors of genetic program, genetic code, and blueprint used to describe explanations of form and development suggest that the form of organisms pre-exists within their genes. Genes encode and transmit the phenotypic form of an organism from one generation to the next. The genes inherited in each generation contain the information which organizes the matter of organisms. The matter is passive and acted upon from within by the organizing force of the genes. Encoded information about the organism’s form exists in its genes; it is the preformed form—the information in the genes which unfolds during the development of the organism.

Although present in the writings of René Descartes, Pierre Gassendi, Karl Nägeli, and Wilhelm His (Fisher 2006: 103-123), this dualist perspective is particularly striking in August Weismann’s work (1885, 1893, cf. Moss 2003: Ch. 1). Weismann distinguishes the organism’s form, which is contained in the chromosomes within the nuclei of the germ plasm, from the material constitution of its body, made up of the somatoplasm. According to Weismann, the germ plasm and somatoplasm belong to two “distinct spheres.” The form of the organism is contained and transmitted only within the germ cells from one generation to the next: “the essence of heredity is the transmission of a nuclear substance [contained in] the germ plasm” (Weismann 1885: 65). This means that although somatic cells participate in the development of the organism, they are tied to the mortality of the organism. Unlike the information contained in the germ cells which is inherited in each generation, characteristics which are acquired in the soma of the organism over its lifetime cannot be inherited (Weismann 1885). Weismann’s dualist perspective holds that organismal form is conceived as both ontologically and ontogenetically prior to the biological matter of organisms.
On this perspective, what makes an organism the kind of organism it is (e.g. what makes a fox a fox) is its form, not its matter. To understand what makes a fox a fox means understanding the directive activities of its germ cells which are the source of its form. In addition to seeming to provide an explanation of what makes a fox a fox, conceiving organisms in terms of a dualism of form and matter means that one can explain why organisms produce offspring which look and behave like their parents (e.g. why foxes produce foxes and not donkeys or butterflies). Foxes inherit their form from the nuclear elements within the germ cells, which are passed on to them during reproduction from their parents, which in turn inherited their form in the same way from their parents.

This neo-Darwinian gene-centred view of the ontogeny of organisms trades heavily on such metaphors as information, code, and program. We may ask what notion of information is being appealed to in these metaphors. It cannot be the notion found in Claude Shannon’s mathematical theory of communication. Shannon (1948) went to great pains to expunge any semantic meaning from his theory. Information was exclusively understood as,

reproducing at one point either exactly or approximately a message selected at another point. Frequently the messages have meaning; that is they refer to or are correlated according to some system with certain physical or conceptual entities. These semantic aspects of communication are irrelevant to the engineering problem. The significant aspect is that the actual message is one selected from a set of possible messages (Shannon, as quoted in Kay 2000: 96).

So, the notion of information appealed to must be a semantic one. Genes are conceived of as transmitting information with semantic content. Information has semantic content insofar as it encodes a meaningful message (this view has been supported by Sterelny, Smith, and Dickinson 1996, and criticized by Godfrey-Smith 2000, Moss 1992, 2003).

According to the gene-centred view of ontogeny, genes are not just parts of DNA molecules that play an important role in making proteins, they code for the traits of organisms and determine their development; they are therefore appropriately described as the text of the so-called book of life.
Understanding genes as uniquely coding for traits involves taking genes to be the main source of information necessary for their development. However, it is not clear why it is only genes and not any other epigenetic or environmental factors which play a significant role in development. There seems to be no metaphysical basis that may be used to justify the privileging of one type of cause as primary and another type of cause as background. Whether one privileges genes over other factors is determined by one’s interest. Instead, there is a “causal parity” among many different kinds of causes and influences (Griffiths and Gray 2001: 195). That is, organismal development is the result of a number of causes which include but are not limited to genetic causes. Different influences might include cellular, metabolic, climatic etc. influences and those that result from intraspecies (e.g. siblings, mates, parents) and interspecies (e.g. predators, prey, bacteria, viruses, endosymbionts) interactions.

The second metaphor is that of the environment as shaping the forms of organisms over genealogical history. This metaphor is appealed to when describing selection and adaptation. Adaptation is often understood in terms of the action of natural selection as moulding a species to fit particular conditions within an external environment. The external factors which mould and adapt the organism’s form to the environment exist within the ecological niche prior to the organism’s occupation of it. The metaphor of the environment moulding or shaping organisms relies on the pre-existence of an ecological niche which shapes the organisms within it. According to Leigh Van Valen (1986), information is contained not just in the genes, but also in the environment. Differences in “environmental variables produce different phenotypes (or none at all) just as do differences in DNA sequences. Therefore information resides in the environment as well as in the genome” (Van Valen 1986: 67). The information in the environment moulds organisms to fit the requirements of living within that niche; e.g. environmental information such as the presence of thalidomide, overpopulation, or the scarcity of nutritional sources moulds the organism by inhibiting growth, or increasing aggressive behaviours. Constant changes in the environment mean that species are continuously adapting,
trying to keep up with these changes (Van Valen 1973). The upshot of this view is that ecological niches are understood to be autonomous entities; able to be defined without any reference to the organisms which live within them. This has lead to the use of such phrases as a “vacant niche” (for criticisms of this view see Griffiths and Gray 2001).

Both metaphors—ontogeny as an unfolding of an internal program and the external environment as something that moulds organisms over time—involves preformationist commitments. The view that the genes contain information about the form of organisms prior to their development is conceptually analogous to the view that organismal form arises from the divine designing power of God, and the view that organismal form is contained in a pre-formed homunculus (Oyama 2000: 55-83).

Likewise, the metaphor of the environment as something that moulds organisms is also committed to preformationism. The preformationism of the metaphor of development as unfolding consists in the prefiguring of organismal form within the genes. In contrast, the preformationism of the metaphor of the environment moulding organisms consists in conceiving the environment as independently specifiable from the organism. The information within environmental niches can be described without reference to organisms (Griffiths and Gray 2001). This information determines the form of an organism prior to the mode of living or career of organisms within it. In this sense, explanations of why organisms evolve as they do can be described using the metaphor of the environment’s selecting certain characteristics of organisms to fit within it.

One might think that what has been referred to as the interactionist consensus (Sterelny and Griffiths 1999: 99) or conventional interactionism (Oyama 2000: 2-6) can deal with these points. Interactionism is the view that organismal development is the result of the interaction of both genetic and extragenetic factors. It acknowledges the important role of both in development. However, interactionism still maintains a dualism between genes and environment as two ontologically distinct causal factors. This kind of interactionism remains wedded to the underlying preformationism of the two metaphors discussed previously. It holds that genes and
environmental niches exist prior to their interaction with each other and can be described independently of one another. This is because for genes to interact with the environment, they must not be a product of it but must exist prior to the organism’s life within it. Only by conceiving of genes as isolatable units can they be understood as independent factors which interact with the external environment.

The view of the biological world already mentioned, in which these two metaphors are combined conceives of development as the unfolding of information contained in the genetic program and evolutionary change over time as a consequence of the environment shaping organisms (cf. Dawkins 1989, 1996; Mayr 1982; Dennett 1995). It is this combined perspective that I offer an alternative to.

This is not to deny that this perspective has facilitated a great deal of scientific discovery and progress within biology and has provided helpful heuristics for scientists’ empirical research (Maynard Smith 1999). However, philosophers of biology can ask whether the metaphors of development as the unfolding of information contained in the genes and the environment as shaping organisms over time are the appropriate ones to use in describing organismal development and evolution.

Challenging Mayr's use of the genetic program Lenny Moss does just that arguing:

the self-organizing and self-developing capacity of living things have been projected into an abstraction called the genetic program which, as an informational analogue of the preformed homunculus, is housed in the nuclear germ of every living cell (Moss 1992: 345).

If the genetic program is understood in this way—as a metaphor or heuristic, then it cannot be something that empirical science can either ratify or deny. It is, in Immanuel Kant’s terminology, a regulative principle, (Moss 1992: 347) and as such, must not be evaluated in terms of something which can be judged to be true on the basis of empirical evidence, but in term of whether or not it aids our reflective judgment about biological development.
Rather than viewing organisms as outcomes of the separate causal forces of the internal unfolding genetic blueprint and the external factors present in a pre-existing environmental niche, we can instead view organisms as being both cause and effect of their own construction within their environments. Organisms are responsive to both their internal and external environment. This responsiveness runs in both directions. According to Mary Jane West-Eberhard (2003) this sensitivity, or what she calls “phenotypic plasticity,” means that organisms have certain capacities to interact and respond in certain ways to certain genes, cells, hormones, parasites, offspring, parents, and other organisms, etc. The organism’s genes do not orchestrate organismal development. Genes are constrained by the responsiveness of the organism to other genes or extragenetic factors. The effects of gene action depend not only on the specificity of the genes but on the plasticity (the organized flexibility) of the organisms’ phenotype. The impact of gene expression at every stage of the life cycle depends on the presence of a structure susceptible to change. There is no stage of development in any organism without an organized phenotype capable in specific circumstances of some specific, active response (West-Eberhard 2003: 94).

It is this interactive responsiveness which is necessary for both the ontogeny and evolution of organisms.

1.2 AN ORGANISM-CENTRED PERSPECTIVE

Some have suggested alternative ways to understand genes, organismal development, variable morphology, inheritance, and evolution which rely on different metaphors (cf. Griffiths and Gray 1994, 2001; Ingold 2001, 2004; Lewontin 1983, 2001; Moss 2001, 2003; Oyama 1985, 2001; and Taylor 1995, 2001). Richard Lewontin (1983) and Susan Oyama (1985) separately suggest that we conceive of development using the metaphor of organismal construction. They argue that the development of organisms is not best described using metaphors which locate the important source of causal power within the genotype. Metaphors of blueprints and codes lead
one to think that there is a concentrated source of causal power which forms passive organisms. This view does not deny the important role of genes in development, but it does deny that genes are the source of an organism’s form which exists prior to its development. Taking Lewontin and Oyama’s metaphor of organisms as constructing themselves as a starting point, Peter Taylor (1995, 2001) extends this metaphor to form his own conception of “heterogeneous construction.” Something is constructed heterogeneously if it builds itself out of diverse resources and has multiple causes.

The metaphor of construction can be used to describe both the ontogeny and the evolution of organisms. This leads to what I call an “organism-centred perspective.” Viewing development and evolution from this perspective does not just highlight the diversity of resources utilized in the organism’s self-construction. It also provides the means to explain how these resources come to be the distributed causes of the organism’s form and behaviour. The causes of organismal form are those resources which are linked together in the ontogeny of the organism.

What does it mean to say that an organism’s ontogeny can be understood using the metaphor of construction? An organism builds itself using a diversity of interacting resources. These resources include but are not limited to the nuclear chromosomes, cytoplasmic structures and organelles within the cellular membrane, cell walls and membranes, mitochondrial DNA, organizing areas for basal bodies and microtubules, DNA methylation patterns, metabolic pathways (Jablonka and Lamb 1995), as well as ecological, behavioural, and cultural resources. Genes are but one resource which the organism uses in its construction. The importance of the genes as a resource comes not from the genes themselves but from their use by the organism’s cells which determine what parts of the DNA count as genes and how these are used; e.g. there are different ways the same DNA molecule can be used by a cell. Genes do not direct the ontogeny of organisms by the unfolding of the information contained within them. The causes of organismal form are not localized in a single source—they are distributed over many available resources which the organism uses in its construction. There are “multiple points of intervention or engagement that
could modify the course of development ... [C]ausality and agency are distributed, not localized [to one cause or one resource]” (Taylor 2001: 316).

An organism is the product of multiple intersecting causes and interlinking resources which are cumulative over the organism’s lifetime. Organismal ontogeny is the constant process of construction and reconstruction. Ontogeny as described with this metaphor means that organisms are continually building upon what is already constructed by many interlinked and intersecting processes: “construction is polyvalent, things involved in one construction process are implicated in many others” (Taylor 1995: 307). The development of organisms is thus a set of various historical contingencies where each stage depends on the causal pathways, processes, and resources that were utilized by the organism in a previous stage.

An analogy to the making of a suit may help. Consider the crafting of a bespoke suit in a tailor’s workshop. In the making of the suit, the materials for its construction, e.g. the textiles, cutting and sewing equipment, tape measure, and buttons are all available. But their presence in the workshop does not constitute a completed suit, nor does it include all relevant factors which the tailor uses in making the suit. For instance, the suit’s construction is constrained by the size of the client and his or her measurements, which styles are popular considering what time of year or what is in vogue at the moment, and the career of the client. Its construction also depends on how material is cut, whether it is a summer or winter weight suit, the pattern of cloth, which part of the suit is sewn first, second, third, how the inside hems and tapes are stitched and whether there are cuffs. Even once finished, the suit may be altered given the increasing girth of the client, his or her transfer to a country with different customs or climate, accidental damage, or the change in fashion over time.

The interlinking processes that lead to the construction of the suit from diverse resources are analogous to an organism’s own construction with two important exceptions. There is no superintending master or mistress overseeing the construction of the organism and there are no easily determined boundaries where resources are located as there is with the
tailor's workshop. The resources available to the organism for its construction include genes, cells, intercellular pathways, gut bacteria, trees, shrubs, grasses, and other organisms.

Organismal construction, like the construction of a suit, also depends on a contingent sequence of events, within a particular context. How the organism constructs certain aspects of its ecological context affect other aspects of both the organism's own construction and may contribute to the construction of its offspring. An organism may change part of its environment; e.g. it may build nests or galls. Many female insects help construct the environment of their offspring by choosing to lay her eggs on a particular plant which provides the habitat and nutritional source for her larvae. Not only does her choice of oviposition help make the environment of her growing larvae, it also affects the form of the plant which is the site of her egg-laying (West-Eberhard 2003: 109). For example, this is evident in the presence of galls on trees which develop as a result of the female or larvae of certain flies and wasps. Although the insect’s oviposition is required for the development of a gall, some trees (e.g. oaks) are more susceptible to galls than others (e.g. maples or larches). Insects do not construct these galls on their own. The development of galls is contingent on whether a plant has a particular susceptibility to galling from certain insects: “specific properties of the plant genome or environment must play a role too ... not all [plants] are hospitable or responsive to galling insects” (West-Eberhard 2003: 109). Construction of organisms and their environments is heterogeneously caused by many interconnected causal resources supplied by factors in the environment, relationships between parents and offspring and other species.

The construction of the organism, like the suit, continues even after it appears to be finished. Organisms may continue to construct themselves and their environments over their lifetime. They may do this by altering their outer appearance by dramatically changing the colour of their skin (chameleons) or the seasonal moulting of the fur of some arctic animals (arctic hares) as a means of camouflage, by migrating to another location (Canadian geese or flamingos), by hibernating underground (desert toads) or
in caves (black bears), or by altering their environment by building webs (spiders), dens (foxes), nests (wasps, robins), warrens (rabbits), or dams (beavers). The analogy of the self-constructing organism to the tailor’s construction of a suit has some obvious limitations which make it, like most analogies, incomplete. Although the analogy serves to highlight some aspects of the external construction of organisms and their niches, it probably fails to illuminate the nature of their internal construction and maintenance (e.g. the organism’s utilization of different homeostatic mechanisms, the organization of its molecular, metabolic, and cellular activities).

Use of the metaphor of construction is not limited to describing the ontogeny of organisms. It can also be used in describing the evolution of organisms, variation over time and the striking suitability of organisms within their ecological niches. Rather than describing the variation among organismal phenotypes and fit to their ecological niches as due to their being shaped by certain factors within the environment or selected by the environment, the metaphor of construction provides a new way to understand the evolution of organisms and their ecological niches. It provides a way to understand these factors as resources which organisms utilize over generations. In this way, environments do not shape or choose the traits of organisms, they are used by organisms in constructing themselves and their niches. The causal importance of these environmental factors as resources comes not from the environment but from the organisms’ use of them: “organisms do not adapt to their environments: they construct them out of the bits and pieces of the external world” (Lewontin 2001: 64). Organisms actively construct their own niches through their interactions with both the animate and inanimate components of their environment and their responses to different situations. They may change what is included in their ecological niche depending on what is available to them and what is needed. For instance, a rattlesnake may use tortoise burrows as a refuge during brush fires. Unable to dig burrows itself, the rattlesnake utilizes the burrows dug by the tortoise which has claws which allow it to dig burrows wide enough for its own protection but
which are also used by rattlesnakes and other animals as a refuge. In this way, the tortoise’s burrows become appropriated as part of the snake’s ecological niche which it uses for its survival. Organisms organize and link various interdependent causal resources for their own construction and the construction of their niche.

As the above example of the rattlesnake illustrates, some of the resources an organism inherits are not transmitted to it from its parents. What an organism inherits is also not limited to nucleic acids transmitted from one generation to the next. Both genetic as well as extragenetic resources are inherited and contribute to the organism’s mode of life. The inherited resources which are transmitted include genes, cellular interactions within their embryological environment, disease resistance gained from mother’s milk, intestinal endosymbionts obtained by coprophagy (Griffiths and Gray 2001: 195), features of their ecological environment (e.g. grasses, seeds, sand, bushes), the knowledge of which type of food is most nourishing, the system of warrens or burrows built by either previous generations of its own kind or by other kinds of organisms within its niche, and the transmission of behavioural patterns (e.g. hunting practices, nest building, migratory destinations).

The organism-centred view is an historical-ecological perspective: it takes ecological dynamics to underlie biological ontogeny and evolution. This perspective is historical because it explains current states of affairs in terms of a combination of organisms’ past use of contingent resources. It is ecological because “all organisms live in an ecological context ... [P]hilosophy of biology depends on some conceptualization of ecology” (Taylor and Haila 2001: 521).

Instead of locating the causal source of form internally, within the genes, or externally, within the selective power of the environment, the organism-centred perspective rejects the view common to both: that there is one localized cause of organismal organization—genes in development and the environment in evolution. The organism-centred perspective fleshes out the metaphysical consequences of taking Taylor, Oyama and Lewontin’s metaphor of construction seriously.
There is no one privileged source which is the primary cause of an organism’s development. When we say, for example, that the nest-building behaviour of birds is either the result of primarily genetic or environmental causes, we do not speak meaningfully about the causes of this behaviour. Rather, nest-building behaviour arises from causes distributed among various resources which may include genetic, environmental, acquired through learning or copying from observing the nest building of other members of its species. Nest-building may also be “responsible for modifying some of the sources of natural [construction] in the environments that subsequently feed back to [them]” (Laland, Odling-Smee, and Feldman 2001: 122). The phenotype of nest-building is not simply the result of the one-way process of environment’s shaping phenotypes of organisms but rather the result of reciprocal feedback from populations of organisms to their environment and back.

Referring to this perspective as organism-centred does not mean that the organism is the source of all causes of its development and form, but that the organism is the vantage point from which to understand and describe evolution, phylogeny, and ontogeny. What it intends to pick out is the ontological centrality of organisms. Organisms are ontologically central because it is in their use of the resources available to them that organisms determine what are and what are not causes of their development and evolution. Organisms, rather than anything else, organize the use of the various resources available to them for their own development and evolution.

Before summarizing the chapters that follow, I locate the organism-centred view with respect to developmental systems theory (DST). DST does not pick out one theory but refers to a collection of theories that share some central commitment (see papers in Oyama, Griffiths, and Gray 2001). The most widely held commitments are to the dissolution of dualist thinking in developmental biology (e.g. Griffiths and Gray 2001: 195, Ingold 2001: 255-61) and to a strong antipreformationism which takes organismal form not to be contained in the information found within the genes (e.g. Oyama 2000: 28-35, Moss 2003). We can distinguish between two aspects of DST.
DST refers at once to both: on the one hand the scientific theory about biological systems which suggests a new mode of empirical research, new heuristics that aid in forming testable hypotheses; and on the other a “philosophy of nature” that provides a new perspective, metaphors, and categories of thought applied to our existing empirical knowledge (Godfrey-Smith 2001: 283-84). Philosophy of nature in this sense, “comes after empirical science and tries to redescribe structures in the world that have already been described by the sciences” (Godfrey-Smith 2001: 284). Although “philosophers are at liberty to make novel empirical suggestions” “a good philosophy of nature makes no empirical claims that are inconsistent with those made in the relevant sciences” (Godfrey-Smith 2001: 284). It is the general philosophical perspective of DST that I espouse in this thesis. Thus, the organism-centred view is a version of the philosophical project of DST, a philosophy of nature in the sense that Peter Godfrey-Smith articulates. This approach aims to dissolve the boundaries between genes and environment, nature and nurture, and biology and culture. It offers an alternative way of thinking about organismal organization, inheritance and development which does not depend on privileging one type of cause over another or conceiving of them as separate causes.

1.3 Chapter summaries

1.3.1 Chapter Two: Kantian origins of the organism-centred view

The organism-centred view is not unique in taking the organism to be both cause and effect of its self-organization. The notion that the causes of organismal form and organismal development are circular rather than linear not only pre-dates Lewontin, Oyama and Taylor, it also predates Darwin. It is prefigured in the Critique of Judgement (1790) in which Immanuel Kant argues that organisms are mutually interdependent means and ends of their own self-organization.
In Chapter Two I discuss some of the views on biological organization that Kant puts forward in the *Critique of Judgement*. Some of these are motivated by his more general metaphysical framework; however, they can be accepted even if we do not share his specific motivation. Neither do we need to adopt Kant’s notions of biological organization wholesale. Pre-dating Darwin, some of them are limited in their applicability to a Darwinian view of evolution and so must be revised. However, careful consideration of the Kantian notions of purposiveness and common generative capacity provides a philosophical basis for the notion of distributed causality that underlies Taylor’s view of organisms as constructed from heterogeneous resources.

Kant’s view of the self-organization of organisms has two central components: 1) purposiveness and 3) common generative capacity. Biological entities, in contrast to inorganic entities, have what he calls an internal purposiveness (zweckmässige). This internal purposiveness is the organism’s directedness towards a telos. Kant believes that we understand organisms as simultaneously both means and ends of their own self-organization because we compare them to ourselves. We understand ourselves as self-directed subjects, so, by analogy we understand organisms as self-organizing ends in themselves. Purposiveness constitutes a teleological understanding of organisms in terms of their ends. Kant believed that we need to use teleology as a regulative idea to understand biological organization: “we use this term only to designate a kind of causality of nature by analogy with [our own self-directedness]” (Kant 1790: Ak. 384). Teleology and mechanism are heuristics we use to study the biological organization (cf. Lenoir 1982). According to Kant, we can never know the intrinsic purpose of nature. “When we study nature in terms of its mechanism [or purposiveness], we keep to what we can observe or experiment on in such a way that we could produce it as nature does, at least in terms of similar laws; for we have complete insight only into what we can ourselves make and accomplish according to concepts” (Kant 1790: Ak. 384).
The second component of organismic self-organization is common generative capacity. For Kant, organisms can be grouped together in terms of their common generative capacity or original stock of *Keime* (germs) and *Anlagen* (dispositions or capacities). All variations and modifications which are made to an individual and its descendants are contained in its original generative capacity. In this sense, organisms cannot possess novel characteristics. Kant rejects the view that the traits of organisms vary as a result of the selective pressure of the environment. He holds that the variation in an organism’s traits is present in the original generic potential. This notion does not imply a preformationism of an unfolding homunculus which specifies the definitive set of an organism’s traits. A shared generative capacity consists of a generic set of resources available to the organism.

Karl Ernst von Baer built on and extended Kant’s teleomechanist framework (cf. Lenoir 1982). For von Baer, what the organism will ultimately become determines how it behaves and reacts over its life cycle. He argued that biological wholes are better understood in terms of their goals rather than ends. From insight drawn from his work on embryology, von Baer understood biological wholes as becoming over time and developing towards a goal. Against Kant, he argued that ends do not exist in themselves in the biological world. They exist only as the interactive developmental processes of organisms towards goals. This resulted in von Baer altering Kant’s conception of causation from ends (*Zweck*) and means (*mittel*) to goals (*Ziele*) and means (*mittel*). Taking this revised account of Kant’s view means that we can conceive the purposiveness of organisms in terms of real phenomena of nature rather than simply heuristically.

I discuss how this revised Kantian approach can be interpreted as a distant ancestor of the organism-centred views of Oyama (2000), Taylor (2001), and Moss (2006). I conclude by articulating the main claims of my own organism-centred view in light of these.

In the remaining chapters I discuss how this organism-centred view provides a new approach to understanding the evolution and development of
organisms; specifically the origin of analogous and homologous traits, and a reconceptualization of the categories of species and race.

1.3.2 Chapter Three: Extending the Meaning and Reference of the Concepts of “Trait” and “Homology”

There are longstanding debates within comparative and evolutionary biology about the meaning of the concept of homology. Homology is defined as similarity that is due to common descent from a shared ancestor. For example, although human forelimbs and cetacean flippers have different functions and appear to be very different, they are considered to be homologues because they share a common mammalian ancestor. It is not this definition which is the subject of these debates but the meaning of the concept of homology, the criteria used for identifying instances of homology, and how homology is to be distinguished from analogy (c.f. Owen 1843, Boyden 1943, de Beer 1971, Fitch 1970, papers in Hall 1994, Jardine 1967, Patterson 1982, 1987, Roth 1984, 1988, Reidl 1978, Van Valen 1982, Wagner 1989, 2007). Much of these debates seems to centre on whether the common descent from a shared ancestor is broken or unbroken. Broken ancestry refers to the absence of the similarity in some generations, e.g. recurrent traits (West-Eberhard 2003: Ch. 19) or latent phenotypes (de Beer 1971, Roth 1984). Unbroken ancestry requires the similarity to appear in every generation (Hennig 1966, Patterson 1982, 1987). But recent discussions have highlighted the fact that the traits which are compared as homologous are rarely exactly the same trait from one generation to the next. For instance, the same traits in different organisms may share similar cellular or developmental processes but utilize different genes. Many traits which are not considered to be completely homologous may in fact be the result of different recombined elements which have been inherited from more than one ancestral trait (Minelli 2003, West-Eberhard 2003). This has led to the controversial suggestion that if we want our conception of homology to reflect this mixed ancestry, it should be extended to include partial, combinatorial and mixed homologies (Sattler 1986, Minelli 2003, and West-Eberhard 2003 respectively). In this chapter I argue
that once we recognize that traits are constructed from multiple resources, we will welcome these extensions to our conception of homology.

Homology may be contrasted with analogy. Analogy is typically defined as similarity which is due not to shared ancestry but rather to the result of processes such as convergent evolution; e.g., bat wings and bird wings have the same function and appear similar but are considered to be analogues because the wings of birds and wings of bats evolved independently—the former from reptilian ancestry, the latter from mammalian ancestry. A human’s arm is homologous with a whale’s flipper because these two organisms share a common ancestor from which both have inherited the same forelimb structure. What Richard Owen (1843: 374-79) calls “the same organ” was later described by Darwin (1859: 435-38) as the sameness of structure due to descent from an equivalent structure in the common ancestor. But what does saying that a human arm and a whale’s flipper are the same structure, or have remained relatively continuous (with obvious modifications in each organism), mean? It means that whales and humans have inherited from a common ancestor an arrangement of bones in their respective forelimbs that are isomorphic to one another. The positions of the human’s phalanges, metacarpals, radius, ulna, and humerus are isomorphic to the positions of the same bones in the whale’s flipper. This is not the case with respect to the wings of bats and the wings of birds: the bat’s wing consists of thinly stretched skin between its digits (metacarpals and phalanges) whereas the bird’s wing is made up of hollow bones (humerus, ulna and radius) and primary and secondary flight feathers. That is, the bat is kept aloft by the collapsible umbrella-effect of the thin skin stretched between its fingers, while the bird’s flight is facilitated by its light bones and the air resistance of its feathers (Owen 1849: 7-8).

Using the metaphor of the selecting and moulding environment, convergence is described as the cause of the analogous wing structures of birds and bats. These wings represent similar solutions to the problem of flight posed by the pre-existing aerial environment. The environment
moulds organismal traits and causes the striking similarities between bat wings and bird wings.

According to the organism-centred view, birds and bats construct themselves in ways which allows them to traverse their environment by producing wing structures which provide wind resistance and facilitate propulsion through air, enabling them to glide and fly. The wings are analogous because both bats and birds are subject to the same constraints, namely gravity, atmospheric pressure, and wind resistance. This means that if their bodies are a certain weight and size, they must construct wings having a certain length and breadth if they are to be aerodynamic. The wings of birds and bats are similar, not because they have both been moulded by similar pre-existing niches but because both have similar resources and are subject to the same physical constraints in their self-construction. This provides an alternative to the metaphor of the moulding environment which takes the causal source of wing development to come from the pre-existing environmental niche of both birds and bats which selects and shapes the morphology of wings to fit the environment. The organism-centred view takes there to be multiple sources of wing development which include the physical constraints of flying, the difference in air pressure of high flying birds and cave dwelling bats among the resources which are used in both birds’ and bats’ wing development. The birds’ and bats’ environmental niches do not pre-exist them. The organism co-constructs itself and its niche over many generations.

It may seem fanciful to say that organisms construct themselves and their environments over evolutionary time. But this impression arises from a misinterpretation of the metaphor of trait construction as conceiving of traits as being built de novo within a limitless space of possibilities. This is not what trait construction implies. Bats cannot build gossamer propellers or brocade zeppelins attached to their feet to carry themselves through the air. Trait construction occurs within a confined possibility space, partially restricted by the physical laws of nature such as gravity, the available resources in the environment, nutrition, limitations of bone mass, tissue thickness, and organism’s genetic and extragenetic resources.
Homologues and analogues are traditionally believed to arise from two completely separate and non-interacting processes: shared ancestry and convergent evolution respectively (c.f. Hennig 1966, Patterson 1982, 1987, papers in Hall 1994). Homologues are important in determining how closely two individuals are related because homologous traits are understood to be conserved from one generation to the next. Two individuals that possess homologous traits share a common ancestor from which each has inherited this trait via an unbroken (or “linear”) route from the ancestral generation. This is obviously an oversimplified account of the conservation of homologues as it is strictly incorrect to say that the same trait is conserved and passed down from one generation to the next. Organisms are constructed in each generation—so what is retained or conserved has been the subject of much debate within the study of homology and philosophy of biology (Hall 1994, Griffiths 2007, Love 2007). While some believe that the conservation of homologues depends on the organism’s genetic inheritance (Hillis 1994), others believe it depends on the organism’s structural morphology (Owen 1849, Remane 1952), while some believe it depends on the developmental processes and mechanisms (Gilbert and Bolker 2001).

Instead of assuming the continuity of structures from one generation to the next, the organism-centred view takes the generationally repeated structure of homologues as explicable in terms of what Taylor calls the “contingent outcomes of intersecting processes” (Taylor 2001: 313). Applying this notion of construction to the discussion of homology and analogy allows us to highlight the contingent processes which lead to the construction of homologous traits. The continuity or conservation of organisms’ homologous traits over a series of ancestors and descendants can be explained as the result of these organisms’ use of similar genetic, behavioural, and environmental resources in its construction. Understanding traits as constructed from various resources offers a new way of interpreting the increasing evidence that there may be diverse routes leading to the same traits. Specifically, an organism-centred view further illuminates what West-Eberhard (2003: 358-74) identifies as “recurrent
traits.” She shows that the route from ancestor trait to descendant trait can be broken (e.g. traits can be absent in one generation but recur in another) and need not be continuous, as traditionally assumed. This view also accommodates Alessandro Minelli’s (2003: 59) conception of the different “temporal mosaics” which include both homologous and analogous components.

The organism-centred view of traits as heterogeneously constructed also provides an alternative to the standard either/or thinking within comparative biology—that similar traits are either completely homologous or are not homologous at all (but may be analogous). If an organism’s traits are self-constructed from multiple interacting resources under similar constraints, the sharp distinction between homologous and non-homologous traits may not be possible. In Chapter Three I consider recent suggestions to extend the concepts of homology to include homologies of process as well as complete, partial, and combinatorial homologies and analogies. For instance, if a trait is the result of a combination of different structures and processes, it may not be best described as completely homologous or completely analogous to another trait in another organism which is generated by a similar process but which possesses a different structure. Conceiving of these two organismal traits as partially homologous and partial analogous is a better description of their nature.

In contrast to the standard either/or thinking about homology, I argue that what have been traditionally thought to be independently evolved structures (analogues) may actually be the result of a combination of various ancestral traits synthesized together to form an amalgam trait in the descendant. This constructed amalgam trait is the partial descendant of a number of different ancestral traits. For example, both humans and octopi have camera eyes. Their eyes possess certain striking similarities of general structure and function. The camera eyes of octopi and humans both have lenses and retinae with photoreceptors. However, the photoreceptors of humans face the back of the eye, while those of octopi face the front (Nilsson and Pelger 1994: 56). Some of the ontogenetic origins of octopi and human eyes also differ. Whereas octopus photoreceptor cells differentiate
from the epidermis, those of humans differentiate from the nervous system (Land and Fernald 1992). Because of these and other differences, octopi and human eyes are widely believed to have evolved independently rather than being inherited from a common ancestor (Kirschner and Gerhart 2005). They are thought to be analogues not homologues.

An organism-centred view helps us make better sense of the similarities in structure and developmental resources found in both organisms. Conceiving of octopi and human eyes as analogues and not homologues offers a limited description of these similarities. There is much evidence suggesting the homology of the structural organization of visual systems in octopi and humans (Land and Fernald 1992). Vision in humans and octopi is the result of light on organs which are photosensitive. The retinæ of both organisms use rhodopsin for photoreception. Rhodopsin is a type of opsin. Over 1000 different opsin proteins have been found in different animals (Terakita 2005: 213). What is striking is that in each and every animal, the opsin is connected to the same 11-cis-retinal chromophore (Terakita 2005: 213). The 1000+ opsins are grouped into five types or families; all of which are thought to share a distant common ancestor possessing multiple opsin types (Menon, et. al. 2001). Apart from the deep homology of the opsins across a wide range of organisms, similarities in the neurological structure of the visual system of octopi and humans have also been found. Exposure to light produces a chemical change in both octopus and human retinæ. This change produces voltages that are transmitted to the brain through a network of neurological events (Dawson 2006: 66). In addition to the structural similarities in the visual systems of octopi and humans, eye development in both (as well as a range of other organisms including fruit flies) is initiated by the Pax-6 gene (Quiring et al. 1994).

These findings reveal that distinguishing the eyes of octopi and humans as either homologous or analogous means ignoring certain aspects of their development or structure. The organism-centred view conceives octopi and humans as utilizing the same resources in the construction of eyes in different arrangements. Their eyes can be understood as homologous because the resources used in their construction are present in
all bilateral organisms, all of which share a common ancestor. Put another way, they share a common generative capacity—a stock of *Keime* and *Anlagen*. Although octopi and human eyes initially appear to be analogous, it is perhaps more accurate to understand them as partially homologous due to their use of similar tissues, genes, cells, proteins and organization of their visual systems, and partially analogous due to the different ontogenetic pathways which lead to the construction of similar outcomes.

This is admittedly highly controversial and may sound Lamarckian to some. However, neo-Darwinists of many stripes avoid the accusation of being Lamarkian by maintaining a distinction between inherited traits and acquired traits which is not ontologically justified. The idea that some organismal traits are inherited from common ancestors (through transmitted genetic information) while others are the result of environmental pressure relies on a dualist assumption that there are two independently specifiable sources of form, criticized above. Considered from an organism-centred perspective, most identifications of homologous and analogous traits are more likely to be partial (Sattler 1994) or combinatorial (Minelli 1996, 2003) rather than completely homologous or completely analogous. Traits are instead constructed from multiple resources, some homologous, some analogous, some neither.

### 1.3.3 CHAPTER FOUR: REINCORPORATING ONTOGENY BACK INTO A CONCEPTION OF SPECIES

Species have been conceived of in a number of different ways and there continues to be much debate concerning their nature (cf. the papers in Ereshefsky 1992; Claridge, Dawah and Wilson 1997; and Wilson 1999). Although frequently criticized, Mayr's biological species concept (BSC) remains the one to which other conceptions are compared. Mayr defines species as groups of interbreeding or potentially interbreeding organisms that share a gene pool. Species are populations of organisms that are genetically and reproductively isolated from members of other populations. According to the BSC, species are sharply separated from one another.
They are “protected gene pools” (Mayr 1992: 24). The environment provides the usual conditions that facilitate the exclusive interbreeding among individuals that share the same gene pool. Species separateness is ensured by “isolating mechanisms” which “protect [the species] from harmful gene flow from other gene pools” (Mayr 1992: 17). He cites hybridization and horizontal gene transfer as examples of the kind of harmful gene flow which breaches species boundaries and threatens species separateness. Mayr argues that “species have reality and an internal genetic cohesion owing to the ... evolved genetic program that is shared by all members of the species” (Mayr 1992: 17). The central criterion for species membership is genetic. A “species is a genetic unit consisting of a large intercommunicating gene pool” (Mayr 1992: 17).

In Chapter Four, I contrast the gene-centred BSC with a new ecological perspective on species that combines consideration of an historical-ecological view of species found in the early writings of Georges-Louis Leclerc, the Comte de Buffon (1744-1749) with the notion of heterogeneous construction from Taylor (2001). Buffon claims that a species is the succession of individual organisms each of which constructs itself within its life cycle according to a particular form of life. Individual life cycles of organisms are materially connected with each other by a series of repeatedly generated developmental processes. This meant that a species is the physical and temporal series of individual organisms which shares a capacity for sustaining themselves in a particular way within their environmental context (Buffon 1749). He argues that species are not defined in terms of shared morphology but on the basis of their way of life. Buffon is one of the earliest thinkers to emphasize the role of behaviour, climate, environment, and nutrition in determining species habitat. He believes that to understand a species, one must consider the morphology, internal activities (e.g. digestion), external activities (e.g. locomotion), and the mode of living (habitus) of the members (organisms) of the species within their environment.

The organism-centred view of species combines Buffon’s historical-ecological view of species with Taylor’s metaphor of the heterogeneous
construction of organisms. On this view we can reconceive species as the recurrent succession of self-constructed and reconstructed organismal life cycles embedded in particular ecological contexts. Species are collections of organisms that use the same resources in the same way in their development. I do not discuss whether on this view species are epiphenomenal or not.

This organism-centred approach is historical insofar as it takes species to be understood as a recurrent succession of organisms; it is constructive insofar as it denies that the environmental niche and the form of species is preformed but is instead the outcome of ontogenetic and phylogenetic processes of organisms in the world. A phenotypic trait of species $A$ may cause changes to its environment. These changes may provide resources that are used in the natural construction of subsequent generations of species $A$. These changes may then affect the phenotypes and genotypes of organisms within species $A$. For instance, a phenotypic trait of beavers is that they build dams. Dams change the beavers’ environment by changing the depth and course of the river in which it is built. The dam may cause the water to pool into a small pond. This provides a new resource that the beavers which built the dam, as well as other organisms (e.g. plants, birds, fish, newts), may use in the construction of their environment. The dam and the pond may be inherited by later generations of beavers thus affecting the resources available to them, as well as other organisms, for the construction of themselves and their niche.

This historical-ecological perspective holds that a species is not best understood using Mayr’s notion of species as a protected gene pool maintained by a stable environment. Instead, a species is ecologically embedded within a dynamic environment. A species is ecologically embedded insofar as its situation within the environment is the result of interconnected relationships, e.g. relationships of inheritance, interactions with conspecifics, learned behaviours, and relationships with other resources within its ecological niche such as prey and predators, trees, lakes and rocks. According to Taylor, the ecological structure (of species) has a history.
To say that the ecological structure has a history ... [is to say that] it changes in structure and is subject to contingent, spatially located events, while at the same time the structure constrains and facilitates the living activity that constitute and ecological phenomenon in its particular place (Taylor and Haila 2001: 526).

A species is the constructive outcome of a contingent historical sequence of past resources and relationships.

Rather than being understood primarily as groups of interbreeding organisms that share a gene pool, this alternative perspective allows us to understand species as sequences of dynamic ecologically embedded populations that share similar resources in constructing and reconstructing themselves generation after generation. On this view, the shared gene pool is one of many resources the species uses in its contingent historical construction and reconstruction over each generation.

Some members of some species may hybridize or horizontally transfer genes across species boundaries. They may utilize the genes acquired from the gene pools of other species. Although not widespread, there is much evidence within zoology, botany and microbiology of regular hybridization and non-vertical gene transfer between organisms of different species, for example ducks (Mallet 2005), flowering plants, and grasses (Stace 1975). Rather than viewing hybridization, as the BSC does (Mayr 1992), as a detrimental breach of species boundaries threatening species separateness, the organism-centred view describes hybridization as providing another resource that may be used by a species’ members in their self-construction. If we use the metaphor of heterogeneous construction to reinterpret the conception of species, we can conceive of the permeability of species boundaries as allowing organisms access to a wider pool of genetic resources. For instance, hybridization has allowed members of one South American species of butterflies (*Heliconius cydno*) to mimic the phenotypes of the members of two different species (*Heliconius sapho* and *Heliconius eleuchia*). This means that it allows *H. cydno* butterflies to avoid being eaten by birds that have developed an aversion to eating the foul-tasting *H. sapho* and *H. eleuchia* (Mallet 2005, 2007). The colour pattern of these butterflies is the result of a number of resources including the behaviour of
predators, the rate of development of the structure of scales on their wings, the expression of pigment, and their genes (Janssen, et. al. 2001: 415).

According to the organism-centred view of species, the co-construction of a species’ members and their environment is the result of the interplay of a wide variety of resources. These resources may take many forms, for example the genetic inheritance from the offspring’s parents, horizontally transferred islands of pathogenicity between different species of bacteria, a female insect’s choice of oviposition for the environment of her developing larvae, disease resistance of the mother that is supplied in her milk passed on to her own (or another’s) infant, the acquisition of symbionts and intestinal bacteria after the infant’s birth from its parents’ regurgitant or faecal matter, the ecological inheritance of burrows, nests or treeless moorland constructed by previous generations, or the transfer of behavioural patterns within a community (e.g. nut burying and retrieval in squirrels, foraging behaviour in finches, the wagglendance of honey bees). The members of one species may also utilize resources from different species. For example, the tadpoles of spadefoot toads (*Scaphiopus multiplicatus*) begin life as omnivores, but when they ingest the thyroid hormone of their main food source, various species of algae and pond detritus (containing bits of shellfish), they develop a more carnivorous morphology. The thyroid hormone affects the prey as well as the predator. *S. multiplicatus* has evolved in such a way that the ingestion of this hormone contributes to the development of a carnivorous morphology allowing it to feed on small animals such as shrimp (West-Eberhard 2003: 111).

The members of a species are the organisms which share similar resources, a similar habitus, a similar capacity for sustaining themselves and a repeated generative process. Whereas the BSC assumes that the members of a species form a cohesive unit because they share a gene pool, the organism-centred view redescribes species as a contingent succession of individual organisms each of which reconstructs itself within its life cycle.
Taking the organism-centred view and its dissolution of the dichotomous thinking which separates form from matter, biology from culture, and nature from nurture has significant implications not only for the so-called biological concepts of homology, analogy, and species, but also for those which have been separately partitioned as the so-called social scientific concepts. In Chapter Five, I consider what effect this view has on the various conceptions of race. Historically, “race” has been used to group people on the basis of many different kinds of criteria, e.g. their morphology, religion, cultural heritage, geographical origin, language, and more recently, genes.

To avoid the racist thinking based on the preponderance of theories available at the time, which held cultural differences to be the result of pre-determined factors in one’s biology, Franz Boas (1940: 65) explicitly separated conceptions of race into the “biological” and the “cultural.” Conceptions of race have been traditionally grouped into two different categories depending on whether they employ criteria from the putatively natural sciences (e.g. morphological, genetic, biomedical) or the putatively social sciences (e.g. cultural, behavioural, familial). The dichotomy of the natural scientific-centred race conceptions and the social scientific-centred race conceptions often results in one set of criteria being privileged over the other. Within different conceptions of race there have also been suggestions that there is interaction between what is considered natural and what is considered social. An interactionist conception of race holds that humans possess characteristics of two distinct kinds—cultural and biological—that interact with one another. So the cause of racial features of human populations is understood in terms of percentages, e.g. racial characteristic X is 30% biologically and 70% sociologically caused. This means that 30% of the differences within members of a population are due to biological effects and 70% due to sociological effects. These are two different causes of the variation within populations—not within individual organisms. The interactionists using this kind of statistical distinction maintain the
ontological distinction between environmental and biological causes as separate and independent sources of racial differences.

Boas separated the biological from the cultural in order to avoid the racist conclusions of his contemporaries who purported to show that racial differences are correlated with biological differences (e.g. differences in intelligence or athletic ability). Such worries still arise from publications such as *The Bell Curve* (Herrnstein and Murray, 1994). However, as Tim Ingold (2001: 260) argues, what is incorrect about making such conclusions is not that race or culture may have a biological basis. Biological factors such as nutrition, mode of living, environmental distresses caused by aridly or frigidly inhospitable climates, the isolation from other people in rural communities, or the following of a vegetarian diet on the basis of one's religion are widely considered legitimate contributing causes of cultural differences. What must be avoided is the racist implication that arises from the attribution of “cultural characteristics to the influence of genetic inheritance” (IUAES 1996: 19-20, as cited by Ingold 2001: 259). What is incorrect is not the use of biological factors to understand cultural differences *per se*, but rather conceiving of those biological factors as genetically inherited. The problem with thinking that cultural characteristics are genetically inherited lies in conceiving of one's genetic inheritance as causally most important and cultural characteristics as being simply the result of the unfolding preformed program contained in a person’s genes. This is not to say that people do not inherit genes from their parents; obviously they do. But genes do not contain a pre-existing program which specifies the racial form of humans. Rather, they are stretches of DNA that are resources used by the organism within its ecologically embedded developmental process of construction.

According to the organism-centred perspective, the form a human being takes is dependent not on the preformed code contained in her genes but rather on her own self-organized development. The organism-centred view conceives of the biological as including a whole range of factors, including nutrition, behaviour, mode of living, and ecology rather than just genetic factors. This perspective takes inspiration from Ingold’s (2001,
conception of humans as “organism-persons” making themselves within their world. Humans are not organisms plus culture or organisms plus social interactions or organisms plus language ability—humans are organisms without remainder.

Considering human organisms from this point of view means that our putative cultural, biological, and behavioural aspects are all aspects of our being organism-persons. Humans, like other organisms, are understood in terms of their mode of living or habitus. A human-organism’s habitus within a particular ecology includes various aspects of how she lives, e.g. her racial and gender identity, language, religious and political beliefs, practices and rituals which affect methods of slaughtering or cooking animals, farming, land ownership, lending schemes, marital customs, familial groupings, etc. The conception of an organism-centred human habitus, or one’s situatedness within the world, is not one which has been clearly articulated in the West. But the concept of *tahna*, as it is used in southern Thailand, comes close. *Tahna* refers to “the functional cultural capital of each person and expands in a close-knit way into community culture, varying with the forces of nature and of power base in a correlation of circumstance, place, and time” (Pongpai boon 2004: 10). In this chapter, I use Ingold’s conception of humans as organism-persons to defend an alternative conception of race which does not separate the natural and social aspects of humans. This view combines Ingold’s conception of organismal personhood with Taylor’s conception of heterogeneous construction.

The organism-centred view is an alternative to a preformationist perspective of race which sees characteristics and behaviours as the unfolding of pre-existing information contained in the genes passed down from one generation to the next. Within discussions concerning the concept of race, this preformationist view takes the form of the widely held Western conception of race as determined by one’s parents. That is, we “assign people to races in a way that is governed by the rule: if your parents are of the same race, you’re of the same race as your parents” (Appiah 2006: 364). But this is an incomplete notion of race. There is much that is not included if one restricts one’s criteria of racial membership or identity exclusively to
ancestral relationships. These do not provide us with any information about familial relationships apart from reproductive ones. For instance, they do not tell us whether parents live in close proximity to offspring, live halfway across the world from one or more of their offspring, whether parents and offspring live in families with steps, adoptive children, unrelated friends or partners of one or both parents, or have even met one another. Using ancestral relatedness as the crucial criterion of racial membership or identity between the race of the parent and offspring is thought to pick out a direct route of inheritance and therefore of morphological and cultural characteristics. This relies on a preformationist conception of race as contained within one’s genes and transmitted from parent to offspring. Kwame Anthony Appiah (2006) highlights how this conception is based on a view of race that is “essentialized” or determined. This view takes the fact that children inherit their genes from their parents as evidence that racial identities are passed on within this genetic inheritance. Relying on purely genealogical or genetic criteria for race membership and identity unjustifiably privileges ancestral relationships over all other kinds of relationships. Fixing one’s racial identity in one’s genealogy relies on viewing ones’ genealogy as the preformed source of ones’ racial characteristics that exists prior to one’s life. This is a preformationist conception of race that explains racial continuity between generations as ensured by the identity of genes in parents and offspring.

The organism-centred view offers an alternative to this preformationist notion of race. According to this alternative, our identity is not pre-determined by our genes or morphology, and does not pre-exist in the environment—it does not exist prior to our life in the world. We are embedded within the world that we construct ourselves and in the histories we share. This view brings together the heterogeneity of self-construction from Taylor with a sociohistorical conception of race from W. E. B. Du Bois (1897). This results in understanding racial identity as a process of development within a web of relationships with other human organisms who share a common history and similar problems, as well as different genetic and extragenetic resources that may include but are not restricted to
one's parents, culture, religion, language, or way of living within a particular ecology.

Racial identity, like the other concepts discussed, is the outcome of heterogeneous self-construction. Unlike the other concepts, this construction centres on the self-interpretation of human organisms themselves. A human organism self-reflectively constructs her racial identity utilizing and interpreting the different resources available to her, including her genetic, developmental, familial, cultural, geographical, community, and political resources (amongst others). This means she is responsible for both the organization of resources in constructing or reconstructing her identity and also for choosing and interpreting what contributes to her identity. This does not mean that race is an inevitable source of identity. An individual may choose not to identify herself with any racial group. However, if a person does, she uses various resources which may include her morphological features, familial relationships, and community relationships to form her identity. She may choose to straighten or plait her hair, participate in community groups, listen to a particular form of music, speak the language of her parents or adopt the vernacular of her peers. She may have her mother’s hair, but this does not mean that she necessarily identifies herself in the same way her mother does when it comes to her racial identity. Information about a person’s race does not pre-exist within her genetic information inherited from her parents. It is not pre-determined by her genes; neither does it pre-exist in her morphological traits—it is self-made. A person may have some of the same morphological traits as her parents but this does not necessarily mean that she has the same racial identity as they or her siblings have. This is because the physical similarity or identity of a person’s morphological traits or genes to those of her parents is not equivalent to her personal racial identity.

Not only does an organism-centred view explain the similarity between parents and offspring in terms of their contingent use of similar resources, e.g. similar genes, similar traits, similar development, and similar relationships with other people or organizations used to construct their own racial identities in similar ecological contexts, it also provides a
way to understand multiraciality. Instead of relying on conceptions of race that demarcate race in terms of “pure lines,” this view conceives race without assuming identity is homogeneously experienced. In focusing on the individual as the centre of his or her own racial self-ascription, it easily accommodates such identities as discussed by Linda Alcoff’s (1995) in “Mestizo Identity.”

What is considered a significant identifier of one’s race is what is thought by a particular person or group at a particular time to be indicative of race. The attempt to fix a definitive set of either natural scientific or social scientific criteria for race fails to recognize both the self-interpretation involved in the construction and reconstruction of racial identity and the changeability of racial identity over time. Racial identity is not static. Its construction is a continuous process that does not stop. Self-identification and recognition of a person’s race may change depending on where one lives, e.g. which country one lives in or visits, the local beliefs and activities of people within local and surrounding communities, and histories. Racial identity is a continual construction built on what and who came before. A person’s identity undergoes continual construction over her lifetime and depends on the changing resources and relationships which contribute to her self-identification.

The arguments within each of these chapters share the common philosophical perspective of the organism-centred view set out in Chapter Two. However, they may each be taken as stand alone arguments that do not depend on accepting the arguments set forth in the others. This overarching perspective provides a philosophical alternative to those based on metaphors of ontogeny as the unfolding of information contained in the genes and evolution as the environment’s moulding of organisms. However, it is possible to use different perspectives to understand different aspects of the natural world. One may choose to accept some but not all of my reformulations of the concepts of homology and analogy, species, and race. One might continue to use perspectives employing these preformationist metaphors for some while make use of the organism-centred perspective for others.
CHAPTER TWO

Kantian Origins of the Organism-centred view

2.1 ORGANISM AND ORGANIZATION

Our understanding of what constitutes an organism has been intimately tied with our understanding of organization from its initial dubbing by the plant morphologist, Nehemiah Grew:

Wherefore, the Organism of a Body, although it hath nothing to do, in the production of Life: Yet is necessary, that every Body should have its Organism, agreeable to the Species of Life, ... wherewith it is endowed. So as hereby to be fitted to receive from, and transfer unto Life, all manner of proper Motions and Impressions (Grew 1701, as quoted in Cheung 2006: 324).¹

The capitalized “Organism” refers to the natural disposition of a body to become organized. One recognizes his conception of organism as following an Aristotelian understanding of the organization of organic living beings as

¹ There are earlier uses of “organism” (the Latin “organismus” and “organismos”) in the second and fourth centuries, but these are not of interest for the purposes of this chapter as they do not refer to organic beings but instead to “playing an instrument” or “disharmonic” or “polyphonic voices” (Cheung 2006: 331-32). According to his comprehensive archival studies which include a series of letters between Lady Masham and Leibniz (1703-1716), Cheung uncovers the first instance of the uncapitalized “organism” clearly referring to an organic being. In this correspondence, Leibniz uses the French, “organisme” interchangeably with “organisation,” and the Latin “organismus” to identify an organized animal body. Interestingly, although Lady Masham wrote in English, she used a capitalized version of the French “Organisme” in her letters to Leibniz. This was three years after Grew’s initial dubbing of the capitalized “Organism” (Cheung 2006: 323-326).
the result of simultaneously formal and final causes. It is obvious that this particular conception of organism is antiquated when compared with ours today, however there is something in it that we retain—the notion that organization is ineliminable to our understanding of organisms.

The notion that organisms are organized beings is surely unproblematic. But, how do organisms become organized and what (or where) is the source of their organization are questions which are part of a long history of debates.

How organisms become organized during their development from zygote through their life cycle and how this form appears to be maintained from one generation to the next have been variously understood as either due to a gradual process over time of being formed by the action of a concentrated causal source of internal or external agency or the result of a preformed form which unfolds. Causal sources of the organization of organisms have been located in an internal form contained within an informational program within the genes, located outside the organism in the consciousness of an external designer, or in the selective forces of an environmental niche that carefully moulds the organism to fit it. More recently, a consensus has been reached that concludes it is both the information contained in the genes and the selective power of the environment which interact with each other to impart organizational form to the organism. These interactionists claim

the DNA and proteins carry instructions or a program, for the development of the organism; that natural selection of organisms alters the information in the genome; and ..., genomic information is ‘meaningful’ in that it generates an organism able to survive in the environment in which selection has acted (Maynard Smith 2000: 190).

In this chapter, I outline an ontological alternative to conceiving of the ontogeny of an organism to the adult form as acted upon from within it by the directing causal forces of the genetic program and from without by the selective power of the environment. In a nutshell, the view I defend conceives the organism not as the passive object of these internal and external causal forces, but as an environmentally situated self-organizing nexus of heterogeneous reciprocal causes. To clearly illuminate what this
means requires me to reveal the philosophical lay of the land traversed to arrive at this view. I do not have space for a complete exploration of the history of thinking about biological organization, so I will provide only a whistle-stop tour of the highlights.

In the first third of the chapter, I explore Kant’s view that the self-organization of organisms can be understood as a response to the debates between the opposing views of epigenetics and preformationism. This response relies heavily on Buffon’s contribution to seeing organisms as organizing themselves throughout their lives through the joint action of their organic molecules and the internal shaping of its moule intérieur. In this respect, Kant’s third critique, the Critique of Judgement (1790) is seen as picking up in some way where Buffon left off. It is here that he develops a novel view which incorporates aspects of both epigenetics and preformationism to form a teleological approach to biological organization. The generically preformed part Kant calls the “Keime,” (germs): the more epigenetic, “Anlagen” (dispositions and proclivities). The second third of my discussion centres on what Kant calls his “regulative principles,” their use in understanding organisms as self-directing natural purposes, and various criticisms and amendments to these provided by those studying physiology, comparative morphology, embryology, and cytology. The empirical studies greatly modified the Kantian idea of organisms as reciprocally causing their own organization. In the final third of the chapter, I move to discuss how this Kantian approach can be interpreted as a distant ancestor of the organism-centred views of Oyama (2000), Taylor (2001) and Moss (2006). I conclude by articulating the main claims of my own version of a neo-Kantian organism-centred view.

2.1.1 GRADUALLY ACQUIRED FORM

It has long been observed that different kinds of organisms have different forms and behaviours, and the forms and behaviours of parents are the same as those of their offspring. Foxes produce foxes and oak trees
produce oak trees. These observations have led to what I call the “folk theorem” of the generation of organic beings: like produces like. But what gives us this impression that like produces like? Sustained interest in this question is still palpable today from biomedical testing that attempts to explain how parents “pass on” certain favourable or unfavourable genes or phenotypes to their offspring, to what are the essential phenotypes (or genotypes) of members within a particular group, e.g. the Iroquois tribe. Today, this impression of like producing like still seems to demand explanation. How like produces like and, more particularly what (and where) the causal sources of this continuity of form are, are problems which affect the present day accounts (e.g. Mayr’s, Maynard-Smith’s, Dawkins’ and Dennett’s) as much as they did the ancients’.

How like produce like finds perhaps its earliest analysis in Aristotle’s *On the Generation of Animals*. Providing an answer to this question involves revealing the source of organic form and more specifically, the development of biological organization. In his discussion of the generation and composition of organic beings, Aristotle begins with the observation, “All which are produced by union of animals of the same kind generate also after their kind, ... if like, then their parents ought to have come into being in the same way” (Aristotle 2007: Book 1: 1). In this passage, it is clearly an explanation of this observation that like tends to produce like which Aristotle pursues. *On the Generation of Animals* is a delightfully entertaining record of his detailed observations and speculations on the copulatory and reproductive activities of different animals. His discussion of like producing like is focused in discussions of fertilization and early development of the *sanguinea* or “blooded animals.”

Based on these observations, Aristotle conceived of the organization of the embryo as gradually being formed over time through the cooperative activities of the formal, material, efficient, and final causes. He attributed the four causes to different bodily parts and fluids on the basis of their morphological differences and their contributions to reproduction. For instance, he describes the generation of offspring to be the shaping of the

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2 I discuss issues surrounding race and ethnicity in Chapter Five.
female’s catamenia (menstrual blood) by the male semen. The offspring is “concocted” or divided into parts (Aristotle 2007: Book 1: 19) by the action of the semen on the catamenia. The catamenia provides the material cause, whereas the semen provides the formal and efficient causes. Aristotle likens the activity of the semen to the action of rennet on milk in the process of making cheese. As the rennet causes the milk to coagulate, it splits into various parts (the curds and the whey). In like fashion the semen works on the catamenia forming it into the parts of the animal (Aristotle 2007: Book 1: 20).

Similarly, the generation of an offspring from its parents is not initially completely formed but becomes formed. The form of organic beings is not present in either the catamenia or the semen. The form of a living being is, therefore, not preformed but generated gradually over time. It is the result of the activities of the four causes over time. The material, formal, and efficient causes are present in the union of the semen and catamenia where they constitute the potential that, when combined, provide the organic impetus or life motion needed for the generation of the offspring (Aristotle 2007: Book 1: 20).

Only after their coming together, can the male semen provide the movement necessary to form the unformed matter provided by the female’s catamenia and providing the push forward to start the momentum needed for the continued growth of the organism. The formal cause gradually develops in the organization of the organism over time through the activity of the efficient, material, and the final causes which directs its development to the fulfilment of it. Like the other three causes, the final cause does not arise from outside the organism, but is present within the union of the catamenia and semen (Aristotle 2007: Book 1). The final cause directs development through the formal and functional requirements of organisms according to this teleological potential. It is that for the sake of which all the parts (organs, tissues, limbs) are produced.

In this sense the final cause is both the future end state the animal will attain as well as the present determiner of its organization dictating the order in which its parts are formed in its ontogeny. As Moss emphasizes, it
is the “fusion of formal and final cause within nature ... that shapes and animates materiality from within. Form and finality are inextricably linked in the living organism, and immanent in nature” (Moss 2008). As a result, an organism’s organization, growth, nourishment, and its mode of living in the world all make sense only when they are understood as activities which are both shaped by and directed to its final cause.

2.1.2 SOURCES OF FORM

Aristotle’s characterization of organisms as gradually acquiring their form through the activity of their four causes remained the accepted view until the mid-16th century (Pinto-Correia 1997). However, in the latter part of the 16th and into the 17th century, an alternative to this Aristotelian view arose. This view held that organismal form was neither gradually acquired nor inextricably linked with formal and final causes within the organism itself, but was preformed outside of the organism prior to its ontogeny. According to this preformationism, the source of generation and growth is due to the unfolding of a form which is already present prior to the organism’s organizational development. Instead of relying on the simultaneity of the formal and final causes as the source of form over the organism’s lifetime, preformationists separated the formal from the final causes of organismal organization in an attempt to locate the source of form from without rather than within the organism itself.³ Debates were heated between those who retained the Aristotelian view that organic matter began unformed and gradually acquired its form over time and those who thought that organisms were already formed—their form already existing prior to their life in the world.

The most famous of these preformationist views maintained that the source of all succeeding generations of new life is contained within the

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³ Moss (personal communication) suggests that much if not most of philosophy of biology after Aristotle can be understood in terms of later theorists either separating formal cause from final cause or attempting to bring them back together.
nesting of smaller and smaller organisms (in humans these are called “homunculi”). This was popularly conceived of as a set of Russian matryoshka dolls, each of which contains a smaller and smaller figure of the same kind within itself. Whereas some preformationists believed that the female ovum was the location of the encased homunculi (ovists), others believed it was the sperm (vermists). For preformationists of both kinds, reproduction did not entail the generation of new life forms. It was equivalent to opening up one doll to reveal a smaller doll inside. Strictly speaking, offspring were not generated by the union of their parents’ ovum and sperm (in the case of sexually reproducing organisms). All organisms were created at the same time—all humans were contained in Eve’s ova or Adam’s sperm (depending on whether one was an ovist or vermist), and each animal from the first of its kind in the Garden of Eden (cf. Pinto-Correia 1997). For preformationists, the final cause was located outside of organisms, conceived of as the intentions of the supernatural designer, God.

Although preformationism seemed to be the theory du jour of the 17th century, alternatives began to arise. One alternative that remained close to an Aristotelian view was the epigenetic view of William Harvey (1651). In his Observations on Animal Generation (1651) Harvey retains an Aristotelian notion of organic organization as unformed matter which gradually becomes organized over time. He understood this gradual formation to be the result of the action of a teleological force. This force was the directive activity of something similar to an Aristotelian final cause (cf. Grene and Depew 2004: 96, Moss 2006). In contrast to Harvey’s epigenesis, the epigenesis of Descartes relied on mechanical principles rather than either a teleological force or a vital force. Like Harvey, Descartes also drew on Aristotle’s explanations of reproduction in the sanguinea in On the

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4 In addition to his notion of teleological force, Harvey also used mechanical descriptions of organic functions such as his description of the heart beating in terms of the shooting of a gun. His appeal to machines was used to illuminate the internal purposes of organisms. He did not suggest that the heart’s beating followed the rules of mechanics (Harvey 1847: 31-32).

5 The notion of a vital force (life force) was employed by some epigeneticists as a unique force organisms possess by virtue of being alive. Harvey’s teleological force was, and continues to be frequently and inaccurately misconstrued as requiring a commitment to a vital force. Vinci and Robert (in preparation) make this point.
Generation of Animals. But whereas Harvey retained the notion of formal and final cause, Descartes discarded these, only retaining the notion of material and efficient cause. Using these, Descartes understood the gradual generation of organisms to be due to a linear series of mechanical movements of matter, one following the next.

To understand these movements mechanically meant to understand them as one would the events necessary to explain the action of playing middle C on a standard 88 key piano, i.e. if you depress the white key just to the left of the two black keys roughly in the middle of a recently tuned piano, this causes the hammer over the metal string beneath it to strike the string producing the sound of the note middle C. Descartes believed that organisms are machines which God constructs; however, because we cannot know what His plan is, all we can know is how they operate. For him, both physics and biology were given in terms of a unified theory of mechanics.

Because all movements (inorganic and organic) are explainable in terms of the motion of matter, the laws of mechanics were enough to explain the organization of organic as well as inorganic matter (cf. Gunderson 1964).

For Descartes, human bodies, like all other animal bodies, are machines. However, humans have minds, unlike animals. But because minds are not material, they are not explainable in mechanical terms. Unlike Aristotle's conception of the four causes as conjoined in the activities and development of organismal organization, Descartes' distinction between the material causes of the body and the non-material causes of the mind meant that mind and matter occupy ontologically distinct spheres. Humans are distinct from other animals in that they are the only minded animal. Whereas humans are machines plus mindedness, all other animals are merely mechanical automata (cf. Gunderson 1964). All change in organisms, including their growth and generation, is explicable in terms of the movement and change of position of matter articulated in the universals laws of mechanics. Descartes mechanical view meant all we can know is the local causes of motion (for Aristotle, the material and efficient causes) not universal causes (final or formal causes).

Although most theories of generation after Harvey and Descartes
were mechanistic they remained preformationist rather than epigenetic. In opposition to the growing popularity of the mechanist-preformationism position, Buffon (and others, such as Maupertuis) began to formulate mechanist-epigenetic theories (cf. Pinto-Correia 1997). In 1749, Buffon modified and extended Descartes’ mechanistic epigenetic view; he suggested that organic matter was made up of unorganized organic molecules. These organic molecules were organized by a kind of mechanical force, similar to the way crystals are formed. Buffon observed that crystals grow according to certain fractal patterns depending on their mineral composition. For instance, salt crystals are found in cubes and these cubes are composed of smaller cubes (Buffon 1749: 240). He believed that just as crystals were constrained in the way they form themselves, so too is the growth and generation of organic molecules which compose organisms constrained by the type of organism they generate (Buffon 1749: 243). For both salt and animals, like begets like. His mechanist epigenesis view held that organisms generated a succession of individuals themselves—reproduction was not merely the unfolding of the preformed homunculus. While Buffon denied that the cause of generation exists completely outside the organism, even arguing that the environment contributes to the gradual ontogeny of an organism’s organizational form, his notion of an “internal mould” functions in a similar way to Aristotle’s formal/final causes:

there exists in nature a general prototype in each species upon which all individuals are molded. The individuals, however, are altered or improved, depending on the circumstances in the process of realization. Relative to certain characteristics, then, there is an irregular appearance in the succession of individuals, yet at the same time, there is a striking constancy in the species considered as a whole. The first animal, the first horse for example, was the exterior model and the internal mold [moule intérieur] from which all past, present, and future horses have been formed. But this model, of which we know only copies, could alter or improve itself in imparting its form or in multiplying. The original imprint subsists in its entirety in each individual; and although there have existed millions of these, not one of them is exactly like another, nor consequently, like the model of which it bears the imprint (Buffon 1749: 352).

In the above passage, Buffon focuses his attention on both the form of organisms as well as their functioning and maintenance in accordance with
a particular mode of living. In this way, his view can be seen to approximate Aristotle’s interest in unifying formal and final cause within the organism’s own being rather than locating either externally. His conception of an internal mould (*moule intérieur*) also retains some elements of preformationism in claiming that it both gives shape to organic bodies and is present in all other organic bodies of its type. In like fashion, each individual organism belonging to the same species shares an internal mould.

### 2.2 Prerequisites for Knowledge and Experience of the World

Kant claims in his “Transcendental Analytic,” that all experience and knowledge is ordered by *a priori* principles of pure reason. These are concepts that organize and shape our experience of the natural world and provide the systematic structure necessary for scientific reasoning. He refers to the central *a priori* ideas as the “regulative principles of reason.” These include the thinking subject, God, and mechanism (Kant 1781/1787: A334/B391, A646/B674 and McFarland 1970: 26-30). Kant does not aim to argue for the concrete reality of these ideas. Instead, it is their analogical use that is important. Their ability to enable us to understand what we do not know by comparison with what we do know. Each of the regulative principles is an “analogon,” an ideal by which we can order our experiences of the world.

If ... we assume such ideal beings, we do not really extend our knowledge beyond the objects of possible experience; we extend only a regulative principle. For to allow that we posit a thing, a something, a real being, corresponding to the idea, is not to say that we profess to extend our knowledge of things by means of transcendental concepts. For this being is posited only in the idea and not in itself: and therefore only as expressing the systematic unity which is to serve as a rule for the empirical employment of reason. It decides nothing in regard to the ground of this unity (Kant 1781/1787: A674/B702).

These analoga can be defined simply as ideals whose prime role is to
facilitate reasoning by comparison (Kant 1781/1787: A631-A668, B659-B696). When we think about some entity or process, we do not know its real nature. What we can know, through our regulative ideas, is its relationship to other entities and processes within our experience. These regulative ideas unify our phenomenal experiences.

As to the first of the regulative ideas, Kant believed that our understanding of organisms as directing and organizing their own form is arrived at by reflecting on ourselves as thinking subjects who direct our actions as means to achieve certain desired ends. This reflection is possible only when we conceive of ourselves as thinking subjects which allows us to understand the activities and functions of organisms in comparing them to our own subjective agency. The second regulative idea, God, conceived of as the author of life, provides us with the notion of teleological force and furnishes us with a number of teleological why-questions (McFarland 1970: 25-36). According to Kant, these teleological questions would not be imaginable to us without the notion of God. Lastly, we utilize the regulative idea of mechanism whenever we explain things as mechanical by comparing our experience of objects in the world to a machine (e.g. how the parts fit together into wholes, how some causes regularly produce certain effects). For example, we understand the architecture of an oyster as a bivalve—two shells hinged together that open and shut, when we compare its composition to a simple machine.

These three regulative principles are transcendental ideas of reason which we use to order our experience and make empirical knowledge possible. They furnish an empirically justified and unified science by providing heuristics which enable us to formulate laws and generalizations which frame our observations. Without the regulative principle of the thinking subject we cannot understand the activities and organization of organic matter. Without the regulative principle of mechanism, there is no possibility of gaining empirical knowledge of the world through the Newtonian laws of mechanical interactions.

Each of these regulative principles of reason provides us with a way to formally order our phenomenal appearances. And only by organizing our
ephemeral phenomenal experiences can we have empirical knowledge of the world.

2.2.1 ORGANISMS AS SELF-DIRECTING NATURAL PURPOSES

Whereas in the First Critique Kant outlines the prerequisites for all empirical knowledge and the regulative ideas of reason, in the Third Critique he pays particular attention to our knowledge of organic matter. In the Third Critique, the Critique of Judgement (1790), he conceives of an organism as a self-organizing, self-directed and reciprocally caused natural purpose which shares a common generative capacity with other organisms of its kind. To unpack this statement of Kant’s view requires an explication of its main components: purposiveness, reciprocal causality, and common generative capacity. I begin with purposiveness.

According to Kant, our understanding of organisms is inextricably linked to our understanding of them as internally directed means (mittel) and ends (Zweck) of themselves. This view of organisms relies on the regulative principle of the thinking subject as an analogon for the directedness of the organism. Biological entities have a different causality to that of rocks and other inorganic substances, what Kant called an “internal purposiveness” (zweckmässige). This internal purposiveness is the organism’s directedness towards a telos, or final cause. In the section of the Third Critique entitled “Critique of Teleological Judgement” Kant considers the question, what is the “character peculiar to things considered as natural purposes” (Kant 1790: Ak. 370-76). He concludes, that if there are any natural purposes then organisms are.

Therefore in order for us to judge a body as a being, in itself and in its inner possibility, a natural purpose, what is needed is that all its parts, through their own causality, produce one another as regards both their form and combination, and that in this way they produce a whole whose concept ... could, conversely, be the cause of this body according to a principle so that the connection of efficient causes could at the same time be judged to be a causation through final causes ... Only if a [body] meets [these] conditions, and only because of this, will it be both an organized
and a self-organizing being, which therefore can be called a natural purpose (Kant 1790: Ak. 373-4).

Kant explains the self-organization of organismal growth by referring to his observations of organisms with birth defects and teratologies: “if birth defects occur, or deformities come about during growth, certain parts ... form in an entirely new way, so as to preserve [erhalten] what is there, and so produce an anomalous creature” (Kant 1790: Ak. 372). Kant understood the ontogeny of the form of these teratological organisms as attempting to conform to a particular end state (Zweck) through whatever means possible.

Kant was aware of the criticisms concerning the use of teleological explanations and their associations with natural theology and vitalism. To avoid the assumption that teleology must be connected with a transcendental plan or vital force, Kant restricts his notion of teleology as a study of ends, or (something akin to Aristotelian) final causes to screen off strong preformationism. His teleological view takes the determination of biological organisms to come from the organism itself over time rather than originating either externally from a master designer outside of it or internally from some preformed plan.

2.2.2 ORGANISMS AS RECIPROCALLY CAUSE AND EFFECT OF THEIR OWN SELF-ORGANIZATION

To say an organism is a natural purpose means that its causes and effects only make sense in light of its final products. We understand these as causes and effects only when we consider them as fitting into a unified plan of directed actions towards a final end (Zweck) or final cause. In organic beings cause and effect are mutually interdependent. The definition of “organized beings, is: An organized product of nature is one in which everything is a purpose and reciprocally also a means” (Kant 1790: Ak. 376) Organisms are organized in such a way that each of its component parts is ordered in relation to the others as simultaneously means and ends: “each part exists only as a result of all the rest, so we also think of each part as existing for the sake of the others and of the whole” (Kant 1790: Ak. 374).
As such, the causal connections in biology occur in reciprocal series rather than in the linear series as they are usually thought to occur in inorganic matter. Growth over time is understood as causally synergistic. But what does Kant mean when he says that organisms are reciprocally self-forming, and how are the causes of organic being different from those of inorganic entities?

Understood in terms of a purely mechanistic view of the world, causes are understood always to precede their effects. These effects may in turn be causes of later effects if and only if each cause is necessarily temporally prior to its subsequent effect. Machines possess what Kant refers to as a “motive force.” Kant argues that unlike machines and other inorganic matter which can be sufficiently understood in terms of linear causes, organic entities cannot be understood solely in terms of a mechanical (or efficient) causality as a linear series of causes followed by their effects. This is because organic beings possess both a motive force as well as a self-formative force.

Now it is entirely possible that some parts in (say) an animal body (such as skin, bone, or hair) could be grasped as accumulations governed by merely mechanical laws. Still the cause that procures the appropriate matter, that modifies and forms it in that way, and that deposits it in the pertinent locations must always be judged teleologically. Hence everything in such a body must be regarded as organized: and everything, in a certain relation to the thing itself, is also an organ in turn (Kant 1790: Ak. 257).

Inorganic and organic entities have different causal forces. A machine only has a motive force. Machines can neither propagate themselves nor compensate for missing parts. They cannot repair damaged parts. This is because the cause that produces a machine and its form does not exist within the nature of the machine itself. Machines gain their form and motive force from external sources while organisms have within themselves an internal formative force (as well as a motive force). An organism’s formative force “imparts to the kinds of matter that lack it (thereby organizing them). This force is therefore a formative force that propagates itself—a force that a mere ability [of one thing] to move [another] (i.e. mechanism) cannot explain.” (Kant 1790: Ak. 374).
organism’s teleological force means that it can propagate itself, heal damaged limbs or organs, and compensate for missing parts. This self-forming teleological force or capacity of biological entities cannot be explained using the standard mechanical understanding of linear causality which sees cause and effect as unidirectional. To do so amounts to a category mistake. Trying to explain biological organization in terms of linear causality misidentifies the direction of causality as linear when it is reciprocal. Whole organisms, unlike whole machines, are not understandable in terms of their parts and processes, without remainder. The purely mechanical view is inadequate because of the underlying assumption that both organic as well as inorganic wholes can be completely understood in terms of their material decomposition. But as Kant argues, nothing like a Newtonian view could be possible for living things. There cannot be a complete physical reduction for living things: “it is absurd for humans even to attempt, or to hope that perhaps some day another Newton might arise who would explain to us, in terms of natural laws unordered by any intention, how even a mere blade of grass is produces” (Kant 1790: Ak. 400). Because living things do not have the same ontological kinds of causes that non-living things have, we cannot fully understand the biological world purely by understanding it mechanically in terms of its material parts.

The circular causality of organisms that allowed effects to precede causes troubled Kant as it appeared to contravene the Humean principle of mechanical linear causation: the view that causes always precede their effects (and a view Kant himself endorses in the First Critique). Whereas the causality of inorganic entities is understood completely in mechanical terms as causes preceding their effects, in organic entities causality involves both final causes which direct the organization of organisms ultimately towards end states as well as mechanical causes of their proximate activities. An organism’s teleological force (a final cause) is both the end the organism strives for and the means by which it is directed to that end. As natural purposes, organisms are reciprocally effect and cause of their own self-organization (Kant 1790: Ak. 374).

This problem seemed to Kant a contradiction between two principles
each of which seems necessary and reasonable. Kant sought to resolve this antimony. He explained that the appearance of a contradiction between our notion of linear and reciprocal causation is only that—an appearance. When we use the regulative notion of the thinking subject as an analogon, we interpret the actions of organisms as being purposefully directed towards achieving a certain end. But, because our principles of reasoning are (only) regulative:

the concept of a thing as in itself a natural purpose is not a constitutive concept either of understanding or of reason. But ... it is a regulative concept for reflective judgment, allowing us to use a remote analogy with our own causality in terms of purposes generally, to guide our investigation of organic objects and to mediate regarding their supreme basis—a meditation not for the sake of gaining knowledge either of nature or of that original basis of nature, but rather for the sake of [assisting] that same practical power in us [viz., our reason] by analogy with which we were considering the cause of the purposiveness in organized objects (Kant 1790: Ak. 376).

A concept is constitutive if it applies to an actual (what Kant calls “noumenal”) relationship in the world—one of quantity rather than of a phenomenal quality. The knowledge we gain of the relationships that we compare using a regulative idea guides us in understanding our own phenomenal perceptions of the world. They are reflective insofar as they occur in our judging our phenomenal perceptions rather than constitutive of the actual (noumenal) world (Kant 1781/1787: A249-A250, B305-307). Therefore, we err in our use and consideration of these principles when we treat them as able to provide us objective principles about the noumenal world. If we regard these regulative principles as constitutive principles antimonies arise.

Kant explains that we are able to dissolve any seeming contradiction by showing that our understanding of organisms as self-directed towards their own organization are regulative ideas which give us understanding of organic being by allowing us to reflect in a certain way on our phenomenal experiences of the world. We make a mistake when we believe that our regulative principles of reason relate directly to the actual (noumenal) objects in the world and give us knowledge which is not mediated by our
phenomenal experiences. Kant cautions against this mistake.

Reason is never in immediate relation to an object, but only to the understanding; and it is only through the understanding that it has its own (specific) empirical employment. It does not, therefore, create concepts (of objects) but only orders them, and gives them that unity which they can have only if they be employed in their widest possible application (Kant 1781/1787: A643/B671).

These regulative “principles of pure reason can never be constitutive in respect of empirical concepts: for since no schema of sensibility corresponding to them can ever be given, they can never have an object in concreto” (Kant 1781/1787: A664/B692). As regulative ideas, they do not provide concrete explanations for the biological organization we perceive. This means that although we grasp organisms as purposeful, we can only explain their activities with mechanical laws of science. Whether Kant manages to do this, or whether amendments to his teleological and mechanistic perspective of the organism are needed, will be discussed below.

Kant solves this problem within a transcendental idealist framework. Whether we need to commit ourselves to this position in order to resolve this antimony of reciprocal and linear causation will be discussed later in more detail. Within the section “From the Kantian ‘Zweck’ to the von Baerian ‘Ziele’,” I consider the metaphysically simpler account of the relationship between the regulative principles and reality itself offered in my von Baerian revision to the Kantian view.

2.2.3 COMMON GENERATIVE CAPACITY

Kant refers to the continuity of form that we observe as like producing like in organisms of the same species or race over generations as “systematic unity” (Kant 1790). This systematic unity is the basic principle upon which natural science and classification is based. In his essay, “Of the different human races” (1777), Kant explains how organisms can be grouped

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Kant states this by saying that our regulative principles are present to our reflective, not to our determinate judgement (Kant 1790: Ak. 386-400).
together into classes (e.g. races or species) in terms of what he calls their “common generative capacity” (Kant 1777, 1790). An organism’s particular bodily form develops according to the generative capacity which is common to all of its particular kind. An organism in one generation of a species shares the same generative capacity to organisms in the previous generation of the same species. Kant argues that the continuity of form within individuals from one generation to the next is due to their sharing the same stock of germs (Keime) and the same capacities and natural dispositions (Anlagen) that together cooperate in the development of organs, limbs, and tissues within a particular set of ecological conditions.

The causes lying in the nature of an organic body (plant or animal) that account for a specific development are called seeds (Keime) when this development concerns a particular part of the plant or animal. When, however, such development only concerns the size or the relationship of the parts to one another, I call them natural predispositions (Anlagen). For example, in birds of the same species which can nevertheless live in different climates, there are seeds (Keime) for the development of a new layer of feathers. These feathers appear when such birds live in cold climates, but they are held back when they live in temperate climates (Kant 1777: 13).

This notion of a common generative capacity forms the basis of Kant’s generic preformationism. This is the view that all groups of organisms originate from a single ancestral stock of Keime and Anlagen. Generic preformationism holds that there is a flexibility of form—the actualization of a capacity for variation already immanent within each biological individual. Unlike the strong preformationists, Kant believed that the Anlagen guide and limit the Keime. Keime and Anlagen can be understood to constrain rather than determine an organism’s form of life. Rather than existing preformed within the organism or its ancestors, Anlagen can be understood to have a fertile adaptability or “Tauglichkeit.” Although Kant does not endorse the strong preformationist views of encasement, he does think that this potentiality of flexible development must be already present in the Keime and Anlagen shared by a species.

Neither chance nor general mechanistic laws could produce such matches [of morphology with environment]. For this reason, we must view this sort of chance development as preformed. ... [A]ny
possible change with the potential for replicating itself must instead have already been present in the reproductive power so that chance development appropriate to the circumstances might take place according to a previously determined plan ... or purposive cause (Kant 1777: 14).

The development of an organism’s bodily form from embryo to adult is the result of a generic set of germs and dispositions that are constant over generations. Rather than relying on a vital or Newtonian force as a source of biological organization, Kant relies on the purposiveness of the dispositions acting on the germs and organizing them gradually in ontogeny. An organism’s teleological force (final cause) exists immanent in the fertile adaptive potential of the dispositions and germs. The particular notion of a teleological force which directs organic development of form from embryo to adult Kant adopts from Blumenbach’s idea of a formative force (*Bildingstreif*). It is important to note that Kant’s notion of *Tauglichkeit* is quite dissimilar to the modern notion of adaptation in a very important sense. Kant dismisses outright the idea that races or species can acquire organic modification through their interaction with different environmental conditions—what we conceive of as evolutionary adaptation. For Kant, the flexible capacity of classes is the stock of *Keime* and *Anlagen* which directs its purposive organization. All changes and modification which are made to that individual and all its descendants must be within the original stock of *Keime* and *Anlagen*. Within the *Keime* and *Anlagen* is contained the developmental capacity for all changes in structure or function. Although Kant speaks of flexible capabilities, he believes that new species do not come from others. He did not accept that one species could transform into another. In this way, *Tauglichkeit* can perhaps be best understood as a fertile flexibility of form as it referred to the capability of organisms in different ecological situations to develop differently—depending on what other resources are available (e.g. the ability to grow a new layer of feathers).

What makes Kant’s approach so different from the current view of evolution by natural selection is that on Kant’s view, individuals cannot possess novel characteristics and there are no such things as random
mutations. Individuals cannot possess novelties because mutation or developmental perturbations cannot cause novelty. Nothing can be novel because the capacity for all variation and change which exists is already present in the original stock of Keime and Anlagen. All developmental differences among individuals within a species are present in the original stock. The original stock of Keime and Anlagen contains a wide developmental possibility space such that some organisms may develop certain morphological forms whereas others develop different ones. The other morphological forms which do not develop are still there in the possibility space of the Keime and Anlagen. For instance, the above mentioned ability for some birds of the same kind to develop an extra layer of feathers if they live in a cold climate exists as a potential but latent ability in birds living in temperate climates. The same stock of Keime and Anlagen could be differently instantiated in individuals within the same species given a wide range of environmental conditions. Although Keime are responsible for the different characteristics of different individuals within a species, they are only activated when there are external environmental forces which cause their development and their development is determined by the Anlagen. Morphological and behavioural variations among organisms allow them to “live in every climate and endure each and every condition of the land … these seeds and predispositions appear to be inborn and made for these conditions through the on-going process of reproduction” (Kant 1777: 14). The flexible capacities of the species were what organized the organism’s organs and structures purposively so that it was fit for a specific environment. Organisms which shared flexibility of capacities were related as members of the same species because they shared a similar generic form of biological organization. Kant’s generic preformationism rejects the view that organisms acquire their ability to change to fit itself to its specific environment. Generic preformationism allows change but holds that the ability of the animal to change depending on its environment resources is immanent within the organism’s purposive organization. Therefore, Kant does not believe that chance plays a part in the development of organic organization. He claims that development of
animals that seem to be perfectly fitted to the environments in which they are found can be explained in terms of their common generative capacity. The apparent fit of organism to environment is explicable on Kant’s view by reference to the organism’s generically preformed set of *Keime* and *Anlagen* which self-directs the development of the organisms’ morphological architecture, rather than its form being imposed from outside by the environment.

2.3 CONCEPTS OF BODILY ORGANIZATION: KANT’S SCHEMA, CUVIER’S EMBRANCHEMENTS, AND VON BAER’S TYPES

Offspring are like their parents because they share the same generative capacities. Kant understands the organization of these generative capacities in terms of a “common schema.”

So many genera of animals share a certain common schema on which not only their bone structure but also the arrangement of their other parts seems to be based; the basic outline is admirably simple but yet was able to produce this great diversity of species, by shortening some parts and lengthening others, by the involution of some and the evolution of others. Despite all the variety among these forms, they seem to have been produced according to a common archetype, and this analogy among them reinforces our suspicion that they are actually akin, produced by a common original mother. For the different animal genera approach one another gradually: from the genus where the principle of purposes seems to be borne out most, namely, man, all the way to the polyp, and from it even to mosses and lichens (Kant 1790: Ak. 419).

This common schema provides us with the means to understand why like produces like. Like produces like because they have a common original type or schema. However, it is not just the relationship between parent and offspring which is understood by reference to a common schema. Organisms of the same race, species or genus all share a common schema. Kant’s innovative notion of an original common type identified both the continuity of form over generations and the basis for biological classification. This notion began to influence the biological practice of his contemporaries.

Kant’s common schema might be thought of as the necessary tinder to
the sparks of the series of debates between the idealist Naturphilosoph Etienne Geoffroy Saint-Hilaire and the material morphologist, Georges Cuvier that ignited a revolution in comparative morphology and classificatory thinking. In these heated debates (1830-1840) Geoffroy and Cuvier each proposed what they believed to be the source of organic form, its organization in biological beings, and the continuity of form over generations.

Geoffroy believed that there was one universal or “unified body plan” which all animals have in common (Russell 1916: Ch. 5). The organization of animal form was the expression of one generalized, abstract, universal type. Similarity between the same parts in different animals was possible through what he called the “principe des connexions” (Geoffroy 1796, 1818). According to this principle, one could locate the same limb in two different animals in terms of their identical position within a universal body plan. Any differences in these parts were understood to be due to modifications of the universal body plan.

Whereas Geoffroy relied on a universal body plan to explain our perception of like producing like and the continuity of form in different animals, Cuvier believed form could only be understood in terms of the organism's conditions of existence. From his embryological observations Cuvier concluded that instead of Geoffroy’s one universal body plan, there were actually four fundamental arrangements of bodily organization or “embranchments” (Cuvier 1817, cf. Russell 1916). One of these four body plans is embodied in every organic being. His embranchments were the four ways parts (limbs, organs, tissues) of organic beings were found together in animals. Rather than Geoffroy’s emphasis on the structure and topology of organic architecture to explain animal form, Cuvier believed that an organism’s ontogeny constituted a coordinated set of actions towards an end state. For instance, an animal’s embranchment was correlated with its conditions for existence—the conditions required for the organism’s functioning (e.g. its respiratory organs, forelimbs and the texture of its epidermal layer) within a particular environment (e.g. aquatic, aerial, or desert). Cuvier emphasized the central organizing power of these conditions
of existence. In constituting a principle peculiar to natural history, ... the conditions of existence, [are] commonly styled final causes. As nothing can exist without the reunion of these conditions which render its existence possible, the component parts of each being must be so arranged as to render possible the whole being, not only with regard to itself but to its surrounding relations (Cuvier 1817, as quoted in Lenoir 1982: 62).

Although obviously distinct, I think that Cuvier's notion of embranchments can be gainfully understood as supporting both the Kantian understanding of organisms' continuity of form over generations as being the result of teleological causes in a common schema as well as his forebear in Buffon's view that the cause of organismal form was attributable to a deep architecture of the organisms' interior mould. Cuvier's approach to organisms as functional wholes fits with Kant's whole-organism perspective. In both, organisms were understood to be the result of internally directed teleological self-organization.

Von Baer's extensive embryological work integrated both the Kantian organism-centred view and Cuvier's four basic embranchments into his own comparative embryological work (cf. Lenoir 1982: Ch. 2 and 3). Although he followed Cuvier's approach to organisms as functional wholes in order to understand the positions of their limbs, organs, and tissues, von Baer's particular interest was in securing an empirical basis for his theory of organismal organization. Von Baer uncovered the origin of certain morphological similarities by comparing the embryological stages of a variety of different organisms, including the chick embryo. These embryological investigations provided him with the resources to explain the ontogeny of organisms in terms of their flexible development within a particular body plan. He observes of the chick embryos:

the younger the embryos are that we compare the more variation we find in the structure of essential characters which later affect the whole manner of life of the organism ... [It] is difficult to grasp how all these variations can lead to the same result and how, alongside of complete, well-formed chickens, there are not numerous cripples [teratologies] ... so it must be concluded that the differences somehow cancel each other out and that every variation, as far as it is possible, is conducted back to the norm (von Baer 1828: 147 as quoted in Lenoir 1982: 85).
Von Baer’s innovation was in deducing that the cause of the chicks’ similar arrangements of organs and tissues within different organisms at the same level of embryological development were due to their similar patterns of development. The reason why the chicks maintained their particular body plan despite numerous variations was due to the plasticity of their developmental pathways and processes which reliably “conducted” them to their goal of attaining a particular bodily arrangement (the chicken body plan). Instead of following Cuvier’s usage in calling the organism’s body plan an *embranchment*, von Baer used two terms that picked out the different aspects of the body plan: “type” and “schema.” Von Baer used “type” to refer to the organism’s body plan, and “schema” to refer to the becoming of the organism in its growth within that plan. Von Baer explains:

> In reality, instead of ‘type’ and ‘schema’ I might have used a common term expressing both. I have only kept them separate in order to make it obvious that every organic form as regards its type, *becomes* by the mode of its formation that which it eventually *is*. The schema of development is nothing but the becoming type, and the type is the result of the scheme of formation. For that reason the type can only be wholly understood by learning the mode of development (von Baer 1828, as quoted in Lenoir 1982: 86).

The type is a relational concept which holds between the different positions of the organs, membranes, and systems within the embryo. In an organism’s becoming, it forms relations between the different organs, tissues, and limbs of the embryo and regulates the order and direction of various events in the organism’s embryogenesis, (e.g. the organism’s polarity, that is, which side of the developing zygote becomes ventral and which becomes dorsal).

Von Baer uses type and schema to reveal the formative force driving the organism’s development over time to achieve its bodily organization. Von Baer’s understanding of the concepts *type* and *schema* follows Kant’s own notion that the development of an organism’s form is both driven by and ultimately attains the form of the common generative schema of its kind. But von Baer adds that organisms sharing the same schema also
share a similar ontogenesis. Their ontogeny may not be exactly similar but they may have patterns of development or organ systems (e.g. the same respiratory system, for example one with lungs or gills) which are common to them. He emphasizes the importance of embryological investigations as the source of our knowledge of organic form. It was only through the careful attention to the study of embryological development that von Baer was able to understand the interactions which occur between organ systems and their mutual ontogenesis within the organism, as a whole, as well as its unified directedness.

2.3.1 From the Kantian “Zweck” to the Von Baerian “Ziele”

Von Baer embraces Kant’s teleological view of organisms as natural purposes and marries it with his own embryological observations. He follows Kant in thinking that it is what the organism will ultimately become which directs the order of activities and the development of its form throughout its ontogenesis. He agrees that it is the purposiveness (zweckmässige) of organic wholes that directs their ontogenesis and not simply the gradual accumulation of new parts. Although von Baer followed the spirit of Kant’s teleo-ontological approach to organisms as self-directing their own organization, he revises it in light of embryological research. This more empirical understanding of organisms leads him to challenge some of Kant’s views. In particular, whereas Kant viewed the self-directedness or purposiveness of organisms heuristically, von Baer conceived these qualities as realistically constitutive of life.

Von Baer was particularly concerned with Kant’s notion that organic causes were circular rather than linear and how organic matter was directed towards its purposive finality. Von Baer thought biological wholes did not have ends (Zweck), as Kant thought, but rather biological wholes had goals (Ziele).

Nearly a century ago Kant taught that in an organism all the parts must be viewed as both ends and means [Zweck und mitte] at the same time. We would rather say: goals and means [Ziele
Now it is announced loudly and confidently: Ends do not exist in nature, there are in it only necessities; and it is not even recognized that precisely these necessities are the means for reaching certain goals. Becoming [ein Werden] without a goal is simply unintelligible (von Baer 1865: 231, as quoted in Lenoir 1982: 271).

This is perhaps von Baer’s most significant amendment to Kant’s teleological understanding of biological self-organization. He changes Kant’s ends and means (Zweck und mittel) to goals and means (Ziele und mittel). Von Baer believed that biological wholes were better understood in terms of their goals rather than ends because he viewed biological wholes (from his embryological work) as developing or becoming over time towards a goal. He argued that ends do not exist in themselves in the biological world; but developmental processes towards goals did exist. In addition, Zweck implied a kind of intentional act of the biological whole to which it is applied. Von Baer considered it to be imbued with a kind of vital agency which he wanted to extinguish in the strong teleological approach to organisms. Ziele, on the other hand, does not carry this implication. Ziele is a pre-conditioned result which arises or develops in much the same way as the zygote develops into the embryo and then into a foetus, juvenile, and adult. It is a necessary consequent of the integrated processes of developmental mechanisms, pathways, and networks within the organism as a whole throughout its lifetime. In making the change from Zweck to Ziele, von Baer sought to extract the last bit of vitalist-style talk from the original Kantian approach.

Why is this shift from Zweck to Ziele important for the organism-centred view? For von Baer, this shift was important because he believed that Zweck imported too much intentional agency into his teleological view of organisms. However, I think there is more to this than just a shift from ends to goals. This is a shift in the use of Kant’s regulatory ideas through which he believed we were able to understand biological phenomena. We can understand this if we go back and consider once again the regulative principles of reason, the analoga of the thinking subject, God, and mechanism. Whereas Kant helped himself to the analogon of the thinking subject when trying to understand organisms in terms of their ends and
means, von Baer seems to have made use of both the thinking subject as well as the analogon of mechanism. This amalgamated use of the thinking subject plus mechanism provides an innovative way of conceiving of the organization of organisms while eschewing the intentional agency reflected in the exclusive use of the thinking subject as analogon for organic being and God as the analogon of the teleological force.

Von Baer's swap of *Zweck* for *Ziele* can be understood as an attempt to avoid the seemingly ineluctable tendency of conceiving of organisms with the analogon of thinking subject as having the same intentional agency as human subjects that Kant's original approach perhaps invites. Von Baer's use of *Ziele* can be construed, not as the final intended end of a thinking subject, but purely as an immanent goal—or the endeavour of a teleomechanically construed organized being. What von Baer seems to have brought to the conceptual table is that we not only can use the Kantian regulatory ideas individually but also in combination. Connecting two regulative ideas together seems to be more profitable than to simply use one of the three at a time. In effectively combining the regulative ideas of the thinking subject and mechanism to explain the organized being of organisms, von Baer harnesses more explanatory value from this combined approach than the original Kantian view of organized being understood in terms of the thinking subject. Von Baer's adoption of *Ziele* over Kant’s *Zweck* extends our conception of organisms as internally directed by emphasizing the goal-directed becoming of organic beings manifest in their biological “type” and “schema.”

Taking this revised account of Kant’s view means that we conceive the purposiveness of organisms in terms of real phenomena of nature rather than simply heuristically. I build on this understanding over the remaining sections of this chapter and rely on it for the remainder of this thesis. This still leaves me with an obligation to resolve Kant’s antinomy of reciprocal and linear causation spelled out in section 2.2.2 “Organisms as reciprocally cause and effect of their own self-organization,” something I return to later. My discussion of reciprocal causation will take the form of a reconfiguration of the meaning of organic cause in each chapter of this thesis. The meaning
of reciprocal causation will become clearer when seen in use within biological examples and within the context of an applied organism-centred perspective.

2.3.2 Further extending the neo-Kantian view: contributions from embryologists and cytologists

Before moving on to extend the Kantian view, we might do well to quickly take stock. Kant’s original conception of organisms took the potential form of an organism as immanent in its *Keime* and *Anlagen*. The development of an organism’s form was understood in terms of the interactive activities of the *Keime* and *Anlagen* towards an end state (according to von Baer, goal). The *Keime* and *Anlagen* were conceived of as ontologically interdependent aspects of an organismal whole. Kant did not specify what the material substrates of the *Keime* and *Anlagen* were and whether they were localized in some specific entity or whether they pervaded the organism as a whole.

Those working within the conceptual framework Kant laid out were keen to uncover the material nature of the *Keime* and *Anlagen*. According to von Baer, to reveal the material nature of the *Keime* and *Anlagen* required investigation of the ontogeny of organic organization. To this end, his studies on embryology, discovery of mammalian ova, and his theory that there were different germ layers during development brought new insight into the possible locations and sources of the material structure and potentiality of the hitherto only theoretical notions of *Keime* and *Anlagen* (Lenoir 1982: 89). It was through his study of the mammalian ovum and the germ layers in particular which lead him to conclude that the potentialities (the *Keime* and *Anlagen*) for the existence of the whole organism were located within the centre of the ovum. The ovum itself was the centre of formative activity from which all growth originated.

Von Baer sought to explain the activity of the formative force throughout the becoming of an organism to its final goal state. To this end, he was particularly interesting in what occurred in organisms when their
ontogeny went awry. The unusual ontogenesis of teratological animals enabled him to contemplate how the purposive agency of the whole organism attempts to construct itself in accordance with its type as best it could despite hinderances. His investigations of teratologies, like his observations of the variation in the chicks, provided a new avenue by which he could explain organismal form—this time in terms of the malformed.

The study of teratologies was not new; both Kant and Blumenbach also observed them and speculated on the curious forms they developed. Kant took the malformations of these creatures to be the result of the interplay between the Keime, Anlagen, factors in the embryo’s intrauterine environment (including chemical, disease, and hormonal perturbations), and the developmental activities of the organism towards its goal state. During the organism’s early development all of these may become resources or obstacles which contribute to its embryogenesis. These factors can be variously interpreted as preventing or facilitating the differentiation of the organism’s cells, the growth of its tissues, the positioning of its limbs and head, and the temporal ordering of the growth of these features throughout its ontogeny. The extent of the perturbations and anomalies within the individual may be buffered by the organism’s own ability to redirect developmental pathways to accommodate these deviations. There may be malformations, omissions or duplications, environmental influences or missed embryological stages, and some version of an organism can still be produced. What von Baer observed in teratological animals was that they appeared to utilize other developmental avenues, resulting in morphological, topological, or other developmental aberrations.

Von Baer believed that teratologies showed that although an organism’s ontogeny was dependent on formal preconditions of existence and the specific organization of its type and schema, its developmental patterns and pathways, which it arranged in its purposive activity to attain this final type, varied greatly (Lenoir 1982: 120). Individuals affected by deviations in some of the biological resources necessary for the generation of a fully functioning individual according to its final type may still strive to develop as best they can whilst negotiating the deviations and anomalies
which impede the usual patterns of its development towards its final type. As an illustration of this, consider the congenital craniofacial defects that affect some Burmese kittens (Noden 1986, Sturgess et al. 1997). Taking von Baer’s perspective, we can understand the facial defects in the development of the kitten’s skull as a working out of a new developmental avenue within the kitten’s body plan in its attempt to create a viable well-formed kitten as best it can. If there is some lack, or often among this kind of teratology, an addition or impediment to its development, the developing kitten works with the resources available to it. The different structuring of the cranial bones, ocular structures, and palate mean that the musculature and tissues of the developing cat must fit in a coordinated attempt towards its goal state—a cat body plan that facilitates a well-formed, functional cat able to eat, breathe, purr, and meow, etc. This teratological development points to a more plastic notion of developmental patterns in all organisms. A teratological animal, such as the one just discussed, makes use of a space of ontogenetic flexibility trying to achieve certain goals, ultimately that of attaining a species-specific body plan. As such, the organism’s self-directedness is attributable to the coordinated activities of its interrelated parts striving towards this goal as a functional whole.

Although the founders of cell theory, Matthias Schleiden (1838) and Theodor Schwann (1839), largely agreed with von Baer’s framework, they rejected his reliance on what they took to be vitalist-sounding formative activities at the centre of the ovum. Unlike von Baer, Schwann did not think that there were formative activities or concentrated agency within the centre of the ovum. He thought that there was no localization of this force. Schwann reconceived von Baer’s formative force in terms of what he calls an “idea.” To avoid appeal to teleological forces or an ontological commitment to organic wholes, he provided a more mechanical account of biological organization:

the science of biology consisted solely in the study of order and arrangement of materials in an organic setting acting according to normal physical laws. In this view, life is not something resulting from order and arrangement: nor is it different from order and

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7 Von Baer and Kant both adopted their own notions of formative force or activity from Blumenbach’s own “Bildungstrieb.”
arrangement. Life consists in the order and arrangement of particles of matter *tout court* (Schwann 1839, as cited in Lenoir 1982: 126, italicization his own).

Schwann rejected the need to refer to emergent, and what he thought to be occult and vitalist, forces to explain our empirical observations of the natural world. Instead, he saw order and form as constitutive of biology and explainable in terms of standard laws. In contrast to von Baer’s belief that an organism’s type and schema exist only in it as a developing functional whole, Schwann argued that the organizing principles of the organism were present in all its parts (cells, tissues).

Although departing from von Baer’s conception of the organism as a functional whole, Schwann’s understanding of the organizing principles as distributed potentia throughout the organism remains consistent with Kant’s own conception of the common generative stock of *Keime* and *Anlagen*. But instead of an organism-centred perspective, Schwann’s perspective takes the cell, not the organism, to be the centre of organizational force:

Since all cells grow according to the same laws, the cause of development cannot in one case lie in the individual cell and in another be based in the organism as a whole. Furthermore, since certain individual cells, namely the fertilized egg, which also follow the general pattern of growth of all cells, can develop completely independently, we must assign an independent life to the cells (Schwann 1839 as quoted in Lenoir 1982: 129-30).

In addition to von Baer and Schwann, many other 19th century natural philosophers have contributed to and revised the original Kantian approach (cf. Lenoir 1982). This was not a static view. The study of comparative anatomy and developmental processes, especially within embryology, focusing on cellular differentiation, and cytology, reformed it.

### 2.4 Gene-centred Approaches

In the foregoing, I have outlined a Kantian understanding of the self-
directed development of organismal form and highlighted some amendments. These have all contributed to what can be thought of as a unified neo-Kantian view of organisms which takes the organism to be ontologically central to our understanding of their self-directing, self-organizing form over time. In order to justify the choice of an organism-centred view of organismal ontogeny over any other view, it will be necessary to articulate the genesis and uptake of some of the alternatives. The next few sections highlight the basic gene-centred approach and its underlying dualism which serves to validate the notion that genes are either the sole cause or the most important cause of an organism’s form and organization.

Although earlier work utilized microscopic observations, these were in some sense limited. In the 18th century, microscopes were still plagued with spherical aberrations and distortions of colour which compromised some observational data. However, in the early part of the 19th century dramatic improvements to the design of the microscope meant that there was a reduction in these spherical aberrations and colour distortions when looking through at high settings (cf. Schickore 2003). These innovations are what provided the reliable evidence needed for Meyen (1830), Brown (1831), Schleiden (1838), and Schwann (1839) to propose their cell theories. In particular, it was necessary for Schleiden’s thesis that all plant tissues are built out of cells and Brown’s discovery of the cell nucleus (cf. Wolpert 1995: 229).

These discoveries occurred just before the re-discovery of Mendel’s work on pea plants which focused on theoretically characterizing the source of continuity of form across members of the same species and from one generation to the next in terms of inherited “factors.” He distinguished between the factors that were inherited and responsible for the organism’s morphology and the morphological traits themselves.9 By the 1940s embryology was effectively sidelined by the newer science of genetics which

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8 Mendel’s studies on pea plants were rediscovered in 1900.
9 The distinction between the inherited factors and the morphological traits was formally made by Wilhelm Johannsen in 1909 when he distinguished the genotype from the phenotype. Johannsen himself was an anti-preformationist (cf. Moss 2007).
took genes rather than organisms as providing the causal source of organismal form (cf. Sapp 1987). Scientists utilizing microscopic data began to study the activities of cells and their nuclei in an effort to try to find where these factors were located and whether they had a physical vehicle or substratum which facilitated their dissemination from parent to offspring. Among these early cytologists was August Weismann. Weismann had originally espoused a version of epigenesis but later became convinced that the source of continuous form over generations was contained preformed in the germ plasm located in the nuclei (Weismann 1893). Weismann believed that Mendel’s studies (1856-1865) on the variation and inheritance of pea plants and the variation between individual organisms within the same species were evidence in support of his own preformationism (Maienschein 1986: 75).

Weismann sought to find a material substrate for Mendel’s factors. From his own research and study of cell biology and genetics, he found that organisms began as single cells with nuclei. He argued that the germ plasm is the material substrate which is continuous from one generation to the next: “the essence of heredity is in the transmission of a nuclear substance in germ plasm” (Weismann 1885: 65). The essence of organismal form was contained in the germ plasm within the nuclei and was the source of all directive activities out of which the organism is built.

Echoing the Mendelian distinction between inherited factors and the morphological traits of the organism, Weismann understood the passive somatoplasm of the material body as shaped by the active germ plasm. Keen to distance himself from his Lamarckian successors, who thought that external influences affected both the soma and the germ plasm and that both of these were heritable, he argued that external influences only affect the somatoplasm, not the germ plasm. Only the germ plasm was heritable. Underlying this distinction between the germ and the soma was a dualist metaphysics of organic organization and causality. His metaphysics of organic organization held that germ and soma were spatially distinct or “sequestered” from one another. They interacted, but in the way marbles interact with a glass vase that contains them. The germ in this sense was
contained in the body (either in the body of the cell or of the whole organism). The body was the passive vessel that weakly interacted with but also protected the germ cells from insult by the environment external to the skin of the organism (or extra-nuclear contents of the cell): “For the germ-cells are contained in the organism, and the external influences which affect them [the germ-cells] are intimately connected with the state of the organism in which they are safely contained” (Weismann 1891, as cited in Winther 2001: 525).

The separation of the germ from the somatoplasm underlies a dualist metaphysics of organic causation which takes the germ and the soma to occupy two distinct ontological spheres. This distinction between the passive soma and the active germ leads to Weismann’s reliance on the germ plasm as the primary causal force of organismal development. This view of causality as concentrated in one localized source was neither Aristotelian nor Kantian. It disposed of three of Aristotle’s four causes (i.e. the material, efficient, and final causes) and centres the causal organizing force (formal cause) firmly within the germ plasm, giving no substantive role to capacities, dispositions or common schemas. His dualism was nothing if not decisive. Weismann (1893) defined the somatoplasm as everything that was external to the germ plasm—this included the cytoplasm, organelles, membrane, and the whole of the organism as an extra-nuclear environment (Winther 2001: 519-520). There was the germ plasm and there was everything else. Nothing outside the germ plasm caused cells to differentiate. This was entirely determined from inside the cell nucleus. Once one identified the germ plasm, one had a complete answer to the question how like produces like.

Interestingly, this was not always the case. Rasmus Winther reveals that in Weismann’s earlier work (1881) he held a view which did not split the organism into two distinct parts. Weismann still believed that there was an external environment, but this was external to the whole organism. He defined the organism as internal to the external environment (Winther 2001: 520 ft. 7). But by 1893, he restricts what is internal to the germ plasm. The germ plasm was the sole source of organizational form and
variation. And it alone was ultimately responsible for determining the fate of cells:

a certain cell in a subsequent embryonic stage does not give rise to a nerve, and muscle, or an epithelial cell because it happens to be so situated as to be influenced by certain other cells in one way or another, but because it contains special determinants for nerve, muscle, or epithelial cells [in its germ plasm] (Weismann 1893: 134).

The resultant phenotypes of the cells were not based on self determination of the cells, cells were merely the passive bodies acted upon by the germ plasm. It was this perspective that lead to what is often termed Weismannianism. This perspective extended the strongest claims of Weismann (from 1893 onwards). It took the dualism of germ and somatoplasm to be evidence that any external influences that affected the somatoplasm were, by definition, non-heritable, as it was forever separated from the germ plasm, which was the sole material of heredity. This sleight of hand only succeeds in justifying Weismann’s distinction between the soma and germ by assuming it first, a vicious circularity for which Weismann should not be held culpable (Winther 2001).

2.4.1 THE INTERACTIONIST CONSENSUS AND ITS CRITICS

Although the spirit of Weismannian dualism may infuse the modern gene-centred perspectives, it seems unlikely that any of its advocates would support a purely preformationist or purely epigenetic view of organismal form (as characterized in the beginning historical sections of this chapter). However, this is not the case. It appears the specters of preformationism and epigenetics seem to haunt not only Kant, but many others who try to set up their view somewhere in the space between these two opposing perspectives. This bothersome duo has troubled even one of the founders of Modern Synthesis. Perhaps in an attempt to exorcize them once and for all, Ernst Mayr (1997) proposed that by combining parts of preformationism and epigenetics a more complete understanding of the organization of
organisms can be attained. He wagers modern genetics itself does just that. By offering a view that combines the best parts of both epigenesis and preformationism, it relies on DNA as the preformed causal source of information which unrolls over the gradual epigenetic development of the organism. Mayr claims that the idea of a genetic program which directs the organism’s organization and development relies on the belief that genes rather than anything else are the sources of causal agency (Mayr 1968: 379).

Modern genetics provides this union, as it distinguished between a genotype (the genetic constitution of an individual) and a phenotype (the totality of the observable characteristics of an individual) and showed that during development the genotype, by containing the genes for becoming a chick, could control the production of a chick phenotype. By thus providing the information for development, the genotype is the preformed element. But by directing the epigenetic development of the seemingly formless mass of the egg, it also played the role of the vis essentialis of the epigenesis .... Molecular biology removed the last unknown by showing that the genetic DNA program of the zygote was this vis essentialis. The introduction of the genetic program terminated the old controversy. The answer was thus, in a way, a synthesis of epigenesis and preformation. The process of development, the unfolding phenotype, is epigenetic. However, development is also preformationist because the zygote contains an inherited genetic program that largely determines the phenotype (Mayr 1997: 157-8).

This view is, as Mayr freely admits, preformationist in its thinking that an organism’s form is specified in advance of its ontogeny—arguably, before it is even alive. It is specified as soon as a zygote is formed. The ontogenetic process of the organism’s becoming formed throughout its lifetime is for Mayr, as it was for Weismann, irrelevant to understanding the cause of its form. The environment in which the organism develops within its lifetime is taken to be easily screened-off as non-heritable and not evolutionarily significant (it affects the somatic cells and not the causally salient germ cells responsible for the organism’s form).

Although not without criticism, a version of Mayr’s genes-plus-environment view, or as it is more commonly known, the interactionist consensus, is widely held (for criticisms cf. Lehrman 1953, Oyama 2000, Sterelny and Griffiths 1999, Lewontin 2001, and Moss 2001). In response to
the question how like produces like, an interactionist answers that it is not just genes but the interaction between genes and the environment which causes like to produce like. Opponents of this consensus argue that the ontogeny of an organism is not the result of interactions between the environment and the genes when these are conceived of as standing in two ontologically separate Weismannian spheres. Instead, it results from (the arguably embedded) relationships between the environment and the organism (Lehrman 1953: 345). The main criticism of the interactionist view that proponents of the developmental systems perspective have offered is that the dichotomy between the genes and the environment (as including everything but genes) is a false one (Griffiths and Gray 1994). Interactionism is therefore dead in the water as it relies on this distinction between the environment and the genes as two isolated entities which can then interact with each other. Extending the point originally made by Daniel Lehrman, the interactions or relationships do not exist between an isolated environment and isolated genes—or indeed, an isolated organism—but between the organism within its environment (Griffiths and Gray 1994).

2.4.2 Overemphasizing the Active Subject

In addition to the above, there are other philosophical problems which affect both the interactionist perspective as well as the Kantian perspective. These can be revealed by looking at the perspective from which both are based. Interactionists believe that an organism’s form is the result of the interaction between the informational program contained in the genes inherited from its parents and the information within the organism’s environmental niche. The genetic program actively directs and organizes the unfolding of the organism’s form throughout its ontogeny. The preformed program directs the form and organization of the organismal body through a set of instructions which regulate, trigger, and interact with
the information contained in the environment (Mayr 1997). The form of an organism is acted on from within by this directed unfolding of the preformed program and from without by the selective moulding of the environment. For interactionists, the transgenerational unity we observe as like producing like is the result of the same informational program which is passed from parent to offspring in the genes.

Interactionism draws on an implicit acceptance of the Weismannian dualism as it holds there to be two separate parts of the organism: the active subject which directs the ontogeny of organismal form (the genes), and the passive object of that direct action, (the body). Although not Weismannian, our Kantian approach to organismal self-organization is also committed to a distinction between an active subject and a passive object. We understand the organism as self-directing its own organizational form because we compare it to the analogon of the thinking subject. This way of thinking about the world puts emphasis on organisms as active subjects based on how we conceive ourselves as agents. We interpret our own activities as being caused by reasons to act. Oyama suggests that this amounts to understanding our own mental processes “by placing another ‘we’ inside us, the mentalistic ghost in the machine” Oyama 2000: 88, after Ryle 1949).

An illustration may help to explain what she means by this inner “ghost.” Yesterday, I ran down to the end of the road because I wanted to buy a pint of milk for my morning porridge; I thought to myself, the milkman still hasn’t arrived and I know the corner shop is open early. These reasons were the cause of my running to the end of the road. However, it would be a mistake to think that there is an inner me inside my head directing my actions.

This subjective perspective leads interactionists to posit an internal master controller (genes or genome) as the causal agent that directs the activities and ontogeny of the organism and an external agent directing the organism’s ontogeny externally (the environment or natural selection) as a natural stand in for the supernatural agency of God. In both cases, an agent of causal power is posited to direct the ontogeny of organismal form. This is
facilitated either by “virtue of the meaning of in-formation as ‘shaping’ and ‘animating,’ ... [it] promised to supply just the cognitive and causal functions needed to make a heap of chemicals into a being” or by the moulding of the selecting environment (Oyama 1985: 12). If we are interactionists, what we are doing when we think that the genetic program directs and orchestrates the ontogeny of the organismal form is we consider the genes to be an inner subjective agency located inside the nucleus (Oyama 2000: 87).

For interactionists as well as for Kantians, our experiences of the world are predominantly influenced by thinking of ourselves as subjects to the objects with which we interact. We understand the causes of our own actions and we cite the reasons which lead us to act, e.g. like my episode of running to get the milk. Our knowledge of the world is, inescapably, as agents. For Kant, this is a prerequisite for understanding the world. We understand organisms as purposive, by using our regulative principle of reason, the thinking subject. Our mindedness (conceived of as an invisible internal subject), the external source of subjective superpower (conceived of as the omnipotent power of a supreme being), and the contents of the world that are not us (objects, e.g. other people, animals and trees) are all projections of our own subjectivity—either outwardly or inwardly construed to understand ourselves and the contents of the world. In what strikes me as a particularly Kantian tone, Oyama argues that when we seek to understand the world, we do so by using ourselves as a template—we conceive of our actions to be the result of a super-subjective inner-me directing my actions. How I arrange the contents of the world, my understanding of continuity, causation, and order is, therefore, premised on my own experience as an active subject.

Oyama objects to the kind of dualist perspective perpetuated in the gene-centred and interactionist views, which separate subject and object, form and matter. She argues that “this separation of form from matter underlies and unites all versions of the nature-nurture antithesis that have so persistently informed our philosophical and scientific approaches to the phenomena of life” (Oyama, 2000: 1). What I have called the Weismannian
dualist perspective conceives of mind and body, form and matter, and nature and nurture as antithetical pairs.

Although she does not state her view as such, Oyama seems to both adopt and reject two of Kant’s regulative principles: the thinking subject and God. Used as a regulative principle, the thinking subject appears to be what Oyama refers to as our “mindedness,” “the ghost,” or the “invisible internal subject.” In what could be taken as a challenge to both the interactionist’s dualist perspective as well as the Kantian’s, she argues that this way of thinking “both exaggerates our role as detached subjects and denies our object-like [role]” (Oyama 1985: 76). This causes more than a little trouble for a Kantian. If our subjective perspective overstates our role as subjects and understates our objectivity, this distortion affects all understanding that is acquired using the thinking subject as a regulative principle of reason. But what can we do about it? If this regulative principle is based on reflecting on ourselves as thinking subjects, how can we get away from this arguably entrenched perspective of ourselves as embodied mindedness? And if the way we perceive the world is inherently as subjects, what does this mean for our knowledge of what we think are real objects and order in the world? In particular, how can we justify the veridicality of our knowledge of the world when our perceptions of the world are from an inherently subjective perspective?

If as Kant argues, our understanding and scientific knowledge of the world is only possible through our regulative ideas (of the thinking subject, God and mechanism), then how can we both screen off our experience of the world as thinking subjects and still use the analogon of the thinking subject to order our experience of it as well? In the last remaining sections I introduce some ways of dealing with this problem and suggest that one alternative is that we reconceptualize the regulative principle of the thinking subject.

2.5 TOWARDS A NEW UNDERSTANDING OF CAUSATION: THE ORGANISM AS A NEXUS OF CAUSES
Just before this revision to the neo-Kantian perspective can be laid out, there is some unfinished business to attend to. In what has come before, the problem of the ontogeny of individual organismal form has frequently been expressed alongside the unity of form from one generation to the next, as like produces like. This is not the result of an unintended conflation of ontogeny with phylogeny. It is true that the ontogeny of form in individual organisms and the phylogenetic unity of form over generations are traditionally understood using two different conceptual frameworks. The former understood in terms of the internal instruction of the genetic program and the latter in terms of the external moulding of the environment which selects over generations of organisms. Following Oyama, I argue that this distinction is artificial and does not represent any real causal separation that enables us to isolate the causes of ontogeny from the causes of phylogeny:

Development has conventionally been explained by internalist [genetic] models and evolution by externalist [selectionist] ones. But developmental constancy is no less a product of (systemic) interaction than is variation. In like manner, lability ... [or] variability is not less (interactively) systemic than is constancy (Oyama 2001: 188-9).

Oyama denies that the dualism of internal and external causes, the division between ontogenetic and phylogenetic causes which they underlie, and the dichotomy of environment and genetic causes on which interactionism is based, exists.

Taking Oyama’s anti-dualism to its extreme, I claim that what interactionists endeavour to pick out with their talk of the dual causes of genes and environment is not ontologically divisible. These causes do not exist independently of one another, but only count as causes within the whole functional-developmental perdurance of an organism. In the foreword to the 2000 edition of the *Ontogeny of Information*, Lewontin emphasizes the potency and centrality of this anti-dualism in Oyama’s perspective:

Without organisms there may be a physical world, but there are no environments. In like manner, no organisms exist in the abstract without environment ... organisms are the nexus of external circumstances and DNA molecules that make these physical circumstances into causes of development in the first
place. They become causes only at their nexus, and they cannot exist as causes except in their simultaneous action (Oyama 2000: xiv).

To this end, Taylor (2001) takes up the baton from Oyama, insisting that we cease assuming that the causes of transgenerational continuity and ontogenetic unity can be parcelled out neatly into two separate ontological boxes. He suggests that instead of setting up dichotomous pairs of causes, we would do better to “consider, instead, what would follow if those [causes] were to be explained as contingent outcomes of ‘intersecting processes’” (Taylor 2001: 313).

Taylor echoes Oyama’s criticism of the distinction between subjects and objects and the overemphasis on the active subject. He suggests that understanding the world or the organism in terms of the active subject trades on the assumption that there is one “concentrated” source of causal agency—located in our genes. But concentrating causal agency in one source does not sufficiently represent the nature of causation. Taylor sets out his heterogeneous view of the self-construction of organisms, arguing that there are:

many heterogeneous components linked together which implies that the outcome has multiple contributing causes and thus there are multiple points of intervention or engagement that could modify the course of development. In short, causality and agency are distributed, not localized. Moreover, construction is a process ... components are linked over time (Taylor 2001: 316).

This view substitutes single “concentrated” causes of organismal organization in preference for causes that are “distributed” over space and time. What does it mean to say that an organism constructs itself from heterogeneous causes; and that these causes are distributed? It means that the organism uses different components—genes, proteins, cytoplasmic structures and organelles, metabolic pathways, sources of food (photosynthesis, nutrient cycle, particular kinds of vegetation), learned behaviours, other species, such as predators, prey, branches, leaves, lakes, mountains—as causal resources in building itself over its lifetime. Its self-construction consists in linking certain components of its neuro- logical, cellular (or ecological) development to other components in space and time.
throughout its ontogeny. Components by themselves do not constitute the causes of an organism’s ontogeny; it is only their linkage over time and space which makes them the causes of its ontogeny (Taylor 2001: 316). This series of linkage events and processes is not specified in advance of the organism’s ontogeny, but is a result of it. These contingent outcomes of developmental processes have a history. They have an ontogeny that is dependent on what has come before. This view ties back into Oyama’s; she states that these linked events are “identified by reference to the organism and may emerge only through its activity ... they exist neither in the head nor in the surroundings. They are constructed during an interactional history” (Oyama 2001: 189). Organisms construct their form over time depending on responses in earlier stages of their ontogeny. These responses and their effects on the organismal form then affect later stages of the organism’s ontogeny. Which resources are used as causes and how they are used are determined through the ontogenetic activities of the organism.

Whereas Kant maintained that organisms are means and end, cause and effect, the subjective agents directing their own existence, Taylor and Oyama seem to hold a modified Kantian view in taking organisms to be both the necessary subjects that construct themselves throughout their ontogeny as well as the responsive objects of this constructive process. The construction of an organism’s form is therefore not concentrated just within the organism’s Keime and Anlagen, but is both temporally and spatially distributed among the contingent resources available and dependent upon how these resources were linked in past stages of its ontogeny or in the lifetimes of its parents or littermates.

2.5.1 THE ENVIRONMENTAL EMBEDDEDNESS OF ORGANISMS

This chapter has followed two questions which have occupied thinking on biological organization: how do organisms acquire the form and organization they do, and how do parents produce offspring like themselves. However, criticizing various solutions to these questions, tracing Kant’s own
solution, and evaluating later neo-Kantian perspectives are not the ultimate aim of this chapter. These have been necessary to uncover the conceptual ground (regulative ideas, underlying assumptions about preformed and informed form, and the many dualisms (of subject/object, passive/active, genes/environment, internal/external) on which understanding of the causes of biological organization have been based. Now that this conceptual ground is exposed, I wish to till and turn it over before planting the initial seeds of my own solution. The philosophical writings of Ingold (2002, 2004), Moss (2001, 2006, 2008), and Wheeler (2005) have enabled the cultivation of my revised organism-centred perspective.

My perspective reconstructs the Kantian view of organisms as self-directed and self-organizing in terms of their “situatedness” within their environments. To say an organism is situated means that its self-organization, ontogeny, and all its activities according to its mode of life are dynamically embedded within its environment. In this sense it is an artefact of the language that organism and environment are two separate terms. To grammatically identify this embeddedness it is perhaps better—if linguistically unlovely to talk of the organism-environment.

Talk of situatedness or embeddedness intentionally blurs the distinction between subject and object, mind and body. The nature of all organisms’ self-organization is in their “com[ing] into being with their particular forms and capacities and in which, through their environmentally situated activities, they condition the development of other organisms ... to which they relate” (Ingold 2004: 218). An organism’s becoming formed is not due (as Mayr 1997 argues) to the unfolding of genetic program as its vis essentialis. Instead, it is due to the organism’s way of living in the world, or to follow the trend for Latinate terminology, its modus vivendi (Ingold 2002).

As both Moss and Ingold independently suggest, the difficulties in articulating some of the concepts and kinds of things in the biological world as well as accurately accounting for the directionality of cause and effect discussed do not appear to be a problem specifically plaguing biology or even philosophy of biology. These difficulties seem to be symptomatic of what I
interpret to be an ontological error of judgement—that is, we have for too long mistakenly thought our perception of objects in the world correspond to our concepts of it, without asking why it appears to us this way. Although these transcendental questions of ontology often are considered in philosophy of mind or philosophy of language and form the bread and butter of traditional metaphysics, philosophy of biology seems to have been immune (or perhaps simply quarantined) from such ontological queries.10

2.5.2 A REVISED ORGANISM-CENTRED VIEW

For most of this chapter I have endeavoured to show what is biologically beneficial and valuable in the Kantian view drawing attention to how later perspectives drew inspiration from ideas outlined in the Critique of Judgment and “Of the different human races.” However, a strictly Kantian approach fails to be a sufficient conceptual aid in facilitating our understanding of organismal ontogeny and providing the heuristics necessary for reflecting on many of the scientific discoveries of the 21st century.

The question now to be answered is how can we best understand organisms as simultaneously means and ends, subject and object of their own organic activities and capacities? Is it, as von Baer suggests, through their goal-directed behaviour as organic wholes? If the purposiveness of organic wholes is manifest in the mutual interdependence of their parts, then thinking about organisms as purposes means thinking of them in terms of their Aristotelian final, formal, material, and efficient causes. Is this, as Kant argued, only possible by using the three regulative principles of the thinking subject, mechanism, and God (as teleological force)? Can we think about the nature of the structure and function of the parts of organisms to each other and to other organisms without relying on the regulative idea of the thinking subject?

10 I think this is a fair criticism of much of the Anglo-American discipline of philosophy of biology, however, it is not true of how it is treated elsewhere (cf. Gertrudis Van de Vijver et al. 2005).
To order and understand our phenomenal experiences of the world it would appear that we need some kind of regulative principles (metaphors or heuristics). However, to avoid misrepresentations and unjustified assumptions to creep into the fabric of our scientific theories, we must be vigilant in our choice of regulative principles.

I argue that Kant’s three regulative principles of reason are not enough to structure our phenomenal experience of the world. In assessing and extending Kant’s view, I suggest that in addition to the regulative ideas he proposes (thinking subject, teleological cause, mechanism) a further regulative idea is required to enable our understanding of organisms as ecologically situated and heterogeneously self-constructing themselves from distributed causes. Natural (heterogeneous) construction is a metaphor we can use to understand the organismal self-organization and as such can serve as an additional regulative principle. Its use as metaphor (or analogon) to structure our phenomenal experience of organismal ontogeny and phylogeny is epistemologically equivalent to the other regulative ideas of reason. It is a (normative) ideal which we use to order our phenomenal experience of organisms.

Like the other Kantian regulative ideas, it is prerequisite for our ontological and ontogenetic understanding of organismal organization. Adding natural construction as a fourth regulative idea of reason not only means that we have a further analogon by which to understand organic organization, it also means that we increase our metaphysics of causes. Specifically we add to our linear and reciprocal causality a dynamic, heterogeneous causation of multiply intersecting causes. As a regulative idea it adds to our biological ontology by enabling us to conceive of causality not just as reciprocal (as Kant did) but as arising from heterogeneous sources which are organized as causes by the organism itself. Whereas von Baer interprets the agency of an organism’s development as its striving towards a particular final goal state, using heterogeneous construction we can understand that each causal step and each causal link in the journey to that goal state is determined and orchestrated by the organism. This means, as philosophers of biology, we can reconceive what counts as causes
of the construction of organism-environmental complexes by identifying the contingent linkages this complex makes over space and time among a wide range of resources (including genes, cells, tissues, behaviours, trees, rocks, nests).

For Kant, the organism was defined in terms of as a closed set of interconnecting relationships which did not make use of external resources outside its skin. My own organism-centred perspective can be understood as opening up the organism. Instead of only allowing the internal stock of *Keime* and *Anlagen* to be the resources available to the organism in its ontogeny, I add to these the so-called external resources in the environment which the organism may also avail itself of during the course of its ontogeny.

With the addition of the new regulative principle of natural construction, my organism-centred perspective forms a real alternative to the current trend for conceiving the causes of organismal organization and phylogenetic continuity in terms of concentrated sources of organizing power. It provides a philosophical perspective which says that the causes are distributed among a number of diverse sources and organized as causes by the organisms themselves instead of as concentrated within the genes, genomes, or environments. Utilizing this additional regulative idea of reason enables us to reconceive a number of biological kinds and phenomena. For instance, instead of understanding variation as random mutation, by using the regulative idea of self-construction, we can understand variation as part of the adaptive resources the organism uses in directing its own organization—the organism may either buffer the random mutation or amplify it to serve its needs.

Our revision of a Kantian organism-centred perspective is not yet complete. Following the criticisms of Oyama and Taylor, we need to ask whether or not we can retain Kant’s notion of organisms as purposive, self-organized beings without falling afoul of the troubles of overstating their subjective nature and understating their situatedness within their environment and interactivity with their heterogeneous resources? We must outlaw any regulative principles which rely on concentrated sources of
cause (either in the genes or in the environment) that set up a dualism between that which is active and that which is passive. If we are to retain the thinking subject as a regulative principle, we need to begin by first reconceiving ourselves as embedded in our environment as situated-thinking-subjects. Our situatedness must then be retained in our use of the situated-thinking-subject as a regulative principle of reason. When used as an analogon to understand all organisms (including ourselves), we come to know them through our regulative idea as situated within an environment. This move brings our situatedness in the world to the fore. By doing so, we become aware of our own embeddedness within our environment allowing us to order and understand our phenomenal experiences of the world as reflecting this fact.

Having articulated the understanding and misunderstanding of the causes of organismal organization and the continuity of form for the bulk of this chapter, it is perhaps appropriate to explain the role of the second half of the hyphenated perspective I call the organism-centred view. My use of the word “centred” in this perspective is not what it might initially appear. It is not intended to indicate that it is the organism rather than the gene or the environment that has causal primacy. On the contrary, “centred” plays an ontological role. An organism-centred perspective is one which takes what I have articulated to be the situatedness of the organism-environment seriously. An organism is, in a very real sense of the word, a centre of dynamic, situated activity, or as Lewontin states, the “nexus” of causes. It is important to note that the situatedness of organism-environments is a situatedness in both time and space.\textsuperscript{11}

Over the next two chapters I cash out how this organism-centred view works in reconceptualizing our perspectives of the biological concepts of traits, homology, and species. In Chapter Five I discuss how this perspective might illuminate some of the debates surrounding the controversial concept of race. Chapter Three, which focuses on homology and traits, centres on an updated version of Kant’s idea of a common generative capacity—in particular, the conservation of a common body plan

\textsuperscript{11} This might seem obvious on reflection, as the organism’s ontogeny occurs over its lifetime, but sometimes the obvious needs stating to be brought to our attention.
and the capacity for a wide range of phenotypic and developmental possibilities. Whereas Kant understood this range of possibilities to lie in the original stock of *Keime* and *Anlagen*, I show that these can be interpreted in terms of a developmental space of possibilities or in West-Eberhard apt phrase, the organism’s “phenotypic repertoire” (West-Eberhard 2003: 146). In the following chapters I discuss the implications of the mosaicism of evolution, developmental recombination, the mixed ancestry of complex traits, and the abundance of intraspecific polymorphisms and polyphenisms for our understanding of homology, species, and race. Discussions in each chapter will centre on the purposiveness of flexibly responsive ontogenesis and the self-constructive activities of organisms using diverse resources.
CHAPTER THREE

Extending the meaning and reference of the concepts "Trait" and "Homology"

From early antiquity, it was observed that different animals share striking similarities among some of their traits. Whilst some were thought to be accidental similarities, others were believed to be the result of deliberate design for a specific purpose. For instance, many aquatic animals shared certain traits; such as fins, whilst animals occupying aerial environments tended to have wings, (e.g. butterflies, birds, and bats). Animals as diverse as blow flies, manatees, octopi, and crocodiles all had eyes. And the bone configurations of bats’, whales’, and humans’ forelimbs seemed to be arranged in a similar way to one another.

If the similarities of these traits were not accidental, then their presence in a wide range of animals required some kind of explanation—explanations that identified the reason for these similarities.

Whereas some traits, like the fins of aquatic animals, appeared to share a particular function—enabling the organism to propel itself through water—others, like the forelimbs of bats, whales, and humans, served different functions. If these anatomical structures appear to be the same structure in different animals even though they do not share similar functions, and are not accidental, what is the nature of their similarity?
The observed similarities among these diverse structures were due to the similar positional arrangement of the bones of their forelimbs and their relationships to the other bones of the skeleton. Rather than functional similarity, the reason for their similarity was their shared structural configuration.

This view led to the classical accounts of the comparable functional and structural similarities among organisms. In these, the reason for their similarities was frequently given in terms of their reflection of ideal forms (e.g. references to Platonic forms or Goethe’s idealist Naturphilosophie). The resemblance of individual traits of different animals to one another was explained in terms of their common cause—both traits were the approximated reflections of an ideal form or archetypal trait.

In 1843, Richard Owen provided the first formal distinction between these two kinds of comparative similarity—the functional similarity he called “analogy” and the structural similarity he called “homology.” He identified the cause of the similarity of analogous organismal traits in terms of the common functions they served: “Analogue: ... A part or organ in one animal which has the same function as another part or organ in a different animal” (Owen 1843: 374). Unlike analogy, Owen’s definition of homology contained no such causal explanation: “Homologue: ... The same organ in different animals under every variety of form and function” (Owen 1843: 349). Although his definition referred to homologues as the “same organs,” it provided no reason for this similarity and did not explicitly identify in what way two organs were the “same.”

Although intended to identify the identity of two organs, this notion of sameness was not meant to imply the material identity of two organs. Owen’s use of “the same” was somewhat ambiguous. He referred broadly to the structural or positional identity of organs. After Owen formalized the definitions of homology and analogy, attempts to provide a causal explanation of the similarity of homologues became widespread.

One such attempt was that made by Darwin. Darwin’s theory of descent with modification provided a causal explanation of Owen’s homology and replaced the classical notion of the similarity of corresponding
structures to an ideal form or archetype with that of a common progenitor. Homologues were the result of descent and modification from a common ancestor. And so the study of homology was the comparison of traits of organisms in terms of their similar correspondence due to shared ancestry. The wing of a bat and the arm of a human are homologous to each other because these traits were conserved over many generations of organisms and descended, with modification, from the same forelimb structure in the nearest common ancestor of both bats and humans. However, the explanation of the “sameness” of these forelimbs (i.e. the bat’s wing and the human’s arm) is not contained in the identification of their similar bone structure. It is not their structural correspondence *per se* but their historical continuity—the inheritance of a certain feature with modification from the same ancestor which is then conserved over generations.

This conception of homology as correspondence due to shared ancestry may initially seem an unambiguously straightforward conception of biological relatedness. However, little credence should be given to this initial impression.

Homology is a notoriously elusive concept to pin down (cf. Hall 1994 and papers therein). There has been, and continues to be, sustained debate over the meaning of homology, the nature of correspondence (e.g. whether homology is an all-or-nothing relation or whether it admits of degrees), and the units of comparison (e.g. whole organisms, traits as morphological outcomes, behavioural activities, biochemical mechanisms, developmental processes, or certain properties of traits).

Touching on each of these, the focus of my discussion centres on extending the meaning of homology from the neo-Darwinian all-or-nothing understanding of it. The all-or-nothing approach takes homology to be the relationship between two or more (usually morphological) outcomes that fully correspond to each other in terms of their unbroken inheritance from a single common ancestor. If traits correspond in this narrow way they are homologues. If they do not, they are not. Understanding homology in this way means that homology does not admit of degrees. One consequence of this conception of homology is that partial correspondence, either as a result
of inheritance of corresponding traits through a broken, interrupted ancestor-descendent lineage from a common ancestor, or correspondence due to inheritance from more than one ancestor, all count as non-homologous.

But if instead of taking the linear view of evolution assumed by the neo-Darwinian approach, we take a mosaic (or “combinatorial”) view, the meaning of homology itself must be reconceived and extended to include partial and mixed homology (cf. West-Eberhard 2003: Ch. 7, 25).12

If the resources used in the construction of organismal traits are inherited from diverse genetic, cellular, behavioural, and environmental sources, then the traits that result are equally mosaic. So conceived, they are the product of heterogeneous construction from multiple ancestral sources. As a result, any comparison between these traits must necessarily be expressed in terms of their partial (or mixed) homology (and/or analogy).

Reconceiving evolution and traits as mosaic and homology as mixed follows directly from the organism-centred perspective set out in Chapter Two. These are the conceptual consequences that come from thinking about organismal form as the product of heterogeneous self-construction and a distributed view of organic causation. When viewed from this perspective, the possible mechanisms of inheritance through which resources are acquired are extended to include not just the vertical inheritance of genetic and extragenetic resources, but also horizontally inherited behavioural and environmental resources.

Before laying out the details of this reconception of homology, I begin with a survey of the early classical conceptions as well as some more recent suggestions for a developmental conception of homology. After this historical review, I reveal the underlying linear view of causation relied upon by the neo-Darwinists and analyse how this has both shaped the meaning of homology and restricted the units of comparison.

Next, I discuss some developmental challenges to the linear view and the mosaic alternative. Taking this mosaic perspective to its conclusion, I show how traits as units of comparison may be extended from the

12 The linear view and alternatives to it will be introduced in sections 3.4, 3.5 and 3.5.1.
morphological outcomes of developmental processes to comparisons of behavioural patterns, developmental processes, and life stages. Lastly, I suggest that if traits are the product of heterogeneous and distributed resources inherited from multiple sources, we may find that they can only be compared in terms of mixed (or mosaic) homology (e.g. partially homologous, partially non-homologous).

3.1 COMPARATIVE CONCEPTS FROM BELON (1555) TO DARWIN (1859)

Although the study of comparative anatomy dates back to Aristotle’s system of nature, the earliest record of the explicit structural and positional equivalence between the features of different animals can be found in Belon’s anatomical illustrations of 1555 (reprinted in Panchen 1994: 43, figure 8). These detailed sketches compared the position and arrangement of the bones of a human with those of a bird. What was of particular significance in these sketches was how Belon arranged the bones of both the bird and the human skeleton in the same upright position. The skeleton of the bird was shown in an unnatural position that mirrored the normal upright standing position of the human skeleton: its head, neck and spinal column formed a straight line and the forelimbs hung down on either side of the body ventrally splayed. Rather than picturing the bones of the bird in their natural arrangement in the skeleton of a living bird, the side-by-side upright alignment of both the bird and the human skeleton emphasized the positional equivalence and corresponding topology of the bones of each animal and their similar relationships with the other bones within each skeleton.

Prior to Owen’s formal distinction between homology and analogy in 1843, the most influential discussions on comparative anatomy occurred during the debates between Cuvier and the idealist Geoffroy Saint-Hilaire (c.1830-1833) at the Muséum National d’Histoire Naturelle, Jardin des Plantes in Paris.13 Cuvier and Geoffroy held different views on what they

13 What seems to be a precursor to Cuvier’s own conception of homology can be found in Kant’s *Critique of Judgment*. Unfortunately I do not have space for a full
believed to be the significant relationships among corresponding traits in different animals. A caricature of their positions often given is that Cuvier argued that similar functions are the cause of structural similarities, whereas Geoffroy argued that structural similarity is the cause of the similarity of function. However this perfunctory description of their debate obscures many conceptual nuances between the two views.

To fully understand the basis for these competing views it will be necessary to consider the theoretical bases of their individual positions. I begin with Cuvier's (1812) theory of embranchements. This theory claimed there to be four basic body plans of animal structure: Vertebrates (e.g. bony fish, birds, and humans), Articulates (e.g. lobsters, horseshoe crabs, and dung beetles), Radiates (e.g. sponges, sea anemones, and starfish), and Molluscs (e.g. snails, octopi, and cuttlefish). In positing these four body plans, Cuvier's theory took certain sets of body parts, features, or traits to be found together in certain animals. Traits could not be found in just any arrangement or admixture but only within the constraints of one of the four basic body plans (cf. Russell 1916: 41).

Cuvier's embranchements were not ideal archetypes—they were actual combinations of traits that were found together in particular animals. These groups of traits were not just random arrangements of parts but acted in cooperation with other traits of the organism towards a particular goal or purpose. The upshot of Cuvier's theory of embranchements was that only sets of traits which act together in this way are those which are actually found in nature. This was because the structure and arrangement of traits was dependent upon the environment and conditions for the sake of which they were formed in the animal. Put another way, the traits of animals

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14 I rely here on Russell's (1916) account of Geoffroy and Cuvier's theories as it remains one of the best (but see also Appel 1987 for a more recently published account).
correlated with the conditions required for the organism’s existence within a particular environment.

Cuvier understood the organism’s functional unity and the interconnectedness of structurally identical parts in different organisms in terms of their interdependence with other traits towards a telos. In this respect, he was influenced by Kant’s view of organisms as natural purposes:

Cuvier was indeed a teleologist after the fashion of Kant, and there can be no doubt that he was influenced ... by Kant’s *Kritik der Urtheilskraft* [Critique of Judgement] ... Teleology in Kant’s sense is and will always be a necessary postulate of biology. It does not supply an explanation of organic forms and activities, but without it one cannot even begin to understand living things (Russell 1916: 35).

By conceiving homology teleologically, Cuvier understood the similarity of parts between two different animals as due to the similarity of their functional goals or purposes. For him the animal’s mode of living determined the arrangement, position, and relationships of its appendages, organs, and other features (i.e. traits) of its body. For instance, if the animal lived in the deep sea, it would require a soft invertebrate body plan so as to withstand great pressures and suctioned tentacles for easily grasping prey in low light. Thus, a body plan characteristic of Molluscs. The purposes for which these traits are used by a deep sea living animal, such as an octopus, might include the ability to dive to great depths, collapse its body to fit through small openings between rocks, capture slippery prey with little or no light, quick propulsion through an aquatic environment, and the ability to attach itself to various surfaces. These are what determine their structure (e.g. a soft invertebrate body with eight leg-like appendages with suckers along the underside attaching to the base of the head surrounding the mouth).

In contrast to Cuvier’s four *embranchements*, Geoffroy believed that there was only one body plan common to all animals. All animals (and all organs, appendages, and other traits) were based on the same shared universal plan (cf. Russell 1916: 54-64). For Geoffroy, the organization of animal form was the differential expression of one generalized, abstract, universal type. Homological correspondence between the same organs in
different animals could be explained as the result of animals sharing the same universal body plan. Two organs are the same (i.e. homologues) if they are located in the same position in the bodies of the two different animals being compared. Any variations among these organs were due to the independent modifications of each animal from the universal body plan.

There may be an infinite variety of modifications observed among different animals. These are different aberrations in the structural form or function from the ideal. Geoffroy expected wide variations in form and function of homologous organs. What mattered in the comparison of homologues was only that their position remained constant: “an organ can be deteriorated, atrophied, annihilated, but not transposed” (Geoffroy 1818: xxx, as quoted in Russell 1916: 53).

The centrality of positional continuity formed the foundation of Geoffroy’s theory of homology, the keystone of which was his principe des connexions. The homology of organs is determined by their positional relationship within the body and its topological relationship to other organs: the trunk with its organs can, as it were, move bodily along the vertebral column, so as to be found in one class near the front end of the vertebral column, in another about the middle, and in a third near the end, then I can show you in detail that the constituent parts of this trunk are found in all classes to be invariably in the same positions relatively to one another (Geoffroy 1818: 1, as quoted in Russell 1916).

Whereas Cuvier’s notion of homology focused on whether interdependent structures share a common functional goal or purpose in different animals and its particular embranchement, Geoffroy’s reliance on an abstracted notion of a universal body plan meant that the homology of organs in different animals depended ultimately on their relative position to other organs and features of the body in comparison to those of another. Cuvier’s body plans were discrete and fixed. There were no transformations and no intermediates between the four embranchements. For Geoffroy, the universal body plan was almost infinitely flexible, producing a continuum of intermediate transformations and modifications to this body plan.

Shortly after the debates between Geoffroy and Cuvier, Owen provided a formal distinction between homology and analogy: “Homologue: ... The
same organ in different animals under every variety of form and function” (Owen, 1843: 349) and, “Analogue: ... A part or organ in one animal which has the same function as another part or organ in a different animal” (Owen 1843: 374). Owen believed that although the Geoffroy-Cuvier debates drew attention to the importance of the concepts of homology and analogy to comparative anatomy, they also beclouded their meaning. Owen’s aim was to provide a clear and consistent definition of homology and analogy, something that had not been done previously. This was necessary as it was the habit of Geoffroy to use “homology” and “analogy” interchangeably to mean the same thing. Geoffroy’s (1818) theory of homology was entitled, “Théorie des analogues,” but in 1825, Owen showed that Geoffroy’s use of “homologue” was identical to his own conception of “serial homology” (Geoffroy 1818, as cited in Owen 1848: 5).15

Despite these criticisms, Owen makes explicit use of Geoffroy’s principe des connexions in distinguishing homology and analogy. Owen’s definition of homologues as “the same organs” is intended to capture their positional and topological orientation and structural correspondence in different organisms. Homologous organs, such as the wing of a falcon and the foreleg of an ox, were identified in terms of their corresponding topological location within the falcon and the ox in relation to their other features (e.g. the position of the humerus and its attachment by ligaments to the ulnae and radii, claws and hooves of each animal).

In contrast, the biological concept of analogy was defined in terms of the functional similarity of two organs in different organisms. For instance, the wings of a blow fly are analogous to the wings of a hummingbird. These are identified as such because of their similar functional role in enabling the animal to manoeuvre itself around an aerial environment.

Owen drew inspiration from Cuvier’s theory of embranchements, as well as Geoffroy’s principe des connexions. Cuvier’s influence was apparent in Owen’s conception of a “homological compound” (Owen 1843: 105):

All those bones which are formed by a coalescence of parts answering to distinct elements of the typical vertebra are “homologically compound” when developed from more than one

15 I discuss serial homology below.
centre, whether such centres subsequently coalesce, or remain distinct, or even become the subject of individual adaptive modifications, with special joints, muscles, etc., for particular offices ... the result of a special organising force ... [and] teleological structure (Owen 1843: 106-8).

But because Owen did not believe that Cuvier’s teleological point of view sufficiently explained the similar topological correspondence of organs’ positions across a variety of different animals, he augmented it with Geoffroy’s notion of the universal body plan—what Owen called the “archetype.”

Apart from formally distinguishing homology and analogy, Owen also provided the first account of the three kinds of homological relationship between the compared organs of organisms. “General homology” was the comparison of two or more organs as similar where their similarity to each other was caused by their similarity to the same organ in the archetype (cf. Owen 1849: 40-42). “Special homology” was defined as the comparison of the same organs within two different organisms. This relationship does not include the comparison to the same organ in the archetype, but consists in “the correspondence of a part or organ [as] determined by its relative position and connections, with a part or organ in different animals” (Owen 1848: 7). The third kind of homology Owen specified was called “serial homology.” Serial homology was the similarity between different parts or organs within the same organism (these parts are thought to possess the same basic structure). Serial homologues arose from the repetitive construction and development of an iterative part (e.g. the vertebrae or the leaves of a plant).

Comparative embryological studies of the morphological features of many organisms’ early anatomy lead both Haeckel (1866) and Darwin (1859) to reconceive Owen’s concept of homology in terms of the historical continuity of traits over generations of ancestors and descendents. However whereas Haeckel’s historical notion of homology was based on the theory of

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16 Although Geoffroy does not explicitly refer to an archetype, his universal common type is widely thought (Russell 1916, Hall 1994) to be the precursor to Owen’s archetype.
recapitulation, Darwin’s was based on the theory of descent with modification.

Darwin was keen to distance himself from the idealism of Owen and Geoffroy and their particular use of the archetype. Avoiding this idealist notion meant that in order to integrate the concept of homology into his theory of evolution he needed to make some alterations to its meaning and reference.

Although Owen’s special homology made no reference to the archetype, it also provided no causal explanation of the topological correspondence of organs in different animals. It was merely a description of their similar correspondence. The only kind of homology characterized by Owen that had a causal explanation within its definition was that of general homology—the similarity of two corresponding organs in different animals to each other was caused by their similarity to the same organ in the archetype.

Although Darwin sought to avoid these commitments to idealism, he does not rely on Owen’s notion of special homology (which does not refer to the archetype) for the basis of his own account of homology. It was instead Owen’s general homology that Darwin used. Looking at the role homology plays in Darwin’s theory reveals why. For Darwin, homology is not just a description but a causal explanation: organs correspond to each other because they both correspond to the same common cause—a shared ancestor. Darwin’s concept utilizes the same form of explanation as Owen’s general homology but interprets the archetype differently—in terms of the historic notion of a shared common ancestor rather than the idealist notion of the archetype:

suppose that the ancient progenitor, the archetype as it may be called, of all mammals, had its limbs constructed on the existing general pattern, for whatever purpose they served, we can at once perceive the plain signification of the homologous construction of the limbs throughout the whole class (Darwin 1859: 435).

In the above passage Darwin does not shy away from making use of Owen’s concept of the archetype in his historical conception of homology. The historical notion of Darwin’s “ancient progenitor” replaces Owen’s idealist “archetype.”
According to Darwin’s historical notion of homology, the traits of two different organisms are not homologous because of their shared function or form—which may differ greatly—and not because of their position or orientation. These traits are homologous because they have both been inherited (and modified) from the same trait in an ancestor common to them both.

3.2 The Cladist Conception of Homology

The historical conception of homology has gone through a number of amendments. Initial changes were designed to remove any last traces of the idealism of the lingering notion of an archetype. In the 1960s, Darwin’s historical notion was reconceved in terms of an historical-analytic conception of homology. The theoretical basis for this reconcevation was cladism, Willi Hennig’s novel theory of systematics (Hennig 1966). More recent variations to Hennig’s initial cladist conception remain popular (cf. Nelson and Platnick 1981, Patterson 1982, and Lauder 1994).

Cladism conceives of evolution as a series of speciation events over evolutionary time, represented as the branchings of a bifurcating tree. According to cladists a natural group is a branch of this phylogenetic tree called a “clade.” A clade is a group of individuals related by a continuous common phylogenetic lineage. Clades include all and only those individuals descended from an unbroken ancestor-descendent lineage from a single common ancestor (referred to as a “monophyletic” lineage).

Understanding homology from a cladist perspective entails different restrictions on both the meaning of homology and its application. These restrictions are intended to disambiguate the confused meaning of similarity and continuity in the classical and the original historical concepts. A cladist
approach narrows the relationship of homology to that of the corresponding similarity of traits due to the unbroken descent from a single common ancestor. It restricts the meaning of homology to traits that are inherited through a monophyletic lineage—the result of a continuous unbroken linear inheritance from one shared ancestor possessing the ancestral trait to all (and only) its descendents: “homology ... is defined not in terms of similarity, correspondence, or ancestry but in terms of monophyly” (Nelson 1994: 127). Restricting the conception in this way means that traits which are the result of broken, non-linear, or mixed inheritance are dismissed as non-homologous.

Cladists tend to restrict the units of comparison to the morphological outcomes or end results of organismal developmental processes. In addition to limiting the units of comparison to outcomes, the cladist view also restricts the meaning of homology by taking an all-or-nothing approach to homology. It groups all traits that are not the result of monophyletic lineages together—referring to them collectively as “false homologies” or “homoplasies”: “Homoplasy [is defined] as the possession by two or more taxa of a character derived not from the nearest common ancestor but through convergence, parallelism, or reversal” (Mayr and Ashlock 1991: 418).

Homoplasy refers to the analogical similarity of corresponding traits due to inheritance from multiple ancestors through parallel or convergent evolution. But it also refers to structural correspondences of traits between organisms that have inherited the trait from more than one ancestor (i.e. are polyphyletic), as well as traits inherited through a broken lineage from a shared ancestor (e.g. recurrent traits that do not occur in every generation).

A clear dichotomy between unbroken (monophyletic) lineages and broken lineages means that homology does not come of degrees. Traits in different organisms either share a common ancestor and are therefore homologues, or they do not and are not homologues. There is no room for partial or mixed ancestry. Therefore, partial homology is prohibited.
3.3 De Beer’s Challenges

Vocal critics of the historical and cladist views of homology focused on the inability of these views to account for developmental perturbations, phenotypic modifications, environmental influences, and the different mechanisms by which homological traits were inherited. Rather than focusing exclusively on the phylogeny of organisms or simply black-boxing development, Gavin de Beer (1971) reasserted the importance of the role of organismal ontogenesis. What was absent in both the historical and cladist concepts of homology was a clear understanding of the causal routes of inheritance and modification leading to morphological outcomes from a common ancestral form. Remedying this omission required careful consideration of the role of development in the construction of these morphological traits in individual organisms.

In his Oxford Biology Reader, Homology: An Unsolved Problem, de Beer identifies particular limitations of these views. He objects to the practice of using corresponding developmental processes or similar cellular tissues to justify morphological homology. De Beer argues that problems emerge when one tries to identify similar developmental processes or cellular substrata as “evidence” for morphologically corresponding homologues. He reveals these problems using a number of examples. The ontogenetic pathways and processes of different organisms may be used in producing what appear to be homologous morphological structures. Although these structures may be homologous, their developmental pathways or the genetic or cellular resources they use in the construction of these morphological structures may not correspond in the same way. For example, the alimentary canal in vertebrates is constructed from the roof of the gut cavity in the shark embryo. However, it is formed from the floor of the gut in lampreys, from both the floor and the roof in frogs, and in birds it is formed from the lower layer of the blastoderm (de Beer 1971: 10-13).

Relying on the same underlying cells, the similar position of these cells in the embryo, or corresponding parts of the zygote from which the different structures are formed, does not guarantee the homology of the
morphological structures which are constructed from these (de Beer 1971: 13). Relying on the homology of these cellular structures as evidence for the homology of the morphological outcomes of them also implies that if morphological structures are the result of different cellular substrata or diverse developmental processes which do not correspond as similar, then these morphological structures are not homologues. De Beer countered these assumptions, arguing that this non-correspondence on lower levels did not mean that the morphological structures that resulted from these were not homologues: “homologous structures can owe their origin and stimulus to differentiate to different organizer-induction processes without forfeiting their homology” (de Beer 1971: 13).

Relying on the same cells, cell position, area of the zygote, or the same genes as evidence for homology encourages the erroneous assumption that homology at one level (e.g. morphological traits) is caused by the homology at another level (e.g. the same cells or genes). Revealing the falsity of this assumption were de Beer’s studies of the incongruities between the corresponding similarities of morphological traits, developmental patterns, and genes in his studies on **eyeless** mutants of *Drosophila*. Observing eye development in fruit flies with the **eyeless** mutation, de Beer found that while some with this mutation do not develop eyes, other **eyeless** mutants develop fully functioning eyes identical to those of the wild type.

He realized that there were sets of genes in some of these mutants, which he referred to as “modifier genes,” that when present, resulted in the **eyeless** mutant developed fully functioning eyes. Although this result was initially unexpected by de Beer, this phenotype was not uncommon among the **eyeless** mutants. His observations were startling, not only because the mutant **eyeless** fruit flies developed eyes, but because their eyes developed through a different developmental route utilizing different genes than the wild type. The different use of the “replacement set” of genes in the development of the mutant resulted in the same phenotypic outcome as the differently developed wild type. Studying similar phenomena in both fruit flies and other organisms, de Beer’s “modifier genes” have also been referred to as “deputized genes” (Roth 1984, 1988, 1991):
New genes, previously unassociated with the development of a particular structure, can be deputized in evolution; that is, brought in to control a previously unrelated developmental process, so that entirely different suites of genes may be responsible for the appearance of the structure in different contexts (Roth 1988: 7).

In this way, the fruit fly's flexible use of different genes in the construction of its eyes means that this trait can become highly conserved over generations despite changes to the genetic and developmental resources available. The gross morphology of fruit fly eyes remains continuous among mutants and wild types despite their different genetic, developmental, and mechanical causes. This means that at the gross morphological level the fruit fly eyes in mutants and wild types are homologous. But at the developmental and genetic level they are not.

De Beer's investigations of the eyeless fruit flies call into question the common assumption that the gross morphological similarities or correspondences between organisms' traits is caused by the same developmental or genetic mechanisms and the congruity of homology of different levels of organization (e.g. genetic homology does not ensure developmental homology and, in turn, developmental homology does not ensure morphological homology). The assumption of a clear causal connection between genotypes and phenotypes was misplaced: “homologous structures need not be controlled by identical genes, and homology of phenotypes does not imply similarity of genotypes” (de Beer 1971: 15).

More evidence for the incongruity of different levels of homology was revealed in extensive studies on fruit flies in the 1980s and 1990s. In a much cited paper by Stanislav Tomarev et al. (1997), eyeless in Drosophila is compared to Pax-6 of the squid. In this, the Pax-6 of the squid (Loligo opalescens) is said to be homologous to eyeless in the fruit fly (Drosophila). Pax-6 is necessary for the development of the eyes, olfactory organs, brain, and the arms of squid. When the squid Pax-6 is implanted in the fruit fly this leads to the development of ectopic eyes on wings, antennae, and legs. Tomarev et al. argue that this is evidence for the conclusion that the Pax-6 in the squid and eyeless in the fruit fly are homologous genes:
Our data support the idea that morphologically distinct eyes of different species have arisen through elaboration of a common, conserved \textit{Pax-6} dependent mechanism that is operative at early stages of eye development and that the anatomical differences among eyes arose late in evolution (Tomarev et al. 1997: 2426).

The implantation of the squid \textit{Pax-6} shows that there may be a homological relationship between these regulatory genes. Within a wide range of organisms, including the mouse, and other vertebrates, there are orthologues (gene homologues) (cf. Doboule 1994). But these genes may only be considered to be homologous (orthologous) to one another in terms of a small role they play in development. In this sense, this research repeats the similar points made by de Beer—one cannot venture beyond homology at one level as evidence for homology at another.

Although the regulatory genes \textit{Pax-6} and \textit{eyeless} may be considered homologous (though this has proved to be controversial; cf. Wagner 2007), the regulatory and developmental networks within which these regulatory genes function in the squid and fruit fly are not homologous. The regulatory networks and developmental processes of the fruit fly and the squid are not homologous because they evolved independently from one another. Neither are the morphological outcomes of the developmental processes utilizing these regulatory genes. The arms of an octopus are not homologous with the eyes of a fruit fly.

Ever since de Beer revealed that homology at one level does not imply homology at any other level of organization, there has been constant debate over which level is \textit{the} source of homology, e.g. genetic, cellular, developmental, or morphological. This debate betrays a complete misunderstanding of de Beer’s findings. There is no privileged level of organization which is causally responsible for homology at all other levels. It is instead a relationship that can hold independently on a number of different levels:

Homology ... is studie[d] at all levels of biological organization from molecules through genes, cells, organs, embryos, organisms, populations, communities, behavior, even biogeographical regions. Homology therefore informs gene regulation, ontogeny and phylogeny, morphology and physiology, molecular and cell biology,
botany and zoology, systematics and classification, ecology and biogeography (Hall 1994: 2).

Homologies at different levels of organization are independent of one another (e.g. developmental pathways, morphological traits, regulatory networks, or genetic sequences). Each of these is a potential unit of comparison. Limiting the units of comparison to the morphological outcomes (as the historical and cladist views do) encourages the inference from an homology at one level to one at another and the assumption that there must be a privileged level of comparison or cause of morphological homology.

3.4 THE LINEAR VIEW OF HOMOLOGY

What I referred to in Chapter One as the “neo-Darwinian” perspective further reconceived the historical notion of homology in light of a new synthesis of Darwin’s theory of descent with modification and modern genetics. This gene-centred view understands evolution to be the change in gene frequencies (Mayr 1993). Natural selection is the result of the moulding factors in the environment acting on phenotypic traits which are coded for in the organism’s genes. The genes are passed on from one generation to the next. Phenotypic features of the organism are the outcomes of continuously inherited genes from ancestor to descendant. This neo-Darwinian conception of evolution and inheritance assumes that the historical continuity of phenotypic traits is grounded in an underlying continuity of genes or genotypes which serve as the blueprints for building these morphological traits. Implicit in this view is the belief that nothing else is reliably inherited except genes. And so it is the genetic continuity which must be the cause of the historical “continuity” of morphological traits over generations.

This gene-centred perspective of homology relies on an underlying preformationist view of trait construction. Understood from a gene-centred, neo-Darwinian perspective, homology is the comparative similarity of the
inevitable phenotypic outcomes of developmental processes directed by the underlying preformed program contained within the conserved genes. In this sense, each homologue can be traced back to a certain set of genes in the genome. Because only genes are reliably inherited generation after generation, they are the replicators of the phenotypic traits that are compared as homologues. This perspective effectively sees that continuity of descent with modification as merely an epiphenomenon of the continuity of vertically inherited genes (cf. Roth 1984).

Central to the understanding of variation over evolutionary time and the diversity of species, this conception of homology enabled the reconstruction of phylogenetic lineages by assuming morphological traits were underpinned by genetic continuity. Underlying this view is a commitment to preformationism discussed in the previous chapters. The form and structure of traits exists prior to the organism’s life in the world, contained in the coding information in its genes.

Understanding the study of homology according to this perspective commits proponents of the neo-Darwinian view of homology to a linear view of causation: “the linear mapping of genes onto developmental schedules and of developmental schedules onto phenotypes” (Minelli 1998: 340). Traits are the outcomes of the linear inheritance of instructional programs for building phenotypic traits. Homologues are the phenotypic outcomes of the same genes that code for these traits which are vertically inherited from one generation to the next in an unbroken ancestor-descendent lineage.

This neo-Darwinian view effectively reduces the homology of morphological parts to the homology of genes: “Reducing organ homology to gene homology is conceptually and methodologically equivalent to reducing species phylogeny to gene phylogeny, a fault of which systematists are increasingly aware” (Minelli 2003: 231).

Conceiving homology in this reductive way both overestimates the control of genes over the construction of phenotypes and undervalues the role of all other extragenetic processes throughout organismal ontogeny. It sees the genetic level as the basic level of organic causation which directs developmental pathways to produce morphological outcomes. But, as de
Beer’s examples have shown, the homology at a so-called higher level of biological organization (e.g. the homology of morphological traits) is neither explained nor implied by the homology at a lower level (e.g. the homology of genes).

Morphological traits can be conserved, maintaining their continuity in successive generations in spite of basic changes to developmental and genetic resources. The same gross morphological traits may be present in two different organisms but each may be the result of different developmental pathways and genetic resources.

This linear view of organic form conceives of homologues as fundamentally underpinned by the unbroken vertical transmission of certain genes or gene complexes from a single common ancestor. Restricting homology in this way limits homology to an all-or-nothing relationship between traits. Traits are either homologous or they are not.

Opposition to the study of partial homology has been a sustained consensus view with few challengers (namely Minelli 2003 and West-Eberhard 2003). Partial homology has been vociferously objected to as a threat to the Modern Synthesis: “Partial homology is incompatible with standard evolutionary views, according to which structures are either homologous or not” (Donohue 1992: 172, cf. Patterson 1987, Lewin and Foley 2004). This anti-partial homology consensus is broad. It includes not just neo-Darwinians but some proponents of developmental systems perspectives (cf. Griffiths 2006: 7, Ereshefsky [personal communication]). Even if partial homology is accepted with regard to the comparison of genes, it is widely believed that “[p]artial homology does not occur with morphological characters” (Lewin and Foley 2004: 122). In the next few sections I explore a possible alternative to the linear view of the neo-Darwinian perspective and consider the consequences of this alternative view for a reconceived notion of homology.

3.5 PLASTIC THINKING
An alternative perspective to this neo-Darwinian linear view of homology from which evolution can be understood has been suggested by studies of developmental and phenotypic plasticity:

The possible role of phenotypic plasticity in the evolution of phenotypic novelties may offer an excellent system in which to apply both the experimental and the comparative methods to tackle the intimately related problems of homology and the origin of new traits (Pigliucci 2001: 377).

New insight into the developmental plasticity of the ontogeny of organisms, as well as its role in facilitating evolutionary variations, has forced hard questioning of the widespread assumption that evolution is, for the most part, linear. In particular, recently acquired understanding of the role of developmental recombination, phenotypic plasticity, recurrence (West-Eberhard 2003, Kirschner and Gerhart 2005), homeosis, deputized genes (Roth 1988, 1994), temporal mosaics, and heterochrony (Minelli 2003), pose new challenges to the linear perspective of evolution and homology as it is currently understood.

The plasticity of developmental processes and phenotypes may alter our conception of the causes of evolutionary variation, the notion of historical continuity, the mechanisms of inheritance, our conception of species, and the relationship between traits of organisms and the comparison of traits between different organisms. Recognizing the role of plastic development in evolution may affect what are taken to be the units of comparison, whether the underpinning of morphological continuity by genetic continuity is empirically justified, and also tests the conceptual assumptions underlying the linear view of evolution on which the widespread opposition to partial homology is based.17

If all organismal traits constantly fluctuate throughout their ontogenesis and continuously change throughout evolution, then our comparison of these traits may only ever be made in terms of varying degrees of homology and/or analogy.

17 As I will go on to suggest in section 3.7.3 “Degrees of homology,” if understood from a developmentally plastic perspective, partial homology—far from being incompatible with evolutionary theory—may turn out to be indispensable to it.
3.5.1 A NON-LINEAR VIEW OF EVOLUTION

Viewing evolution linearly means the changes in phenotypic features of organisms, understood in terms of the change in gene frequencies, are believed to be the result of vertically inherited random genetic mutations which have been stabilized under selection. On a non-linear perspective, novel phenotypic variations of traits may also arise from the reorganization of developmentally flexible phenotypic features depending on the organism’s genetic, extragenetic, and environmental resources:

Much of the skepticism over the years about the capacity of random mutation or genetic reassortment to generate phenotypic change has arisen from the assumption that genetic changes must create very specific, multiple, complex phenotypic changes. Our view is that specificity and complexity are already built into the conserved processes (Kirschner and Gerhart 2005: 142).

On this view, an organism may recombine some of its phenotypic features in a novel way or make use of new genetic or extragenetic resources and variations within its environment. The organism rearranges its own phenotype using the resources available to it. Novel phenotypes may be the result of the rearrangement and reorganization of old phenotypes and old resources linked together in new ways. Rather than genetic mutation, the motor of evolution on this plastic view is the capacity of organisms to reorganize and recombine their phenotypic resources:

[re-]combinatorial evolution raises the possibility that derived traits may often contain elements of more than one ancestral trait, and that what was formerly seen as a de novo modification actually involves the recombined expression of preexisting traits (West-Eberhard 2003: 485).

If the direction of evolution is understood in terms of a non-linear view rather than a linear view, certain assumptions, such as the continuity of ancestral lineages based on a linear view, may be undermined.

3.5.1.1 RECURRENT TRAITS
Homologues are important in determining how closely two individuals are related because homologous traits are conserved from one generation to the next. And according to the neo-Darwinian view, two individuals that possess homologous traits share a single common ancestor from which each has inherited the same trait via an unbroken route from the ancestral generation.

This is obviously an oversimplified account of the conservation of homologues as it is strictly incorrect to say that the “same trait” is conserved and passed down from one generation to the next. Organisms are constructed and reconstructed in each new generation. So what is retained or conserved? And why must it be conserved via an unbroken lineage?

The assumption that homologues must be conserved via continuous, unbroken ancestral lineages can be questioned. Phenotypic traits in numerous species may be the result of phylogenetically discontinuous inheritance over broken lineages. While some generations of organisms of the same species may have one phenotypic trait, this trait may be absent in the next generation. Organisms of the same species may vary their phenotypic traits such as their wing patterns, body size, or sexual behaviours. This kind of developmental flexibility enables the organisms in each generation to construct various wing patterns depending on their particular environmental needs (e.g. to avoid a preponderance of predators, enable it to compete successfully with other conspecifics in securing a mate, or providing an alternative feeding behaviour if its preferred food source is scarce).

In some species, or in some pairs of closely related species, a variety of phenotypic variations may be possible, but not all exist in any one generation. In these species, traits are not continuous but are “recurrent” (West-Eberhard 2003: 358-74, also referred to as “latent homologies” by Roth 1988). Although not all appearing in the same generation, all of these phenotypic variations may descend from a single phenotypically and developmentally plastic common ancestor. They may in this sense be considered homologues. However, their discontinuity disqualifies them from
being considered homologues according to cladist or neo-Darwinist concepts of homology. For example, we may wish to compare the recurrent wing patterns of many *Heliconius* butterflies that have evolved in two closely related species (*H. melpomene* and *H. erato*) (cf. Brower 1994).

The recurrent identical wing patterns of different species of *Heliconius* butterflies are “convergent” in cladistic terms ... but they [may be homologous] ... in the broader sense of being based on shared physiological determinants of wing patterns (West-Eberhard 2003: 357).

Recurrence contradicts the impression of concordant phenotypic evolution sometimes given by the taxonomic and phylogenetic practice of arranging groups of organisms in lineal and hierarchical series to approximate a genealogy ... This may unwittingly encourage a lineal view of evolution, when in fact the phenotype often evolves in a mosaic, combinatorial and intermittent fashion (West-Eberhard 2003: 369).

Far from being uncontroversially non-homologous, the recurrent patterns among these different species may be due to a shared common phenotypically plastic ancestor. If these butterflies have a set of developmental resources—a veritable back catalogue of developmental and phenotypic capacities from which their phenotypes are constructed—then the recurrent variations are connected by a discontinuous lineage from a common ancestor.

Recurrence is just one example of how evolution may not be conceived linearly. A new plastic approach to evolution and development challenges the systematic privileging of unbroken linear descent over non-linear broken descent from a common ancestor held by cladist and neo-Darwinian perspectives.

### 3.5.1.2 Homologies of Process

Only within the last few decades has the study of homology been extended beyond anything besides morphological outcomes (Gilbert, Opitz, and Raff 1996). Until the recent emphasis on developmental systems
perspectives and the reincorporation of development into evolutionary theory, this restrictive view of homology was widely accepted. Restricting the study of homology to the corresponding similarities between morphological outcomes, as the privileged units of comparison, was the result of the lack of attention paid to the role of development in the neo-Darwinian synthesis.

In restricting the units of comparison to outcomes, the neo-Darwinian view systematically excludes homological comparison between developmental processes, complex mechanisms, life stages, behavioural patterns, and constructed environmental artefacts.

In opposition to this narrow view of homology, one particularly promising suggestion is that rather than thinking of homology exclusively in term of the corresponding similarities of static morphological outcomes, we can instead view these morphological structures as locations of activity. Organismal activities or movements may be slow, like growth and decay, or fast, like cell differentiation, digestion, and photosynthesis (cf. Woodger 1929, Sattler 1994: 451). In focusing on the correspondence of similar morphological structures, the neo-Darwinian and cladist views limit the units of homological comparison to the structural outcomes of an organism’s developmental processes. In contrast, a processual view of homology takes processes to be the constructive activities of organisms that combine different processual activities that result in an organism’s form (Sattler 1994). On this process view of homology, developmental processes themselves—rather than just the outcomes of developmental processes—may be considered possible units of homological comparison:

Whereas classic homology has been one of structure—be it of skeletons or genes—the homology of process goes into the very mechanisms of development. Whereas classical homology looks at the similarity between entities, the homology of process concerns the similarity of dynamic interactions. The result is that although organs (such as the vertebrate and arthropod eye, the vertebrate and arthropod leg, etc.) can be structurally analogous, they may be formed by processes that are homologous! (Gilbert, Opitz and Raff 1996: 364).

Comparing morphological outcomes relies on abstract static features of organisms. By focusing only on the end products of a particular
constructive activity of the organism, the neo-Darwinian view assumes a static metaphysics of organismal organization. It conceives the end products of an organism’s development as finished stable entities rather than dynamic processes. The comparison of morphological outcomes is the comparison of abstract entities.

This seems to run counter to our empirical experience of the biological world and our understanding of it in terms of descent with modification. Organisms constantly change throughout their life cycles from embryo to death and throughout the various chemical, cellular, and behavioural activities required of living beings. The homological comparison of traits as morphological outcomes amounts to the comparison of temporally suspended snapshots of the organisms’ traits at one point during their lives.

Rather than relying on morphological outcomes as the units of comparison, we may take this suggestion and focus on dynamic processes instead. Morphological outcomes could still be compared as homologues but would be compared as “process combinations”: “a [morphological] structure is the process combination” (Sattler 1994: 457). In this way, two processes can be compared as homologues if both processes have been inherited from the same common ancestral developmental process, the same combination of ancestral processes, or if their complex processes or process combinations share some but not all of their ancestral processes.

### 3.5.1.3 Multiple developmental pathways

De Beer has shown that the assumption that homologous phenotypes must be constructed from homologous genes, gene complexes, or developmental pathways is untenable. Homology at one level does not guarantee homology at another level of biological organization: “the same genes can be involved in the development of nonhomologous characters” (de Beer 1971: 15).

Morphological traits that are homologous may be the outcomes of different developmental pathways and different genes (that are themselves
not homologous to each other). Reflecting on de Beer’s work leads one to question how the concept of historical continuity can explain the ubiquity of these developmentally plastic pathways and whether this affects what we mean when we talk about the concept of homology.

Given the only recent interest in developmental plasticity, it seems the implications of de Beer’s research are only just beginning to be realized. However, evidence for de Beer’s conclusions, and criticisms of the historical, cladist, and neo-Darwinist concepts of homology can be found as far back as the 19th century.

During the late 1820s and early 1830s Johannes Müller carefully studied the organs of the urogenital system of various vertebrate embryos comparing them to the urogenital system in the adult stage of organisms of the same species (Lenoir 1982: 103-11). At the time of his investigations, it was widely assumed that there were vestigial organs in the embryos of vertebrates which corresponded to adult organs. These were thought to be the primordial tissues from which the adult organ was formed. For example, the Wolffian body (also called the “mesonephros”) was believed to be the substratum from which the kidneys and all internal sexual organs of both adult males and females began. Although the mesonephros did indeed serve as a kidney in the growing embryos of both male and female vertebrates, Müller disputed the causal relationship between it and the adult kidneys and internal sexual organs.

Through his comprehensive studies, Müller found there to be no material or developmental continuity of the tissues of the mesonephros and the adult kidney. Through further investigations, he found that among male vertebrates the deteriorating mesonephros was coopted by the developing animal as a resource to be used in the construction of its internal reproductive organs, e.g. the epididymis, seminal vesicle, and vas deferens. However, Müller found that in females the mesonephros simply disintegrated. Not only was it not used in the construction of the kidneys, it played no part in the development of the female’s internal sexual organs. He found that the ovaries, uterus, and fallopian tubes were formed from a completely separate embryological structure, what he named the
paranephric duct (now known as the Müllerian duct) (Lenoir 1982: 109). Because there was no direct causal connection between the material of the Wolffian duct and the adult kidneys, Müller argued—contra received opinion at the time—there was no transformation of the cellular material from the Wolffian duct into the adult kidneys.

What both de Beer and Müller's investigations show is that the historical continuity of traits within different organisms may be the result of different evolutionarily conserved developmental resources, such as the growth of eyes in fruit flies, or the functionally similar but morphologically discontinuous development of the embryonic mesonephros and adult kidneys in the same vertebrate animal. In both cases, historical continuity or "sameness" of organ is discontinuous—the result of different developmental pathways and genetic resources to conserve the morphological trait of eyes in fruit flies and the discontinuity of cellular matter composing the embryonic kidney and that of the adult kidney. This means that the historical continuity of morphologically homologous traits is not due to the sameness of their genetic resources or cellular substrata.

Throughout an organism's development there are various genetic, cellular, and environmental changes. The organism may accommodate the changes in the resources it uses by recombining different features of traits in the construction of new traits.

One might be able to trace the developmental path of a particular trait which is the morphological outcome of its ontogeny through various intervening stages of development. But one would not be able to identify the portions of the genome or original cellular material which were the causes of the development leading to the eventual construction of the adult trait.

Comparing traits usually identified as functional parts of organisms with past ancestral functional traits invites confusion when trying to trace their historical continuity over generations (Gould and Lewontin 1979). If there is no genetic or extragenetic substrata underlying the continuity of these parts, then identifying the causes of its repeated construction in each
generation will not be as straightforward as the neo-Darwinian view suggests.

More recent evidence against the assumption of material continuity and linearity can be found in research on the multipotency and bipotentiality of cells. Different populations of cells retain the ability to express different, multiply possible end states of differentiation. This is particularly pronounced in the case of the neural crest, which consists of self-renewing multipotent populations of stem cells (cf. Hall 1999, Kirschner and Gerhart 2005). Neural crest cells do not have predetermined cell fates that are simply the result of gene action.

Identification of a cell lineage or cell population is not a demonstration of a single state of determination for that lineage. Of course, cells only ever do express one differentiative phenotype, but many such subpopulations are at least bipotential and may remain bipotential even after differentiating along one pathway [e.g. lineage tracing does not necessarily equate with determination of cell fate] (Hall 1999: 130).

Neural crest cells retain their multipotentiality and have less predictable trajectories than other cell types. These cells are reciprocally responsive to other cells within the self-organizing systems of the organism. Their differentiation into cell types is based on their exploration of the organismal body plan, cell-cell interaction, and their responsiveness to different physiological signals:

The exploratory nature of the neural crest involves physiological variation and selection. The wide responsiveness of neural crest cells to signals and their capacity to undertake any of numerous paths of development in response to signals constitute their form of variation (Kirschner and Gerhart 2005: 205).

The developmental integration of crest cells means that they act in alliance and are flexible with regard to their end cell form. Morphological outcomes are not the result of genetic coding or “genes for” nerve cells. The flexibility of these cells to vary their cell type depending on other cell populations, interactions and location in the organism’s body ensures that the organism’s phenotype is highly conserved. This capacity for flexible and responsive development means that the organism’s phenotype remains stable despite changes in its genetic, extragenetic, and developmental resources.
A linear view of evolution, assumed by cladists and neo-Darwinians, brings with it a particular understanding of: the continuity of traits, the units of comparison, the nature of the relationship between genes and traits, and the meaning and reference of “trait” and “homology.” These particular understandings no longer follow if we cease to take a linear view of evolution.

3.6 The heterogeneous construction of mosaic traits

The meaning of homology has been intimately related with what are understood to be the natural units of comparison. The relationship of homology, very generally, is an equivalence relationship between two units (Goodwin 1994: 233). Units of comparison are organismal traits. A trait identifies an enduring part of an organism. Enduring parts are those which are conserved over evolutionary time across generations of organismal life cycles.

According to the gene-centred view of homology, the life of the organism itself is transient but its conserved features are not. These enduring features are generated in each generation from the inherited genetic program. Because they are conserved over generations, homologues are used to resolve evolutionary relationships and phylogenetic lineages. Tracing these homologous relationships between the structures of different organisms back to the nearest common shared ancestor enables taxonomists to construct phylogenetic trees of evolutionary relatedness. Homologues, defined in terms of their shared ancestry due to unbroken (monophyletic), lineage are used to identify organisms as conspecifics.

Opting out of both the linear perspective of evolution and the neo-Darwinian gene-centred conception of homology means homologues so construed cannot be used in tracing the ancestral lineages of organisms or in deciding whether an organism is or is not a member of a particular species.
Taking a non-linear, mosaic perspective on evolution results in a restructuring of both our conception of organismal traits and homology. This perspective invites a number of questions including: What are the natural units of comparison?, What are traits?, What is the meaning of homology?, What causes the homology of traits and ensures their conservation over generations?, and How have homologues changed over evolutionary time?

Most of these questions will be addressed in the present chapter. I focus on how a mosaic perspective of evolution and the acknowledgement of the evolutionary significance of developmental plasticity begins to open up a new possibility space within which natural units of comparison can be recognized.

### 3.6.1 **The “Degree of Partness” of Organisms**

Traits are what I will call the “proper parts” of an organism. These are more commonly referred to as the “characters” of organisms (cf. Wagner 2001 and papers therein). Recognizing the significance of development means that those pathways and processes previously thought of as important only as routes by which genes succeed in building morphological outcomes may now be considered proper dynamic features of the organism in their own right. Traits as proper parts can be expanded to include developmental processes, mechanisms, behaviours, and other dynamic parts, not just the relatively static morphological parts of organisms, like forelimbs and vertebrae. From a mosaic perspective, proper parts are conceived of as modular systems rather than structural singularities.

A [proper] part is a system that is both integrated internally and isolated from its surround[ings] ... [it] is integrated to the degree that interactions among components are many or strong, or both ... these may be spatially distributed [such as] a hormone-mediated control system or a local population of crickets chirping in synchrony ... Isolation is a reduction in, or termination of, integration ... Both integration and isolation may vary continuously, and therefore the extent to which a system is a
part—its degree of partness—is likewise a continuous variable (McShea and Venit 2001: 262).

An organism’s “degree of partness” enables it to make changes to certain features while keeping the rest of its body stable. This means that certain features may become sensitive to certain genetic or extragenetic resources which do not affect other components of the organism. These features can be understood as discrete units of variability.

The compartmentalization of the component parts of an organism into relatively discrete units or subunits means that the effects of variations in one subunit may be isolated from those of another. If these are, in turn, inherited as subunits, the degree of partness of the organism may increase over generations.

An organism’s “degree of partness” refers to the relative independence of its parts. The relative independence of an organism’s parts is the result of the weak linkages that hold them together. These weak linkages enable greater developmental or phenotypic variation throughout the organism by allowing many independent variations to simultaneously occur in each of its subunits without adversely affecting others. They facilitate the possibility of differential sensitivity and receptiveness of its parts to different genetic and extragenetic stimuli. Whilst some parts are affected by a particular stimulus or resource, others may be buffered, unaffected by the same resource (Kirschner and Gerhart 2005: Ch. 4).

Organisms with tightly linked, relatively dependent, non-modular parts do not have this buffering capacity. In them, variations in genetic or environmental resources may affect all parts. For instance, a particular environmental stimulus (e.g. direct sunlight) may provide an advantage to some parts of a leafy plant (e.g. increasing the supply of energy for photosynthesis), but they may prove deleterious to others which are simultaneously affected (e.g. drying out the soil and preventing the roots from taking in enough water). If the proper parts of the organism are tightly integrated with all other proper parts, any positive effects on the organism will be thwarted if the deleterious effects on other parts prove lethal to the organism.
In an organism with a high degree of partness, the proper parts of the organism may vary independently within a particular conserved overall structure (e.g. according to a particular body plan). Independent changes may occur in various semi-autonomous parts at the same time without these changes proving to be lethal. If the plant’s leaves can independently vary their shape due to the amount of sunlight, for instance, by broadening the leaf shape and increasing the size of the leaf without affecting the growth of the rest of the plant, this change may increase the likelihood of survival through droughts. The broad leaves may shield the soil below them lessening the effect of the sun in drying out the soil where its roots grow. The increase in the semi-autonomy of an organism’s parts facilitates an increased capacity for this kind of independent adaptation.

The benefits (as well as some disadvantages\(^{18}\)) of the increase in organisms’ degree of partness have been highlighted by what Moss (2008) has termed “detachment.” Detachment is “a measure of the relative independence of an entity from a larger milieu” (Moss 2008). An increase in the level of detachment can be understood as an increase in the level of closure of the parts in an organic system (or within an organism or community) and its connectedness to other parts in the organism’s body (or other entities in the world). A part becomes detached when it increases in both complexity and flexibility within a particular domain (Moss 2008).

By increasing its level of detachment, the part gains greater flexibility because it is able to “buffer itself in relation to possible perturbations, to have a history which is a factor in its subsequent trajectory, and indeed to dispose itself in some way toward its ... future possibilities” (Moss 2008). In this sense, detachment can provide both restraints and liberties, both requirements for a stable structure.

### 3.6.2 The Reconfigurability of Modular Parts

\(^{18}\) Moss (2008) refers to this as the “pain of detachment.” Although I will not discuss this here, the pain of detachment will be explored in the final sections of Chapter Five.
Degrees of partness may increase when speaking of complex traits. Complex traits may be considered “multimodular” or “mosaic” (West-Eberhard 2003: Ch. 4). This means that different subfeatures of the same trait can evolve independently of others. They may change in diverse ways to the other subfeatures, evolve at different rates, or utilize different resources in their construction. These discrete features may be weakly linked to other features of a particular part of an organism. Because they are weakly linked, one feature of the trait may dissociate from it and may then be used in association with a different trait. This “reconfigurability” of modular features (as subunits of traits) constitutes a highly conserved core capacity of organisms (Kirschner and Gerhart 2005: 136). In Kantian terms, these core capacities are included within the organism’s original stock of Anlagen.

The possibility of dissociating these modular units and their subsequent rearrangement into novel combinations by the organism to serve other purposes further increases the organism’s ability to vary its growth to meet new needs. Understood in terms of an organism’s degree of partness, variation can then be understood to be the organization and reorganization of modular parts.

One example of this can be found in studying the sexual organs and behavioural characteristics of sexually dimorphic adult vertebrates. These traits are the result of mosaic evolution, the product of diverse resources. Both male and female genitalia share the same undifferentiated structures in their embryological stages. These structures may develop differently though the organism’s ontogenesis depending on their reciprocal interactive processes with a combination of different resources including chromosomes, hormones, adjacent tissues, environmental conditions such as temperature, number of potential mates, food consumed in early development, maternal behaviour, and structural and topological location in the various compartments of the organism’s body plan. Saying that a complex trait like the sexual traits of dimorphic adults is mosaic means that it is composed of “developmentally dissociable” subunits (West-Eberhard 2003: 261). Evidence of this trait mosaicism can be found in the dissociability of
the wide variety of primary and secondary sexual characteristics found in mammals of the same species. This variability among the dimorphism of mammals is almost infinite, resulting in an array of intermediate phenotypic traits between female and male (e.g. body size, musculature, hairiness, dominance, aggression, and other behavioural traits) (cf. West-Eberhard: 260-62).

Mosaic traits are organized in their development. They are “choreographed” by the organism “through [different] causal factors giving rise to morphological associations” (Atchley and Hall 1991: 137). Different features of the same trait capable of independent variation may have different developmental pathways and may be responsive to different genetic and extragenetic resources but remain coordinated by the organism. For instance, cranial and jaw bone development in rats varies at different rates of growth. In the early development of the rat pup these exist as separate and independent structures. However, in the adult rat they form a mosaic complex trait. These two previously separate bones are now used by the organism in a coordinated way so that the length of the jaw correlates with the growth of the skull. Linking the two structures provides the organism the means to accommodate the new feeding behaviour it learns after weaning. Instead of requiring morphological structures that allow it to suckle milk from its mother, the coordinated growth of its jaw and skull enables it to masticate solid food (Zelditch 1988, Zelditch et al. 1992).

Another example of the mosaic construction of organismal traits from diverse sources is the construction of plant leaves from different histogenic layers of the meristem:

[each histogenic] layer of the meristem makes a [different] contribution to the formation of leaves. In dicots, the L1 layer contributes only to the epidermis, whereas the L2 and L3 layers contribute to the internal tissues of the leaf. The contributions of individual layers are not strictly lineage dependent, however. A cell from one layer occasionally invades a neighbouring layer, where it contributes to lateral organs in a manner characteristic of the new layer rather than the original layer, demonstrating its lack of commitment (Smith and Hake 1992: 1017).

The initiation and determination of the organism’s leaves are the product of diverse cellular, genetic, and environmental resources and the
organization and reorganization of the organism’s patterns of development. These include its hormonal changes, rates of cell division, changes in the plant’s polarity, position in relation to other leaves, and environmental influences (e.g. sun exposure, submersion underwater). Understanding traits as mosaics requires treating them as the product of the heterogeneous construction of self-organizing and reorganizing organisms.

Using the notion of heterogeneous construction, we can describe many traits as constructed by organisms from diverse sources. Traits are the product of contingent processes, the novel recombination of subfeatures or units, and the organism-directed choreography of distributed genetic, behavioural, and environmental resources.

3.7 WHAT DOES IT MEAN FOR HOMOLOGY TO BE MOSAIC?

Taking mosaic evolution and mosaic traits seriously opens up a new conceptual possibility space for comparative biology. Although proponents of a new developmental perspective tend to agree with West-Eberhard’s suggestion that evolution is mosaic rather than linear, they have not taken this combinatorial view to its inevitable conclusion.19 The upshot of this mosaic perspective is that the gene-centred, linear conception of homology no longer fits our conception of evolution. To fit, homology must be reconceived according to a mosaic view:

The traditional idea of homology visualizes a linear series of changes whereby an ancestral trait has been transformed into a descendent one ... By this idea different homologues may appear differently modified on different phylogenetic branches, but each descendent homologous trait has at its core a single ancestral trait (West-Eberhard 2003: 485).

‘Mixed’ homology departs from [the cladist and neo-Darwinist] tradition in recognizing that a single derived trait contains parts that are collectively homologous with several ancestral ones, not just one or a lineal series (West-Eberhard 2003: 491).

19 Only West-Eberhard (2003: Ch. 25) and Minelli (2003: Ch. 10) have made this suggestion.
Understanding the roles phenotypic and developmental plasticity play in mosaic evolution means rethinking the relationship between genes and phenotypic traits and the nature of biological causation. Phenotypic traits are not the morphological outcomes of developmental programs tightly regulated by genes. The relationship between genes and phenotypic traits is loose. Traits are developmentally plastic—the dynamic product of the organized construction of various genomic, cellular, ontogenetic, and behavioural resources by an ecologically embedded organism.

So far, I have criticized the neo-Darwinian view of evolution and homology. I have suggested that traits are not genetically prefigured outcomes. If traits are not the result of the unfolding of information contained in the vertically inherited genes, then the homology of traits cannot be determined on the basis of underlying genetic continuity.

I proposed that traits are constructed from contingent linkages and resources by the organism throughout its ontogeny. In the remainder, I draw out the consequence of this view. If homologues depend on descent from a common ancestor—a shared common cause—how can we reconceive the homology of traits if traits are the result of mosaic constructive processes of organization and reorganization?

### 3.7.1 Distributed Causes of Continuity

I have tried to show how the assumption of linear evolution and the privileging of genes as the ultimate source of continuity underpinning the continuity of traits has lead the neo-Darwinian view of homology to overemphasize the importance of genes in the development and evolution of organismal traits. Although obviously a resource used in the organism’s development, genes do not have the privileged role of directing architect or informational blueprint for building a trait. But if genes do not play this role and we cannot rely on genetic continuity to underpin the morphological continuity inherited through generations from a common ancestor, what is
the cause of this continuity—or more pointedly, what causes the homology of traits and ensures their conservation over generations?

Genes are not fundamentally responsible for phenotypic form, but neither are cells or tissues. As the examples above have shown, there is no one level of biological organization, nor one biological resource (e.g. genes, cells, tissues), that can be distinguished from other resources as the privileged causal source of homologues’ continuity over generations. Many different genetic, extragenetic, and environmental resources can contribute to the conservation of complex phenotypic traits. The causal contributions of the same resources may differ depending on the individual organization of the organism or the use it is put to in the construction of particular traits. While in some cases small changes in resources may result in large changes in the phenotypic traits, in others, large changes in the resources may have little or no effect (Pigliucci 2001: 364-66).

The use made of a particular resource (e.g. *Pax-6*) in one organism (e.g. a squid), or the use made of it in one part of an organism (e.g. in the olfactory organs of a squid), does not determine its use in another organism (e.g. fruit fly), or in another part of the same organism (e.g. in the arms of a squid).

Linear thinking and the privileging of genetic continuity assumes that the traits of organisms in each generation are the result of linearly passed on genes or genetic networks. In contrast, distributed thinking about the heterogeneous causes of traits takes traits to be the result of different developmental processes and reorganizing activities of both vertically and horizontally inherited genetic, epigenetic, developmental, behavioural, and ecological resources. Distributed causes are those that come from many different sources—not concentrated in one source:

[M]any heterogeneous components [are] linked together which implies that the [phenotypic] outcome has multiple contributing causes and thus there are multiple points of intervention or engagement that could modify the course of development. In short, causality and agency are distributed, not localized ... components are linked over time [and space] (Taylor 2001: 316).
Genes, cells, tissues, hormones, organ systems, developmental processes, and behavioural patterns are all potential causal resources within the ecologically-embedded organism’s milieu:

affecting each [other] in constant succession ... To regard one as controlling the other is quite illegitimate and introduces that dualism of agent and thing acted upon which runs through and vitiates all theories of nuclear dominance (Russell 1930: 157).

What causes the continuity of homologous traits is necessarily dependent on the organism’s environment and the purposes for which these resources are put to use. This means that what is conserved over generations is dependent on the organism-environment context. Depending on the context, it might be the interacting developmental pathways which are conserved, cellular connections, the use of other phenotypic or developmental resources, or certain generative systems of pattern formation.

Outlining how these concepts and causal connections can be reconceived in light of the mosaic perspective requires situating the organism at the centre of its own self-organized construction. In doing this, we rely on Kantian ideas of purposiveness (organism’s directedness towards a telos) and common generative capacity (i.e. the original stock of *Keime* and *Anlagen*) which provide a generic set of resources available to the organism. Understanding the organism’s conserved structures as a consequence of the purposes required for its mode of living also reflects a Cuvierian conception of homology.

The Kantian ideas of purposiveness and common generative capacities provide a philosophical basis for understanding the nature of distributed causality underlying a new mosaic conception of homology. This perspective conceives of the developing organism “as if it were fulfilling an end or purpose—that of arriving at the typical form and modes of activity of the species; it tends towards this goal in spite of difficulties, and the end is more constant than the way of attaining it” (Russell 1930: 6).

What is responsible for the conservation of homologues in particular contexts is determined by the use organisms make of certain resources in the construction of these traits.
The central point of understanding the construction of traits from the organism-centred perspective is that the purpose for which the organism uses any particular resource is not specified in advance of its use by the organism. Resources become causes only in the organism's use of them in conserving certain activities or resources for the construction of particular traits.

Genes, proteins, hormones, cells, tissues, and ecological resources may be conserved over generations for this purpose. However, this is not to say that the purpose for which a particular resource was used in past generations matches the purpose for which the organism now uses it. The organism may reorganize and recombine the phenotypic and developmental resources available to it for building new traits. To understand and compare any two traits as homologues or analogues, we must first understand which of the organisms' constructive activities correspond with one another.

Comparing the morphological traits or developmental pathways of two different organisms may reveal not one but multiple causal sources of continuity. The conservation of homologous traits, especially complex traits, may be the result of multiple distributed resources. These may be used by each organism being compared in a correspondingly similar fashion (or not). The use of these resources in particular ways by both organisms ensures the continuity of the particular phenotypic traits being compared as homologues. If the resources or developmental pathways being compared are due to some shared common resources or pathways, then they are homologues.

By focusing on the directive activities of the self-organizing organism, we capture the importance of the role of developmental plasticity as a generic capacity for constructing and reconstructing organisms given diverse and changing resources. Predating this perspective, Kant's ideas of fertile flexibility (Tauglichkeit) can be understood in terms of an updated discussion of developmental plasticity and his common generative capacity corrected and amended by providing cellular specificity and differentiation.
This mosaic, organism-centred view diverges from a strictly Kantian approach to organismal organization by extending the resources available to the organism in self-construction to include not just the organism's internal stock of *Keime* and *Anlagen* but also the environmental resources acquired from interaction with other conspecifics, learning, maternal behaviours, and horizontally inherited resources.

### 3.7.2 Multiple Ancestral Sources

The common ancestor of two or more organisms seems to be something that is easily judged. If one can trace back through many generations of organisms in their genealogical/phylogenetic trees to the same organism in an earlier generation, one may conclude that these two organisms share a common ancestor from which they are both descended. A similar view of shared ancestry is used by the cladist and neo-Darwinian conceptions of homology. This view holds that two traits are homologous if and only if they are inherited (through an unbroken phylogenetic lineage) from the same trait possessed by a single shared common ancestor.

The main difficulty with the neo-Darwinian view of homology is that phenotypic traits are not really “the same” traits passed on from one generation to the next. They are constructed in each organism. Organisms may utilize different resources in the construction and reordering of their traits. As a result, the origins of a mosaic trait are not traceable to a single common ancestor but are the product of heterogeneous resources inherited from multiple ancestral sources.

No single linear route of inheritance can be traced to the source of all these inherited resources because these may be inherited from a number of different genetic, epigenetic, developmental, and ecological routes and from diverse ancestral sources. Mosaic traits may be the product of diverse and distributed inherited resources from multiple ancestral features either in the same organism or from different organisms.
This means that the ancestry of mosaic traits may be traceable to several different sources depending on which feature of the trait is being compared as homologous with that of another. What counts as a common ancestor therefore becomes considerably less straightforward once we give up the neo-Darwinian approach to linear evolution and a gene-centred view of homology.

The mosaicism of evolution and traits, the diversity of ancestral sources, and the different developmental routes by which organisms may acquire these resources in the construction and reorganization of different subunits of its complex traits requires a radical reconception of the notion of shared ancestry. Extending the notion of shared ancestry involves including not just descent from a common morphological structure but also descent from a common ontogenetic pathway or behavioural pattern. Rather than “shared ancestry” a more apt way of describing this relatedness might be a shared common cause, resource, pathway, pattern, or source.

The morphological structures, developmental pathways, or behavioural patterns need not be conserved via the vertical inheritance from ancestor to descendent. The conservation of homologues may be the result of a range of common generative sources or mechanisms of inheritance—both vertical and horizontal. Extending the concept of homology in these ways is admittedly unique and probably controversial. I show in the next two sections, by discussing a number of examples, that the concept should be so extended.

Referring to common generative sources or mechanisms of inheritance instead of “common ancestry” avoids some, but not all, of the problems previous conceptions of homology had in identifying homologues. Because mosaic traits are the result of diverse distributed resources, this notion of common ancestry needs to accommodate their mixed ancestry. Mosaic traits may be compared to each other in terms of their common ancestry, the common generative sources of the subunits of these complex traits, or they may be compared as whole complex traits in terms of their partial homology. This amounts to tracing the histories of individual modular units, morphological parts, or developmental processes of organisms. In doing
this, we identify which subunits of these modular units “travelled together and for how long,” in which organisms and by which routes of inheritance they were conserved (cf. Doolittle 1999: 2124-8).

### 3.7.3 Degrees of Homology

Neo-Darwinism, together with a focus on morphological outcomes assumes an all-or-nothing approach to homology. This neo-Darwinian view took the relationship of homology to be complete correspondence due to descent from a common ancestor by an unbroken lineage. In contrast, partial homology is due to some but not complete correspondence due to descent from a common ancestor (or some common ancestors) by either a broken or unbroken lineage. Partial homology was, according to neo-Darwinians, inconsistent with evolutionary biology (cf. Donohue 1992). With this kind of condemnation, it is perhaps unsurprising that Louise Roth’s suggestion of partial homology (1984, 1988) fell on deaf ears:

> phylogeny has components of both continuity and change. We identify the elements of continuity as homologies; the change is called evolution ... Change occurs by degrees, and “sameness” is relative ... [Whole traits or structures] can be compared ... in terms [of the] ... partial homology [of] properties, individual features, or aspects of development (Roth 1988: 16-17).


This sustained opposition to partial homology meant that the only acceptable way homology could be conceived of was in terms of complete correspondence: “Correspondences are perceived as 1:1, hence for the majority of homology concepts only total correspondence ... is admitted. Everything else is either ignored or arbitrarily forced into the mold of a 1:1 correspondence” (Sattler 1994: 424).
The meaning of partial homology can be expressed simply as some correspondence due to some shared ancestral sources: a morphological structure or developmental process may share some but not all properties with another structure or process. Partial homology may exist among the complex traits of the same organism, traits of different organisms, or properties of traits in either the same or different organisms. Partial homology may be best articulated schematically in terms of a series of relationships. Take, for instance three different traits: AB, BC, and CD, where A, B, C, and D are different properties of these traits:

BC is [partially] related to both AC and CD because it shares one property with each of them. Such a relation also can be seen as a partial correspondence since BC corresponds partially to both AB and CD. The trait which exhibits the properties B and C, partially corresponds to trait AB and CD because it shares properties with both of them (Sattler 1994: 425).

Partial homology occurs when there is some correspondence between complex traits; where some but not all properties of certain traits correspond to each other. This may occur if organisms use diverse resources, (which may be acquired through a number of different horizontal and vertical mechanisms of inheritance), from different ancestral sources in constructing these traits.

In the next two sections I provide three examples of partial homology. I start with the partial homologies which may be found when comparing developmental schedules and life stages.

### 3.7.3.1 PARTIAL HOMOLOGY OF DEVELOPMENTAL SCHEDULES AND LIFE STAGES

Heterochrony is defined as a difference in the timing and rate of developmental stages (West-Eberhard: Ch. 13). I begin with an abstract characterization of a comparison of two organisms in terms of their development schedules—the temporal order of developmental stages over an organism's life history. In this schematic example partial homology will be illustrated.
Consider traits $x$ and $y$ of two organisms $P$ and $Q$. We may compare the individual developmental schedules in $P$ and $Q$ of $x$ and $y$. Suppose the development of $x$ occurs later in $P$ than it does in $Q$. But the development of $y$ occurs earlier in $P$ than in $Q$. In addition to comparing the individual developmental schedules of $x$ and $y$, we can also compare the overall developmental schedules, $P$ and $Q$.

The overall developmental schedules of these two organisms may correspond with one another even though the individual timing of some of their traits do not. Because of this, when we compare these two organisms in terms of their overall developmental schedules we are comparing “temporal mosaics” (Minelli 2003: 59). The overall schedules of $P$ and $Q$ may partially correspond in terms of the timing of certain traits while not corresponding with the timing of others, thereby being only partially homologous with one another.

These differences in the development, timing, and expression of traits in the different life stages of organisms may be evolutionarily valuable. And the dissociation and recombination of different heterochronic traits enables organisms more developmental flexibility and adaptability in the expression of their phenotypic traits resulting in new timing and order of developmental stages within an organism’s life history (West-Eberhard 2003: 241).

To flesh out the schematic example above, consider two different eggs from different egg masses of the red-eye tree frog ($Agalychnis callidryas$). These two eggs may vary significantly in the timing of certain developmental stages when compared to one another. One egg mass may hatch much faster than another, even if these are deposited by the same mother on the same plant. Accelerated hatching behaviour among eggs of the red-eye frog is the result of attack by snakes or wasps predating on the egg mass as the eggs are one of their favoured food sources. If the egg mass is under attack, some (but not all) eggs may hatch early and drop from the leaf the egg mass was clinging to into the water, thus escaping being eaten by the predator (Warkentin 2000: 503-10). The comparison of the timing of the stages of embryological development of individuals from the same
mother may differ greatly due to whether they are under threat of attack or not.

The timing of some of the stages of development in both groups of eggs may correspond to one another as homologues, while the timing of others, such as the time of their hatching, do not. If the overall developmental schedules of both groups of individual’s are compared, the timing of stages throughout their life histories would partially correspond as similar. This partial correspondence may be due to a common set of developmentally generic capacities and resources. But because some but not all of their stages temporally correspond to one another, their overall developmental schedules are only partially homologous. The plasticity in the order of their temporal stages and, in particular, the differential timing of their hatching behaviour means that these two individuals do not possess the complete correspondence required to be considered homologues according to the neo-Darwinian view of homology.

However, the partial homology of their overall developmental schedules is evolutionarily significant. Their partial homology can be explained in terms of a conserved developmental plasticity of hatching behaviour over generations which enables the organism to reorganize certain temporal stages of its developmental schedule for the purpose of avoiding predation.

### 3.7.3.2 THE INTER- AND INTRA-ORGANISMAL PARTIAL HOMOLOGY OF MOSAIC BEHAVIOURAL TRAITS

The mosaic trait of spoken language in humans is the product of the coordinated activities of organisms using distributed causal resources. Language learning of human infants begins with the noisy environments the infant is born into. The sounds in its environment include the speech of many language users as well as the sounds of other animals, machines, and weather conditions. This environment “furnishes the variable conditions for the ... self-assembly, in the course of early development, of the neurophysiological structures underwriting the child’s capacity to speak”
Because its environment is constantly changing, its neurological structures in turn change to accommodate different sound patterns or vernaculars of a particular linguistic context. These changes are coordinated with the development of the soft tissues of the mouth (e.g. tongue, lips, palate), as well as the jaws, teeth, throat, larynx, and the pattern of the organism’s breathing.

Language is a complex trait resulting from the coordination of these resources over the course of the child’s development. This trait is constructed and reconstructed through repeated practice and learning within a particular embedded environment. It can be compared either as a whole mosaic trait or in terms of different decomposable features (e.g. the formation of the tongue or larynx, the production of the sound “o”, or the utterance of an infant’s first word). Because the mosaic trait of language speaking relies on numerous distributed causal resources used in its development, complete correspondence between the language learning of one individual and that of another (even if between monozygotic identical twins), if not impossible, is highly unlikely. Partial homology between these two mosaic traits is the best we could hope for. Partial homology also allows us to compare as similar the development of this complex trait with other complex traits, such as the learning of a signed language, in terms of their partial correspondences.

Partial correspondence of mosaic behavioural traits may also be the result of the organism’s reorganization of certain phenotypic traits for the purpose of new behaviours. In this case, we may compare two different behavioural traits of the same individual in terms of their partial correspondence. This may be possible if certain subparts of behavioural traits dissociate from their original association with one trait and be used as a resource in the production of a new trait. The combinatorial nature of mosaic behaviours has been the subject of much ethological study (cf. Geist 1978 and Cairns et al. 1990). This type of change in phenotype is referred to as “behavioural heterochrony” and involves the co-option of certain behaviours, such as feeding, and the incorporation of these behaviours into courtship displays to attract potential mates. By utilizing known
behaviours in the activity of one purpose for that of another, the organism exploits the recognition of the associated behaviours in feeding in order to attract the attention of potential mates. For instance, female monk parakeets (*Myiopsitta monachus*) in search of mates behave in a similar way to young birds begging for food. Male birds, respond to these females as they would their own young by feeding them. As a consequent, the females acting out this juvenile behaviour are able to entice males into potential matings by exploiting the male parakeets associated fatherly feeding behaviour. In doing so, the female parakeets co-opt this behaviour for new purposes as part of their courtship behaviour (Geist 1978: 54).

In comparing the feeding behaviours of these individuals as young birds to their mating behaviours as courting adults, we find some similar correspondences in certain characteristics of the behaviour, such as the positioning of the body and begging cries, whilst other aspects do not correspond, (e.g. the bird to which the begging behaviour is directed differs from young birds who direct their begging to parents, and courting females who direct their begging to potential mates). This within-organism comparison of the two kinds of begging behaviour shows that although there are non-corresponding features of the begging behaviours of young parakeets and the courting behaviours of adult parakeets, some aspects of begging behaviours do correspond as similar. This partial correspondence means we can consider them to be intra-organismal partial homologues.

3.7.4 A COMBINATORIAL NOTION OF HOMOLOGY FOR PARTIALLY CORRESPONDING MOSAIC TRAITS

Understanding homology from a mosaic, organism-centred view means conceiving of traits as developmental combinations. These traits are the product of organismal self-construction from heterogeneous resources that are conserved over generations of individuals reflecting the fundamentally mixed ancestry and the mosaic nature of their organization, generation, and development. Heterogeneous processes can be compared as similar in terms of their homologous developmental pathways, morphological structure, use of genes, hormones, cellular activities, or
behaviours. A mosaic view of homology reflects the plasticity and heterogeneity of a reciprocal multilevel approach to organismal evolution and development.

Instead of assuming the continuity of structures from one generation to the next, the organism-centred view takes the generationally repeated structure of homologues as explicable in terms of the contingent products of intersecting processes. Applying this notion of construction to the discussion of homology and analogy allows us to highlight the contingent processes which lead to the construction of homologous traits. The conservation of organisms' homologous traits over a series of ancestors and descendents can be explained as the result of organisms' use of similar genetic, behavioural, and environmental resources in the construction of traits.

Mosaic traits result from the organism's mixing and recombining pre-existing phenotypic and developmental subunits for the purpose of building new phenotypic traits using novel linkages between these modular combinations:

Homology may involve not just different degrees of similarity, due to divergent modification, but may be ‘mixed’ … for example, the insect head evolved by the fusion of six ancestral body segments … Tracing mixed homologies requires separately [comparing as homologous] pairs or series of ancestral and derived states for different elements of the same descendent trait, not just lineal comparisons focusing on the modifications of a single ancestral form (West-Eberhard 2003: 485).

Mosaic traits correspond to other traits in terms of their partial homology or partial analogy. Their correspondence may be due to the recombination of diverse resources from multiple ancestral sources within the organism throughout its ontogeny, or due to the horizontally and vertically inherited resources from multiple ancestral sources over its phylogeny.

The organism-centred view of traits as heterogeneously constructed provides an alternative to the standard either/or thinking within comparative biology—that similar traits are either completely homologous or completely analogous. Until Roth's (1984) suggestion that homology
might be partial, the consensus in comparative biology was that homology was a 1:1 relationship of full correspondence of whole traits. This either/or thinking also meant that analogy and homology were seen as dichotomous—similar traits are either completely homologous or completely analogous. If an organism’s traits are self-constructed from multiple interacting resources under similar constraints, a sharp distinction between homology and analogy may not be possible. Understanding organisms as heterogeneously constructing their own traits dissolves the distinction drawn by neo-Darwinists between the two separate and non-interacting processes of shared ancestry and convergent evolution that are used to identify homologues and analogues respectively. It maintains an ontological separation between inherited traits and acquired traits. It takes the correspondence between organismal traits to be either the result of inheritance from common ancestors (through transmitted genetic information) or the result of environmental pressure. In doing so it relies on a Weismannian dualist assumption that there are two independently specifiable sources of form (as discussed in Chapters One and Two).

In contrast to the standard either/or thinking about homology and analogy, what have been traditionally thought to be independently evolved structures (analogues) may actually be the result of a combination of various common generative sources (or ancestral traits) combined together to form an amalgam trait in the descendent. Mosaic traits may be the “partial descendent” of a number of different ancestral traits. This suggests an alternative to standard dichotomous thinking about homology and analogy. It challenges the assumption that phylogenetic lines of descent are ontologically separate from an individual’s ontogenetic life cycle.

Although homologues and analogues are traditionally believed to arise from two completely separate and non-interacting processes—shared ancestry and convergent evolution respectively (inherited, acquired)—these processes are two aspects of the organism’s own ecologically embedded development.
3.7.4.1 Mixed Homologies

The mosaic traits of two different organisms may be partially homologous to one another due to their inheritance of a particular developmental resource from a shared common ancestor, but not share other inherited resources used in the construction of this trait, (such as the genes, cells, tissues), or its structural morphology.

For instance, the camera eyes of humans and octopi are both mosaic traits. The eyes of these organisms possess certain striking similarities of general structure and function. The camera eyes of octopi and humans both have lenses and retinas with photoreceptors. However, the photoreceptors of humans face the back of the eye, while those of octopi face the front (Nilsson and Pelger 1994: 56). Some of the ontogenetic origins of octopi and human eyes also differ. Whereas octopus photoreceptor cells differentiate from the epidermis, those of humans differentiate from the nervous system (Land and Fernald 1992). Because of these and other differences, octopi and human eyes are widely believed to have evolved independently rather than being inherited from a common ancestor (Kirschner and Gerhart 2005). They are thought to be analogues not homologues.

Because of this human and octopus eyes are considered to be homoplastic (not homologous). This conclusion ignores certain aspects of similar correspondences of development or structure shared by these complex traits. For instance, the eyes of octopi and humans utilize some of the same resources in the construction of eyes in different arrangements. Although octopus and human eyes initially appear to be analogous, it is perhaps more accurate to understand them as partially homologous due to their use of similar tissues, genes, cells, proteins, and organization of their visual systems, and partially analogous due to the different ontogenetic pathways which lead to the construction of similar outcomes. Because organisms may inherit resources from different ancestral sources used in the construction of mosaic traits, they may only ever be partially homologous (or partially analogous) to one another.
The traits which organisms inherit are frequently not completely isomorphic to one another. More often, they may be the result of various features of different traits inherited from distributed genetic and extragenetic sources. The comparison of these complex traits as whole traits then results in some being homologous, some analogous, and some neither. Mosaic homology identifies the numerous pathways and levels of organization on which homology can be found for each pair of traits being compared.

Because novel traits may be the result of reshuffling and new linkages between the already-present features of traits or the result of novel timing, the distinction between derived and ancestral traits of organisms may be less clear than the cladist and neo-Darwinian notions of homology have led us to expect.

3.7.4.2 Homologizing Fuzzy Parts and Developmentally Temporary Units

The capacity for developmental and phenotypic plasticity conserved in the organism’s original stock of Keime and Anlagen—in particular its capacity for exploratory behaviour within a conserved body plan, weak linkage, and the dissociation and rearrangement of the subunits of traits—leads to our recognizing that traits have multiple common causes.

Although much has been made of the dissociation of parts or modules, defining homologues as independent evolutionary modules (Wagner 1996) and assuming that a module is a bounded part insensitive to its intracellular and extracellular environment takes this notion of modularity too far. Modularity (West-Eberhard 2003), may invite confusion where I think degree of partness (McShea and Venit 2001) or levels of detachment (Moss 2008) may not. These subunits may be developmentally temporary or have fuzzy spatial or developmental boundaries, for instance: “in the multilayered mosaic of developmental subunits that we can recognise within a developing animal, there is a virtual continuum between the conventional germ layers and the clusters of set-aside cells” (Minelli 2003: 252).
Fuzzy bounded developmental or spatial organismal parts was first introduced with regard to the delimitation of the organismal segments in plants, e.g. leaf, stem, root, and in the tagmata of animals, e.g. head, thorax, and abdomen. “Root,” “leaf,” and “stem” are the names for simplified bodily organs of a vascular plant. They demarcate the plant in terms of their different structural features. Although these are often treated as organs with sharp spatial and developmental boundaries they often overlap with one another. This has been recognized in the study of botanicals, with the result that the fuzzy nature of these organs is now spelled out in the names used by botanists: root, root/stem mosaics, stem, stem/leaf mosaics, and leaf (Fisher 2002).

Many species of angiosperms produce intermediate growths (between what is normally considered a stem and a leaf). Plants of the genus *Chisocheton* have been studied extensively (Fisher 2002). These studies reveal that many species within this genus have indeterminate leaves—structures which are neither strictly leaf nor stem. The structures of *C. macranthus*, *C. pentandrus*, *C. trichocladus*, and *C. ceramicus* (as well as other species of this genus) can be best described as either stem-leaf mosaics or indeterminate stem-leaves (cf. Fisher 2002 and Fukuda et al. 2003). This kind of indeterminacy may also be seen in the formation of the leaf-stem organs of the bladderworts, *Utricularia*, and the root-shoot organs of the perennial river weed *Podostemaceae* especially *Podostemum ceratophyllum* (Ameka et al. 2003), *Zeylanidium lichenoides*, and *Ledermannella bowlingii* (Ota et al. 2001 and Jäger-Zürn 2003), and the leaf-shoots of *Asparagaceae* (Sattler 1984: 383-383).

Among seed plants, a caulome is defined as a stem or the axis of a flower, whilst a phyllome refers to a lateral appendage, (e.g. leaves, petals, or stamens) (Sattler 1994: 432). Comparing these intermediate structures in terms of their similar correspondence with other structures results in a variety of partial homologues:

the position of the leaf and branch may be inverted so that the leaf is more distal than the phyllome-conjunct branch ... [W]e would have to conclude that the inverted leaf is homologous with a shoot [of another plant] and the inverted shoot with a leaf ... [or] the inverted leaf is homologous with a shoot [in terms of its
bilateral position] but homologous with a phyllome leaf [in terms

The possible partial homology can either occur between organisms or within
the same organism at the same time, at two stages of the organism’s life
time, or during different ecological conditions (e.g. between different leaf-
stem structures of heterophyllous plants depending on whether they are
fully submerged in water, laying on the surface, or aerial) (cf. West-
Eberhard 2003: 174 figure 7.6).

Fuzzily bounded, developmentally temporary parts of organisms also
occur among the bodily segments of vertebrates and insects—head, thorax,
and abdomen. This fuzziness makes comparing these parts of organisms in
terms of their similar correspondence with one another less straightforward
than if these were construed as rigidly bounded, spatially discrete parts.

In comparing as similar the corresponding segments of a praying
mantis and a fire ant, we must distinguish which of the organisms’ body
segments correspond to each other. Among insects, the thorax is generally
defined in terms of the second body segment—between the head and
abdomen. The thorax is specifically characterized as the only segment
which has legs. But in some arthropods such as praying mantises and
centipedes, there may be appendages that are located before the legs of the
thorax but not in the head of the organism (Minelli 2003: 79-81). These are
typically used for either capturing prey, tearing and manipulating food, or
poison containing tools (called “maxillipeds” (Minelli 2003: 81). In
comparing the corresponding segments of the praying mantis to the fire ant,
there are a number of equally possible options:

from the point of view of the specialisation of the appendages, one
says that the head of these arthropods [i.e. the praying mantis]
comprises one or a few segments more than the head of [the fire
ant] lacking maxillipeds. On the other hand, [because] segments
with maxillipeds may [be considered] ... non-cephalic ...[or
thoracic], despite the feeding specialization of their appendages ...
Boundaries between conventional tagmata are often less clear
than anatomists would hope” (Minelli 2003: 81-82).

This becomes even more fuzzy when dealing with organisms such as
centipedes and millipedes. There is wide disagreement over how many
bodily regions millipedes have, the answer depending on what is counted as the thorax and trunk. If only strictly bounded modules are possible units of comparison, homologizing these fuzzy intermediates would not be possible.

Comparative biology in general, and homology and analogy in particular, are used to compare corresponding traits of organisms as similar and to reconstruct their common origins in order to identify organisms as members of the same or different species.

The next chapter follows on from the previous (the organism-centred view) and the present chapter, tying together the heterogeneity of organismal trait construction with a mosaic view of evolution in its reconception of species.
CHAPTER FOUR

Reincorporating ontogeny back into a conception of Species

The observation that different species of organisms have different forms and behaviours may seem obvious. But what exactly does this mean and what makes a particular organism the kind of organism that it is? For instance, what makes a fox a fox? What makes foxes develop the characteristics that they do? What makes fennec foxes have large ears, termites consume wood and build mounds, wildebeest migrate, legumes fix nitrogen, or insects choose to lay their eggs on the leaves of specific plants? These traits appear to be reliably passed on from one generation to the next among organisms of the same species. These observations lead to the generalization ‘like produce like’—organisms produce offspring like themselves. How these forms and behaviours are maintained from parent to offspring within a species has been discussed across thousands of years of philosophical discussions and natural history. From antiquity, species have been thought of as quintessential natural kinds. Organisms of a particular kind possess essential features, sets of properties, or relationships shared by all individual organisms of that kind.

This view was found to be less well equipped when it came to explaining similarities among different species of organisms. Many striking morphological similarities shared across species were highlighted in
Haeckel’s work (1866). In his ill-fated recapitulation theory, Haeckel illustrated the remarkable morphological similarities among the same stages of early development in species of vertebrates as different as pigs, crocodiles, mice, and platypuses. He showed that embryos of similar stages of development in diverse species have almost identical morphological features when compared to each other. The embryos of these different species were shown to be morphologically much more similar to each other than to the adult forms of their respective species. These observations challenged the traditional essentialist view that species could be best conceived of as sets of similar organisms that share an underlying essence or a common set of traits.

Haeckel’s observations of the similarities among different species introduced two concomitant problems: members of the same species may vary greatly in their morphological features, and organisms of the same species may display different morphological features at different stages in their life cycle. The first of these problems is widespread among sexually reproducing organisms. The sexual dimorphism such as that between female and male mammals (e.g. women and men, and tigresses and tigers) and birds (e.g. peacocks and peahens) mean that the females of many species share a number of striking characteristics with females of different species (e.g. among mammals: lactation, pregnancy, menstruation, ovaries, uterus) that they do not share with the males of their own species.

In addition to these dimorphic variations among individuals of the same species, some organisms also vary their morphologies within their own lifetime. A similar observation to Haeckel’s own can be made by any amateur Lepidopterist. Consider the larval stage—the fleshy, leaf-eating, crawling, multi-pseudopod form of the worm-like caterpillar—of many species of pre-metamorphosed butterflies and moths. They morphologically resemble each other much more than they resemble the form they later acquire in both their pupal and postmetamorphic adult stage, in which they possess a thin body, six-legs, a long proboscis enabling them to extract nectar, large wings, the ability to fly, and (if female) lay eggs. These widely varying morphological characteristics within species make them
particularly unwieldy biological kinds to be conceived of in terms of a fixed set of features common to all members of the species.

What (if anything) is shared by organisms whose characteristics vary dramatically between different individuals of the same species, and can change depending on a number of different factors, including stage of development, season, temperature, food supply, or environment? As the previous chapter on homology showed, there can be innumerable ways in which organisms can be described and compared as similar to one another. But only a few of these provide generalizations that facilitate the making of hypotheses, directing experiments, and providing knowledge about species.

Rather than relying on wildly variable morphological traits as the essential features of a species, something else was required. This led to the suggestion that what was common among individuals of a particular species was their behaviour, in particular, their ability to generate new offspring through sexual reproduction with conspecifics. This suggestion was first articulated by John Ray in the 17th century (cf. Sloan 1972). A century later it was revised and reconceived as part of the French naturalist Buffon’s own notion of species as groups of organisms whose members interbreed and produce fertile offspring.

[I]t is neither the number nor the collection of these similar [organisms] which makes the species, it is the constant succession and uninterrupted ... destruction and renewal of beings ... The species is thus only a constant succession of individuals able to reproduce together (Buffon 1753: 355-56).

Buffon argued that our knowledge of species lies in our knowledge of the behaviour of individual organisms. We can extend this knowledge of individual observed behaviours when our senses detect regular or generalizable patterns of activity or form among individuals. Although this appears in many ways a contemporary approach to understanding the nature of species, it was conceived a century before Darwin. Still a product of his time, Buffon, like his contemporaries, conceived of species as static entities which do not substantially change over time.

Changes in species over time by means of descent with modification was an idea introduced by Darwin (1859). Instead of conceiving of
individuals of a particular species as essentially similar or sharing a homogeneous set of traits, Darwin’s theory of evolution recognized that the individuals of a species may vary. If these variations were of beneficial value to the organism—by improving its foraging abilities, skill in avoiding predators, ability to entice mates, reproduce, and increase its fecundity within particular environmental circumstances—these variations will be inherited by the next generation. If beneficial to this generation, they can in turn be similarly passed on to the next generation. (And conversely, those that hinder are not.)

Darwin dramatically illustrated his theory in studies of the variations among the species of finches during his expeditions of the Galápagos Islands. Evolutionary change over time is dependent upon heritable phenotypic variation within species. Phenotypes among individuals of a species can change quickly in a matter of months, depending on food supply or shortage, climate, or ecology. And phenotypes of a species can evolve slowly over generations. The characteristics common to a species at time T1 can be discernibly different from those at time T2 and even more markedly at T10. Organisms are constantly dying and new organisms are born. As a result, the species is not a static entity, but one that is constantly changing its parts (if one’s metaphysics of species is that of individuals) or members (if species are groups or sets).

Mayr explicitly incorporates both a Buffonian and Darwinian notion of species in formulating his own conception of species, the biological species concept (BSC) (Mayr 1942, 1968). In the original form, the BSC stated that: “species are groups of actually or potentially interbreeding natural populations, which are reproductively isolated from other such groups” (Mayr 1942: 120). This conception of species answered the question, What unifies the members of a species?, in terms of an actual or potential physical connection (i.e. in terms of both the copulation of sexually mature organisms and in the generation of new organisms that result). This physical connection between members of the same species was thought to support the belief that there is indeed a natural division in biology upon which a natural classification can be based.
However, there were exceptions to this purely reproductive conception of species. Reproduction can occasionally occur between members of different species. Some of these exceptions were discussed by Buffon (1753). In *The Donkey*, Buffon discusses the infertility of hybrid offspring (e.g. mules) which are the result of the reproductive relationships (either through natural copulation or through artificial insemination) between two animals of different species (e.g. in the case of the mule, a donkey and a horse). But Buffon argued that this exception did not pose the problem for his conception he originally thought as the offspring of the donkey and horse was not fertile (Buffon 1753, cf. Gayon 1996: 224-26). Later amendments to his conception of species to accommodate this and other exceptions shifted the focus onto other behaviours of organisms besides reproductive ones. Their modes of existence and their life activities within an ecological habitat were not adopted by Mayr.

The problem Buffon raised about hybridity did not go away. Mayr’s solution was to deny that hybridization between organisms of different species was evolutionarily significant. He maintained that the majority of hybrids are “totally sterile,” and “successful hybridization is indeed a rare phenomenon” (Mayr 1963: 133). Since hybrids are rare, they only ever amount to “evolutionarily unimportant mistakes” (Mayr 1963: 133). This view was echoed by W. H. Wagner: “hybrids have occasionally appeared, but most have been sterile or ill-adapted ... [a] kind of evolutionary noise is produced” (Wagner 1970: 146).

Although mules and other animal hybrids tend to be sterile, many plant hybrids are fertile. Most hybrids are not completely fertile or completely sterile but display varying capacities of fertility and sterility that fall along the middle of this continuum:

Although today it is often said that ... hybrids are usually or mostly sterile, many show a great deal of fertility and it could be argued that the majority are fertile to some degree. In fact every stage from complete sterility to complete fertility exists, and it is difficult to make generalizations (Stace 1975: 39).

In addition to hybridity, there were further challenges to the reproductive concept of species. Conceived in terms of sexually reproducing organisms,
the BSC effectively denied specieshood to asexual species. Mayr (1970) argued that asexually reproducing organisms were an exceptional case.

But increased understanding of the activities of organisms within the superkingdoms Bacteria and Archaea meant that Mayr’s exceptionalism was grossly misplaced (cf. Woese 1987 and Woese, et al. 1990: 4576-79 for discussions of Bacteria and Archaea). Whereas asexual reproduction is ubiquitous within two of the three superkingdoms, (Bacteria and Archaea) and is common in some kingdoms of the third (Eukarya), sexual reproduction only occurs within some (but not all) multicellular organisms of the subkingdoms Animalia and Plantae (cf. O’Malley and Dupré 2007: 156). Pace Mayr, sexually rather than asexually reproducing species are the exceptional case. The ubiquity of asexually reproducing species added to the pressures on the original reproductive conception of the BSC. This eventually led to the reconfiguration of the BSC from a gene-centred perspective.

After discussing Mayr’s revised gene-centred perspective of species, I show how his BSC and other gene-centred views of species are committed to dichotomous thinking about ontogeny and phylogeny. These commitments entail three core beliefs about species: species are the result of linear genetic causation; strong preformationism; and the claim that species can be best understood by the phenotypes of adults. In the second half of the chapter, I propose an alternative to gene-centred view of species and its underlying commitments. My organism-centred perspective relies on a Buffonian conception of species as a succession of individual organismal life cycles, a Taylorian view of construction, and a revised Kantian view of reciprocal self-organization. It aims to reintroduce ontogeny back into the concept of species. Reconsidering species in terms of this Buffon-inspired view means conceiving of organisms and species as the result of distributed resources, generic preformationism, and the activities of organisms over their whole life cycle. Lastly, I consider and dismiss Dawkins’ (1982) suggestion that organisms’ constructed environments can best be understood as extended phenotypes.
4.1 Mayr’s Gene-Centred Perspective of Species

In the middle of the 20th century a new gene-centred understanding of natural selection, evolution, heredity, and the stability and variation within species became widely accepted (Mayr 1942, 1963, 1970, Dawkins 1976). This neo-Darwinism diverged from Darwin’s original conception of descent with modification by taking genes as the causally most important factors in evolution and in the development of organismal form. In *The Selfish Gene*, Dawkins described how genes, not organisms, were the “motors of evolution.” Genes build organisms that are vehicles for their own replication. This view was later extended to include all morphological traits, behaviours, social relationships, and habitats of organisms; they are merely “phenotypic effects of a gene ... [they] are the tools by which it levers itself into the next generation, and these tools may ‘extend’ far outside the body in which the gene sits, even reaching deep into the nervous systems of other organisms” (Dawkins 1982: vi).

An organism’s phenotype is encoded in the information within its genotype. Genes, as informational programs, code for traits (cf. Moss 2001: 85-87). This focus on genes was thought to be self-evident—natural selection acts on the genes responsible for building organisms. Natural selection occurs by changing the frequency of genes from ancestral generations to descendant generations. It selects phenotypes that confer the greatest fitness. Because genes code for these phenotypic traits and genes, unlike anything else, are reliably transmitted directly from one generation to the next, it is genes, rather than anything else, that are the true cause of organismal form, variation, and change over time. This direct, linear transmission meant that genes were conceived of as the ontologically prior causal force and most important causal factor responsible for organismal stability and variability of species over generations. Ecological and epigenetic factors may only indirectly affect the unfolding of the genetic program but cannot cause changes to genes. Linear genetic causation is unidirectional—going only from genes to organisms.
The widespread influence of this gene-centred perspective is witnessed by the definition of evolution provided in most evolutionary textbooks as the “change in gene frequencies” (cf. Grant 1977, Futuyma 1986, 1998, Ridley 1993).

The inheritance of the same genes from one generation to the next was thought to ensure the stability of species-specific traits. Phenotypic variation among individuals of a species was ultimately due to genetic mutations and genetic variations within the species population. This meant that although species could be considered reproductive or ecological units, the true cause of phenotypic variation among individuals of the same species was to be found in their genes—a species is a genetic unit. The BSC was reformulated from what has by some been called an interactionist perspective:

This concept stresses the fact that species consist of populations and that species have reality and an internal genetic cohesion owing to the historically evolved genetic program that is shared by all members of the species. According to this concept, then, the members of a species constitute (1) a reproductive community. The individuals of a species of animals respond to one another as potential mates and seek one another for the purpose of reproduction. The species is also (2) an ecological unit that, regardless of the individuals composing it, interacts as a unit with other species with which it shares the environment. The species, finally, is (3) a genetic unit consisting of a large intercommunicating gene pool, whereas an individual is merely a temporary vessel holding a small portion of the contents of the gene pool for a short period of time (Mayr 1992: 17).

The interactionist perspective of biological form (what I have also referred to as the “combined view” in Chapter One), is the view that biological form is the result of two ontologically separate but interacting spheres of activity: moulding by a naturally selecting environment and the unfolding of the information contained within an organism’s genetic program. The selecting environment gradually modifies generations of organism’s phenotypic traits on the basis of whether they increase or decrease the likelihood of the organism to successfully mate and pass on its genes to future offspring. Those genes that are reliably passed down from parent to offspring contribute to the species-specific blueprint for building
new organisms of the next generation of the species. The species gene pool is the result of the selecting force of the environment on genetic mutations occurring over numerous generations.

The organizational form of organisms is preformed—written in its genetic code. The organism’s internal genetic code interacts with the external environment through the course of its ontogeny. Organismal ontogeny amounts to translating the information in the genetic code into a design blueprint that can be used to build an organism.

This interactionist perspective sets up the genetic code and the environment as two ontologically separate but interacting sources of information. Although this perspective conceives organismal organization as the result of both genes and the environment, these are not equal interactants. Genetic causes are systematically privileged as the primary source of causal power, whereas extragenetic causes or environmental causes are considered secondary or as contributory to these. They are bracketed off as background conditions within which genes operate. This results in the genes, rather than every other causal factor, being most important (Griffiths and Gray 2001: 195). Mayr emphasizes the fundamental gene-centred perspective of species:

it is important to focus on the basic biological meaning of the species: A species is a protected gene pool. It is a ... population that has its own devices (called isolating mechanisms) to protect it from harmful gene flow from other gene pools (Mayr 1992: 17).

This perspective systematically privileges linear genetic causes of species as providing the “internal genetic cohesion [and] genetic program that is shared by all members of the species” (Mayr 1992: 17). Mayr explicitly states his belief in anti-essentialist and anti-typological thinking from the start. Because of the variability among organisms of any species there can be no set of traits which all organisms of a particular species share (Mayr 1992: 16). Ostensibly, this anti-essentialism commits him to the belief that there are no essential species-specific traits common to all individuals of a particular species.

However, I argue that Mayr’s interactionist revision of the BSC does not escape this kind of essentialist-thinking. He commits himself to two
kinds of essentialism. Firstly, he essentializes genes and gene pools: “species have reality and an internal genetic cohesion owing to the historically evolved genetic program that is shared by all members of the species” (Mayr 1992: 17). Secondly, he essentializes the sexual reproductive relationships among members of the same species: “animals respond to one another as potential mates and seek one another for the purpose of reproduction” (Mayr 1992: 17). Consequences of these commitments will be explored with regard to the assumption that species are cohesive entities over the next few sections.

4.1.1 ESSENTIALIST-THINKING AND THE ASSUMPTION OF SPECIES’ “GENETIC COHESION”

Essentialist-thinking about genetic programs and reproductive relationships is entailed by the underlying ontology of the gene-centred perspective of the BSC. The shared species-specific genetic program is both the cause of a species’ cohesion and gives a species its metaphysical reality. The genetic cohesion of a species is maintained through actual or potential gene flow between its members; this provides a physical connectedness of individual organisms to other conspecifics. Mayr emphasizes the importance of this exchange of genes because he believes “mixing the genes of two different species leads to a high frequency of disharmonious gene combinations; mechanisms that prevent this are therefore favored by selection” (Mayr 1992).20 As such, species are properly understood as protected gene pools. The protection of a species’ gene pool is ensured by what Mayr calls “cohesive mechanisms” that “protect it from harmful gene flow from other gene pools” (Mayr 1992: 17). Organisms that share the same gene pool are thought to have access to any genetic mutations which may arise in individuals throughout the species population. Because genotypes are causally determinative of phenotypes, if the gene pool is

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20 As I will discuss later, the opposite has been observed with regard to bacterial species. In some, it is in the combining and exchanging of genetic materials with heterospecifics that allow individuals of a particular species to acquire resources enabling them to construct evolutionarily advantageous phenotypes.
shared so is the phenotypic expression of these genes. If the phenotypic expressions of the organisms were relatively homogeneous, then natural selection would act uniformly in the population. This would ultimately mean that natural selection would restrict the possibility of persistent and stable polymorphisms among subgroups which could eventually lead to speciation.

Reliance on the restriction of gene flow between members of different species is based on an assumption that unrestricted gene flow between members of different species cannot be sustained. If there is unrestricted gene flow between members of different species, the current diversity of species would cease to exist. Such unrestricted gene flow would result in the two species becoming less genotypically and phenotypically distinct. Increased gene flow between individuals of different species would eventually result in the two previously separate species merging to form one genetically and phenotypically amorphous species (Mayr 1970). If reproductive relationships and gene flow were not restricted to conspecifics, an increasingly homogeneous gene pool shared by organisms of different species would result. By producing an increasing homogeneity of both genotypes and phenotypes of organisms as the boundaries between species eroded, Mayr worries this would result in a decrease in the biodiversity (Mayr 1982).

In contrast, new species are formed when populations become reproductively isolated from one another and gene flow between these groups stops. Species are separated from one another “by a complete biological discontinuity” (Mayr 1992: 20). It is this complete separation from other species which “protects [the species] from harmful gene flow from other gene pools” (Mayr 1992: 17). Different species are sharply demarcated from one another by what Mayr calls a “gap.” This gap “exists between populations that coexist ... at a single locality at a given time which delimits the species ... one finds each species clearly delimited and sharply separated from all other species” (Mayr 1992: 19). He highlights the crucial significance of this sharp discontinuity between species: “Most important, no hybrids or intermediates [are] among these [different] species ... each is a
separate genetic ... system separated from the others by a complete biological discontinuity, a gap” (Mayr 1992: 20).

A similar notion of cohesion forms the basis for an historical conception of species as a lineage of organisms—an evolutionary unit of organisms that is “held together by cohesive forces” and responds to natural selection as a unit (Williams 1970: 357). Mayr, following Williams, understands these cohesive forces in terms of gene flow, genetic homeostasis, and common selective pressure (cf. Williams 1985 and Ereshefsky 1992: 385-87).

Viewing species as genetically cohesive units is not unique to the BSC. A number of other conceptions of species including the isolation, cohesion, mate recognition, phylogenetic, and cladist conceptions of species share this view. The BSC, isolation, reproductive, and mate recognition conceptions of species explicitly rely on the importance of potential or actual physical relationships of sexual reproduction and the exchange of genes between conspecifics it facilitates as justification for internal species genetic cohesion and genetic isolation from members of other species. Reproductive relationships and genetic cohesion are implicitly relied upon as necessary for the neatly bifurcating pattern of unbroken and unreticulated lineages central to both cladistic and phylogenetic species concepts (PSC). Genetic cohesion and genetic isolation are assumed by these species concepts in their definition of species as an unbroken lineage—a lineage maintained by a sequence of reproductive relationships restricted to conspecifics and ensured by exclusive vertical transmission of genetic material from one generation to the next.

PSCs conceive of species in terms of the bifurcating branching tree pattern of evolution. In its weaker form, a PSC conceives of a species as “a lineage (an ancestral-descendent sequence of populations) evolving separately from others and with its own unitary evolutionary role and tendencies” (Simpson 1961: 153). In its stronger form, it relies on identifying species in terms of a group of organisms which share a monophyletic lineage (McKitrick and Zink 1988). A monophyletic lineage is an unbroken sequence of ancestor-descendants that includes all and only the
descendants of one common ancestor. By ruling out polyphyletic lineages, the PSC denies specieshood to any groups of organisms that are the descendents of more than one common ancestor. By ruling out paraphyletic lineages, it denies specieshood to groups of organisms which includes some but not all of the descendents of a common ancestor.

Although intended to explain the unifying features of a species (as well as those separating species from each other), talk of species cohesiveness, cohesive mechanisms, and genetic cohesion does not succeed in explaining this unity of (or the disunity between) species but succeeds only in presupposing it (cf. Ereshefsky 1992: 381-87). The assumptions of species cohesion and the apparent circular arguments on which they are based are held not just by the BSC but by other gene-centred concepts of species as well.

4.1.2 THE ONTOGENY/PHYLOGENY DICHOTOMY

Gene-centred and interactionist perspectives of species take the genetic program to be the essential species-specific inheritance shared by all members of the species. Because they are mortal, organisms are “merely temporary vessels” rather than “immortal replicators” of the species (Mayr 1992, Dawkins 1989). The persistence of a species generation after generation is therefore not dependent on the lives of individual organisms but on the transmission of the species-specific genetic program from one generation to the next. This view replaces Buffon’s view of species as the succession of individual life cycles with the gene-centred perspective. Organisms do not make species, genetic programs do.

This view effectively separates an organism’s phylogeny from its ontogeny—organisms are the species they are not because of their ontogeny but only because of their phylogeny. They inherit their species-specific features from an unbroken series of ancestors. An organism’s phylogeny
traces the ancestor-descendant relationships as the route by which information contained in the species-specific genetic program is inherited. Phylogeny is the history of inherited genotypes. It is the transgenerational transmission of information that is thought to ensure the stability of the organizational form of members of the same species. And it is the reliable passing on of the species specific information of the genetic blueprint from which genes build an organism. This provides a set of instructions for building an organism according to a particular species format that is independent of any environmental context. Conspecifics share something like a species-specific homeostatic genotype that encodes the information to build organisms with the same basic phenotypes regardless of most external environmental perturbations (cf. Ehrlich and Raven 1969, Mishler and Donoghue 1982).

This dichotomous thinking about phylogeny and ontogeny construes the evolutionary causes of species to which an organism belongs to be ontologically distinct and separate from the causal sources of its ontogeny. This often results in the role of phylogeny emphasized almost to the complete exclusion of the role of ontogeny among many of the conceptions of species discussed above. The commitment of the gene-centred perspectives on species to dichotomous thinking about phylogeny and ontogeny entails three core beliefs about species: linear genetic causes are metaphysically distinct and privileged over all other extragenetic distributed heterogeneous causes, strong preformationism, and an adult-centred view of species. These are discussed in turn.

4.1.2.1 LINEAR GENETIC CAUSATION

What I call “linear genetic causation” is the metaphysical view that the causes of species-specific organismal organization are passed on in a direct unidirectional flow of energy or information (cf. Taylor and Haila 2001: 522). The direction of causation is either unidirectional from gene to organisms or from the natural selective factors in the environment. A gene-
centred perspective of species holds genes to be the privileged cause of evolutionarily significant variation among species—Dawkins' replicators. Privileging linear causation over other directions of causation has been referred to as “linear thinking” (Bateson 2001: 149). Linear thinking and the particular metaphysical view which underlies both the gene-centred perspective and gene-centred interactionism—linear genetic causation—takes genes to be the most important causal factors shaping the organic organization of organisms. These views accept that genes do not act alone. They interact with and utilize internal epigenetic factors and external factors in the environment in building an organism. These form the raw materials that are used in the execution of the genetic program. But unlike epigenetic and ecological factors, only the genetic information coded within the organism’s genes is directly transmitted from parent to offspring. This direct transmission justifies the apportionment of causal priority to the genetic factors over all other factors. This kind of linear thinking takes the causes of organismal organization to be one-way.

The environment is simply a constant repeatable context which can easily be bracketed off. It constitutes the usual conditions of development which facilitate normal development, *ceteris paribus*. By bracketing off all causes but genetic ones, it characterizes evolution solely in terms of the change in gene frequencies. This emphasis on linear genetic causation leads to a systematic overestimation of the causal contribution genes make:

It ... assume[s] that the distribution of characters of organisms in an evolving population reflects the frequency of particular naturally selected genes currently found in that population. A consequence of this approach is that only a genetic currency [is used] when describ[ing] evolution (Laland, Odling-Smee, and Feldman 2001: 125).

Privileging linear genetic causes as most important in the construction of species specificity systematically excludes the role of other kinds of causes.

**4.1.2.2 Strong Preformationism of Species-Specific Forms**
These gene-centred conceptions of species are committed to a preformationist notion of species-specific form. An organism’s species-specific form is preformed in two ways: in the inherited information contained in the genetic program that exists prior to the organism’s life in the world, and in the monophyletic pattern of its species tree tracing the unbroken ancestor-descendant relationships from a single common ancestor. I focus on the former source of preformationism: the genes or genetic program.

Genes, or rather genotypes, are conceived of as the inner directing forces organizing the form and development of the organism. The heritable information contained in the genes codes for all the species traits that are transmitted from parent to offspring, ancestors to descendants. An organism’s species-specific form is preformed in the genetic program as a set of instructions for building an organism of a particular kind: “development is the execution of the genetic program for the construction of a given species of organism” (Davidson 1991: 11). It is determined independently, in advance of the organism’s life and development in the world. The form of the organism is contained preformed in the information within the genotype:

Recent results indicate that for several well-studied organs there is a single gene or a small set of genes that specifies the basic form of the organ. These genes are expressed early in development in wonderfully complex patterns that prefigure the complex form the organs will take ... [T]heir key role [is] in generating organic form (Krasnov 1997: 235-6).

### 4.1.2.3 THE ADULT-CENTRED VIEW

The third core belief of the gene-centred, linear perspective of species is that the genetic program is a program for building a complete adult organism. This focus on the adult stage of the organism rather than the embryo, juvenile, adolescent, or metamorphic stages is partially justified by claiming that we must base our species concept on adults as it is the reproductive capacities of sexually mature adults that are responsible for
propagating the species. Viewing natural selection as acting only on the traits of sexually mature organisms that improve or diminish their fecundity means the proper judgment of an organism’s form is a judgment of its adult fitness. This perspective construes natural selection as an external force that designs organisms. Instead of locating the “agency for the acquisition of adapted form in ontogeny—that is, in some theory of epigenesis, [this] view ... expels all manner of adaptive agency from within the organism and relocates it in an external force ... as ‘an algorithm’ of natural selection” (Moss 2003: 6). One that is applied only to adult forms.

4.2 AN ORGANISM-CENTRED CONCEPTION OF SPECIES

The division between phylogeny and ontogeny, the preference for relying on the former over the latter in conceiving of species, and the three core beliefs that follow from the dichotomous thinking of a gene-centred perspective are not the only, or even the best, ways of conceiving of species. In the following I propose an alternative to the gene-centred and interactionist perspectives of species. I argue that the phylogeny of a particular species is neither ontologically distinct nor separate from the individual ontogenies of organisms’ life cycles. In place of these gene-centred, interactionist perspectives, I argue for an organism-centred perspective that conceives of species as the recurrent succession of organismal life cycles which are causally connected in a spatiotemporally ordered series. Understanding species in this way draws its main inspiration from the conception of species found in Buffon. This organism-centred view also relies on reciprocal self-organization of organisms (Kant 1790), the acquisition of resources from distributed rather than concentrated sources, and the metaphor of heterogeneous construction (Taylor 2001).
4.2.1 Species as a Succession of Individual Organisinal Life Cycles

Buffon is perhaps best known for his criticisms of the classification system of his more famous contemporary, Linnaeus. In particular, he criticized the Linnaean system for not being based on real biological entities. Buffon considered it an abstract piece of complicated terminology constructed to facilitate the memorization of plants and animals by giving each a name: “it is at the very most only a convention, an arbitrary language, a means of mutual understanding. But no real cognizance [connaissance réele] of things can result from it” (Buffon 1749: 104). Although admitting that this abstract system was obviously useful as a tool to remember organisms in terms of a hierarchically ordered set of names, he argued that it did not reflect any physical reality or order in the world. The classes of the Linnaean system—kingdoms, phyla, orders, families, and genera—were merely fictions. Only species were “real” concrete biological entities (Buffon 1749, Gayon 1996: 215-25).

Buffon’s natural philosophical project was to reveal the physical reality of a species considered in time: “[a] species … exists only when we look at Nature in its temporal succession” (Buffon 1753: 99). In pursuit of this he relied on extensive observations and descriptions of individual organisms. He argued that it was only after we have studied all the minutiae of an organism’s organization and behaviour that it would be possible to order these facts spatially and temporally, within a particular historical sequence. The generalized facts we glean from these naturalist studies on individual organisms are the “physical truths” of a species. These physical truths are only acquired through the precise description of an organism’s morphology, internal activities (digestion), external activities (locomotion), and its mode of living within its environment—not from ideal abstract knowledge or universal truths (Buffon 1749: 100-11). This view of species was revolutionary. Buffon was the first to conceive of species ecologically, as spatio-temporally extended, environmentally embedded series of life cycles:
[organisms’] conception, the time of gestation, [the] birth, the number of young, the care shown by the parents, ... the places where they live, their nourishment and their manner of procuring it, ... their hunting, and finally, the services which they can render to [them] and all the uses which [they] can make of them (Buffon 1749: 111).

This material connectedness of each individual life cycle—of generation, growth, metamorphosis, maturation, reproduction, and death located temporally within a perpetual series of individual life cycles of organisms—constituted the nature of species as real biological entities.21

A Buffon-inspired conception of species as the recurrent succession of organismal life cycles that are causally connected in a temporally ordered series is the basis for a new organism-centred perspective. It takes as central the whole organismal life cycle, focusing on manifold dynamic processes and developmental changes over its lifetime.

4.2.2 THE SELF-CONSTRUCTION AND SELF-ORGANIZATION OF SPECIES

Rather than privileging relationships of reproduction, a shared genetic program, gene pool, or a set of morphological traits over other factors, this view conceives of a species as a series of self-constructed and reconstructed organismal life cycles. A species is the succession of organisms that share common capacities for sustaining a particular form of life by repeated generative and developmental processes, relationships, and modes of life. Organisms self-construct and self-organize themselves throughout their lifetime utilizing similar heterogeneous resources in similar ways. What resources count as causes of its construction are ecologically embedded and dependent on the temporal stage of the organism’s development.

Whereas the gene-centred and interactionist views of species take evolution to be the change in gene frequencies, this constructive organism-

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21 For Buffon, only species (not genera, phyla, classes, families, or kingdoms) are naturally unified in this way.
centred view takes evolution to be “phenotypic change [that may] involve gene frequency, not [characterized by] just gene frequency alone” (West-Eberhard 2003: 28, italicization her own). The organism self-constructs its phenotype utilizing genetic, epigenetic, physiological, cellular, behavioural, and environmental resources and organizes these over the course of its life cycle. Organismal self-construction and the summed self-construction of species (construed as a succession of life cycles) are the products of distributed causes. The succession of organismal life cycles organize their own construction by selecting similar resources in similar ecologies to preserve similar ways of living utilizing similar generative capacities. In this way, species are generically preformed. They share common capacities that facilitate the stability of species-specific traits, plasticity in their development, and variability among individuals of the same species.

4.2.3 RECONSIDERING SPECIES ONTOGENETICALLY

An organism-centred, self-constructive view dissolves the sharp distinction between ontogeny and phylogeny that has been used to justify the privileged use of the latter in preference to or in place of the former in conceiving the nature of species. Conceiving species from an organism-centred perspective means understanding them as the succession of ecologically-and-temporally embedded organismal activities. This view integrates the individual organism’s ecologically embedded ontogeny back into the conception of species.

There is no significant metaphysical distinction between linear genetic factors and extragenetic or ecological causal factors that justifies privileging one over the other. The apportionment of causal priority to genes as the informational program responsible for the phenotypes of organisms is based on a confusion. It takes a preformationist conception of genes as an “instrumental expression used as if they cause phenotypes” to provide a specific molecular sequence which is responsible for constructing that phenotype (Moss 2001: 87-88).
The confused view that genes code for traits arises when we conflate two distinct gene concepts: Gene-P and Gene-D (Moss 2001, 2003). “Gene-P” and “Gene-D” refer to completely distinct kinds of things. Whereas Gene-P is a heuristic for speaking about a relationship to a particular phenotypic trait, Gene-D is a specific molecular sequence—a “developmental resource” that is phenotypically “indeterminate” (Moss 2001: 88). Once these two concepts are distinguished, the confused basis for privileging genetic causes ceases to exist: “Gene-D is ontologically on the same plane as any number of other biomolecules, that is, proteins, RNA, oligosaccharides, and so forth, which is only to say that it warrants no causal privileging” (Moss 2001: 89).

Species construct themselves from a combination of these and other resources. All of these resources can be conceived of as potential causes of organismal construction and organization depending on which ones are used, how they are used, and when and in what combinations they are used during the course of the organism’s life cycle.

Resources may be inherited vertically or horizontally, they may be acquired at birth, learnt as a juvenile or acquired from interacting with other conspecifics. Sources of resources may be distributed over space and time: “genes are transmitted by ancestral organisms to their descendants, ... but in addition, phenotypically selected habitats, phenotypically modified habitats, and artefacts, persist, [and] are actively ‘transmitted,’ by these same organisms to their descendants via their local environments” (Laland, Odling-Smee, and Feldman 2001: 120). These acquired habitats, behaviours, and artefacts are all conceived of as possible causes, resources that can be used by an organism in its self-construction and in the successive multigenerational constructions of life cycles of organisms. This constructive process is ongoing. As a succession of life cycles, a species is constantly constructed and reconstructed utilizing similar genetic, extragenetic, and environmental resources and similar capacities and activities of organisms that are both vertically passed on to offspring as well as horizontally among conspecifics.

Three principles follow from this organism-centred view: circular and distributed causation; generic preformationism; and the organism as
understood in term of the whole life cycle. These are alternatives to the linear genetic causation, strong preformationism, and adult-centred view of the gene-centred perspective.

4.2.3.1 CIRCULAR AND DISTRIBUTED CAUSES

Rather than locating the causal source of species’ forms internally within the genes, externally within the selective power of the environment, or a combination of the two, the organism-centred view rejects the view common to all of these: that there is a localized cause of species specific form. Rather, the direction of organic cause is circular not linear and the sources of organic cause are distributed across a number of different resources rather than concentrated only in one or two sources. This view of organic causes draws on Kant’s own account of causal circularity in the *Critique of Judgement* (Kant 1790). He illustrates the causal circularity of organic self-organization referring to a species of tree:

a tree generates another tree ... the tree it produces is of the same species. Hence with regard to its species the tree produces itself: within its species, it is both cause and effect, both generating itself and being generated by itself ceaselessly, thus preserving itself as a species.

The leaves, too, though produced by the tree, also sustain it in turn; for repeated defoliation would kill it, and its growth depends on their effect on the trunk (Kant 1790: Ak. 371, 372).

The causal circularity Kant discusses is threefold. Firstly, the organism is both the product of a previous tree’s reproduction and the producer of a succeeding tree; it is both cause and effect of its own species. Secondly, as the organizing agency determining which resources are used in the self-construction of an organism, the organism is both cause and effect of its own individual development. And thirdly, it is both cause and effect of the integrated structure and maintenance of its parts (e.g. leaves, boughs, roots, branches, seeds).

This last type of causal circularity can explain the self-organized growth of organisms. Take fruit trees as an example. Fruit trees organize
their own growth by controlling how different resources are used in different tissues at different times, e.g. they allocate energy first to the construction of new roots; then, as the plant establishes an equilibrium between fixation of carbon and energy from the atmosphere and uptake of water, it directs energy to leaves, then flowers and finally to fruit. Carbon fixed after this goes to roots or is stored as starch. The starch it holds back serves as a reserve to buffer itself from root or foliage damage by insect attack or fire. Nutrients are recycled from foliage which has dropped to the ground and decomposed as humus. Trees shield their roots from being decomposed by constructing them out of the more rigid material lignin instead of cellulose which decays more easily (cf. Berg 1986, Aber and Melillo 1991).

The fruit tree’s inherited resources and its capacities for fixing carbon, metabolic use of sunlight for photosynthesis, and the storage of starch are all partial causes of the tree’s self-organized construction within its embedded environment.

The organism-centred view rejects the division which locates the principal source of causal power in the active genes or genomes, bracketing off other factors as the stable environment—the passive background conditions of the activities of the genes. Viewing the environment as a stable set of background causes that either facilitate or frustrate the primary genetic cause assumes that there is a single unidirectional flow of inheritance facilitated by the vertical transmission of genes from one generation to the next.

Oyama criticizes this view arguing that there are no unique replicators or vehicles of species constancy: “[t]here is no vehicle of constancy (even though the coined term, ‘interactant’ may have an unfortunate particulate connotation), unless the organism and its niche, as they move along time’s arrow, are so conceived” (Oyama 2000:27).

Genes are not exclusive in their reliable inheritance over generations. A diversity of genetic, extragenetic, ecological causal resources and generative capacities are reliably inherited contributing to the organism’s organisation over its life cycle and passed on similarly and over a series of organismal life cycles. Certain phenotypic traits are constructed by
organisms from resources \((Keime)\) and capacities \((Anlagen)\) of the self-organizing organism. The organism explores the developmental possibilities of the resources available to it in time and space and utilizes its capacities for organizing and reorganizing these resources. These resources and capacities partially constrain the organism’s developmental activities but these constraints allow it to maintain a relatively stable form. This stability facilitates the possibility of novel variations in the organism’s self-construction and development.

Rather than systematically privileging genetic factors as most important in the development of an organism’s specific form, the organism-centred view denies that the apportionment of causal significance to any particular resource—whether they be genetic, cellular, nutritive, or ecological—can be judged in advance of the organism’s life. It is dependent upon the organism’s use of these resources and its building on the results of past constructive activities over time.

These resources are potential causes of organismal construction and species construction. Causes are contingent; they vary according to historical trajectories that have led to them; ... particularities of place and connections among places matter; ... time and place is a matter of scale that differs among species; variation among individuals can qualitatively alter the ecological process; ... interactions among the species under study can be artefacts of the indirect effects of other ‘hidden’ species (Taylor 2001: 327).

Resources used in repeatedly constructing and reconstructing stable environments over life cycles and successions of life cycles are not limited to the vertical inheritance of genes from parent to offspring. There is a panoply of resources that can be inherited both vertically and horizontally. A selection of these will be considered.

### 4.2.3.1.1 Vertically Acquired Resources

Many resources are acquired vertically besides genes. One example is the vertical inheritance of epigenetic resources. During the development
of the organism, cells differentiate to become muscle, nerve, cardiac, lung, skin, liver, brain, and blood cells. Whilst these cell types all contain the same DNA base-sequences, when they divide they produce more cells of the same type—liver cells produce liver cells, blood cells produce blood cells. The function of these new daughter cells is passed on to them by the parent cells epigenetically rather than by any information in the genes.

This type of epigenetic inheritance may be passed on through a number of different pathways. One such route of inheritance is the passing on of a particular developmental or ecological stimulus that affects gene activity—genes may either be turned on or off by the cell in response to the stimulus. If these genes are turned on in the parent cell, the genes in the daughter cells and in subsequent descendants will continue to turn those genes on. The result is that there may be “genetically identical cells [that] can be in two alternative states (‘on’ and ‘off’), and both states can be self-perpetuating” (Jablonka 2001: 104). These cell lineages can continue to produce offspring that are “on” even when the original stimulus is no longer present. This continues “as long as the products of the self-sustaining cycle do not fall below a critical threshold” (Jablonka 2001: 104).

What are being passed on are the activities of ancestor cells in each cell cycle. Although the different states within each cell cycle are limited, cells may have numerous different cell cycles. Because of this, there can be an exponential number of possible cell variant states. Cells can also inherit their structure from parent cells epigenetically. For instance, the pattern of cilia on their cell membranes, pattern of growth (e.g. fractal), or chromatin marks on protein or RNA complexes that affect methylation patterns (cf. Jablonka 2001: 103-9).

In addition to epigenetic resources, behavioural and ecological resources can also be inherited vertically. Oviposition and the building of galls or nests are some ways many female insects construct the environments of their offspring—either by choosing to lay their eggs on a particular plant or by constructing galls. The plant on which the female insect lays her eggs (or the gall she constructs) becomes the nutritional source and the habitat for her developing larvae. The larvae vertically
Inherit this environment from their mother. Like the vertical inheritance of genetic and epigenetic factors, it is one of many resources passed from parent to offspring. These resources are utilized in constructing and reconstructing the environments and ecological artefacts of a succession of organismal life cycles. These “constructed components of the environment are both products of the prior evolution of organisms and, in the form of [ecological inheritance], causes of the subsequent evolution of organisms, both products and causes of evolution” (Laland, Odling-Smee, and Feldman 2001: 125).

The construction of nests and galls is dependent on circular and distributed causes because these organic artefacts are the constructed product of contingent interconnected causal resources supplied by the tree, climate, the female insect, and her larvae. The female insect does not construct her gall on her own. The development of galls is contingent on such things as whether a plant has a particular susceptibility to galling from certain insects: “specific properties of the plant genome or environment must play a role … not all [plants] are hospitable or responsive to galling insects” (West-Eberhard 2003: 109).

**4.2.3.1.2 Horizontally Acquired Resources**

Vertical inheritance is only one route by which organisms can acquire resources. Genetic and extragenetic resources can also be acquired horizontally. Organisms can exchange genes, extragenetic, and ecological resources either with organisms of their own species as well as with those of different species. These horizontal routes of resource acquisition may be facilitated by hybridization between organisms of the same genera (interspecific hybridization) or in some cases between organisms of different genera, orders or families (supraspecific hybridization). The exchange of genetic material can occur horizontally among different species of organisms, e.g. between parasites or symbionts and their hosts. Extragenetic, behavioural, and ecological resources can also be inherited
horizontally. These include gut microflora, endosymbionts, learned behaviours or preferences, and constructed habitats.

4.2.3.1.2.1 HORIZONTALLY ACQUIRED GENETIC RESOURCES

Unlike Buffon’s example of the mule, among botanicals, especially flowering plants such as orchids (Orchidaceae), berries (Ribes), cacti (Cactaceae), vascular plants, and many species of grasses and ferns, hybrids are both frequent and often fertile (Stace 1975). But although hybridization among animals occurs less frequently than among plant species, in some it is especially common. For instance, 35% of the butterflies in the genera Heliconius hybridize (Mallet 2007). The two interspecific butterfly species, Heliconius erato and Heliconius himera live within a similar ecological niche and frequently exchange genes through hybridization. Despite regular hybridization and overlapping gene pools, these species remain separate phenotypically distinct stable species. H. erato and H. himera have distinct behavioural characteristics, phenotypes, choice of host plant, and different microhabitat, even though they share a larger ecological niche. Lepidopterists and taxonomists do not consider these to be one intermixing species, but two separate species which frequently hybridize. In doing so, they do not conceive of species using the BSC, which would lump these hybridizing species together into one large polymorphic species.

Hybridization among the different species of Heliconius butterflies has provided a horizontal route by which butterflies of different species have acquired resources that have enabled them to construct their phenotypic features in such a way as to minimize their predation from birds. Some species of Heliconius butterflies are mimics that model their phenotypes on the wing patterns of other species of Heliconius butterflies. The black and white banded H. cydno is a mimic which mimics the model species H. sapho and H. eleuchia. The model species that H. cydno chooses to mimic depends on where it lives. H cydno live in different parts of West Ecuador and
Columbia. The different colour patterns which are present on the *H. cydno* wings are controlled by the same loci as other species of *Heliconius* butterflies (both mimics and models) which occupy diverse ecological niches (Kapan 2001, Kronforst et al. 2006). These model species of *Heliconius* are less likely to be eaten by predator birds that have learned that these butterflies are particularly foul-tasting. Birds recognizing the particular colour pattern on the wings of foul-tasting butterflies are avoided. Species of *Heliconius* which are palatable to birds have acquired the same wing colour pattern to those which are foul-tasting. Hybridization between species of foul-tasting models and palatable mimics has facilitated the acquisition of certain genetic and extragenetic resources that have provided species such as *H. cydno* the means to construct its phenotype mimicking those of the foul-tasting butterflies. Living in similar environments with similar risks of predation means these mimics enjoy similar protection from bird attack because the mimics share almost identical colour patterns on their wings as those of the foul tasting species (Jiggins et al. 2001, Gilbert 2003).

Whilst some non-hybridizing species of sexually reproducing animals may still be definable in terms of a conception of species based exclusively on reproductive relationships and genetic isolation, it fails for hybridizing species such as those discussed here. But its deficiency does not end with hybridizing species. It fails for the majority of species in the world. In particular, the BSC faces significant problems when dealing with microbial and bacterial species. Bacteria reproduce asexually by budding or the binary fission of the single parent cell into two daughter cells rather than by the formation of a zygote, the product of two gametes. Bacterial species do not produce gametes and do not go through meiosis. Genes are passed vertically in asexual reproduction from parent to offspring but they can also be passed horizontally between different bacterial species by means of transformation, transduction and conjugation.\(^\text{22}\) These provide other means of resource acquisition in addition to vertical inheritance.

\(^{22}\) Transformation is the process by which bacteria pick up DNA from their environment. Transduction is the process by which bacterial DNA is moved from one bacterium to another by means of a bacterial virus (bacteriophage).
Organisms of one species exchanging genetic material with an organism of another is not accommodated easily by the BSC’s conception of species as groups of organisms sharing a genetically isolated gene pool and a species specific set of genes. The difficulties for the BSC raised by the horizontal transfer of genetic resources are not confined to bacterial species: bacterial and viral DNA are constantly being integrated in the chromosomes of plants and animals today, by the known genetic mechanisms of conjugation, transformation, and transduction, (in evolutionary terms, retroviruses and other ... viruses are exact parallels of bacteriophages). It can be concluded that eukaryotes possess the same capacity and similar mechanisms for effective horizontal gene transfer as prokaryotes do (De la Cruz and Davies 2000: 132).

Although significantly rarer, horizontal gene transfer (HGT) has been found to occur between organisms belonging to different kingdoms such as between eukaryotic species and bacterial species. Eukaryotes may obtain genes horizontally from mobile genetic elements in the food they consume, retroviruses, and disease causing parasites such as trypanosomatids (cf. Doolittle et al. 1989, Doolittle 1998 and Hannaert et al. 2003). Although striking, it is a mistake to overemphasize the role of HGT. Not all genes can be horizontally transferred, in fact, only a small minority of genetic sequences are able to be horizontally transferred. However, HGT is notable because it provides organisms with another route by which genetic resources can be acquired. And it provides bacteria important access to genes from a number of different organisms (either of a similar species or even of a different kingdom). They contribute widely distributed genetic resources that the organism can use in its self-construction.

One of the most conspicuous and widely studied examples of HGT is the acquisition of virulence. Some plasmid and bacteriophage vectors carry the genetic materials necessary for virulence. The resources necessary for the construction of the virulent phenotype are horizontally transferable. These chunks of genetic resources are called “islands of pathogenicity” (Hacker et al. 1997). These islands of pathogenicity can be passed

Conjugation is the transfer of genetic material from one living bacterial cell to another and requires physical contact between the two cells (De la Cruz and Davies 2000: 132; cf. Timmis and Scott 1984).
horizontally from a virulent bacterium of one species to a non-virulent bacterium of another species. The acquisition of these pathogenicity islands by the recipient bacterium provides it with the resources to become virulent. This dramatic change in the bacterium’s phenotype (from non-virulent to virulent) means that it can now occupy an entirely new ecological niche.

4.2.3.1.2.2 HORIZONTALLY ACQUIRED EXTRAGENETIC AND ECOLOGICAL RESOURCES

Organisms horizontally acquire various extragenetic resources. For example, some organisms acquire microorganisms horizontally. Ruminant mammals such as cattle and sheep and other mammals inherit symbiotic microflora that they utilize in digestion. These microflora are inherited from multiple sources (both horizontally and vertically). These may include ingesting the milk from the mother; from other related and unrelated conspecific females of the same group (e.g. within prides and packs); in the regurgitant of carers, siblings or other conspecifics peers (or other individuals besides parents); or the ingestion of faecal matter that is the product of different organisms (which may include both conspecifics and heterospecifics). In cattle, the symbiotic microflora live within one of the stomachs, the rumen. The microflora aid in digestion of the copious amount of rough vegetation cattle consume. These symbionts partially decompose tough plant tissue allowing the cow to absorb energy and nutrients from cellulose that would otherwise be indigestible (Aber and Melillo 1991: 230-31). This increases the amount of energy the cow gains from the vegetation it consumes.

The acquisition of beneficial resources that may be used in the construction and organization of organisms is not limited to mammals. The horizontal transfer of γ-proteobacterial endosymbionts occurs among many insects especially the microsporidia that are present in a wide variety of arthropods and the parasitic fungi of several plants (Werren 2005: 291). The symbiotic microorganisms of termites quicken the rate of decay of high-
lignin substances. Termites use this to their advantage. This quicker decay rate facilitated by their symbionts allows the hosts to consume large amounts of wood.

These symbionts can be passed on from one organism to the next exclusively by horizontal transfer, but they can also be passed on by a mixture of partially vertical and partially horizontal inheritance. Symbionts such as the nitrogen-fixing bacteria *Rhizobium* of some legumes, algae-bearing symbionts of some corals, and the γ- and α-proteobacteria *Rickettsia* and *Wolbachia* of arthropods and nematodes are acquired through a mixture of heritable routes (Werren 2005: 290-98).

Some of the most well-known horizontally transferred symbionts are of those of the bacteria *Rhizobium*. These are acquired when the bacteria infect the roots of leguminous plants (e.g. peanuts and soybeans) causing the plant to grow root nodules. These root nodules serve to protect the acquired microbes from the acidic conditions of the surrounding soil (Aber and Melillo 1991: 149). In this protected environment, the microorganisms carry out the fixation of nitrogen gas from the atmosphere. By doing so, they provide the plant a greater amount of this valuable nutrient than is possible from the regular uptake of nitrogen by the plant from the soil in the absence of these microorganisms.

Behavioural resources may also be inherited horizontally as well as vertically. In addition to the vertical acquisition of food preferences by oviposition or through the mother’s placenta, or in her milk, these preferences may be acquired horizontally (perhaps “diagonally” is better) among organisms that cross-feed. Horizontal acquisition of behavioural patterns such as nut burying of squirrels and chipmunks, the waggledance of honeybees (used to communicate the location of food sources to other bees in the hive), the courtship behaviours and songs of grasshoppers and crickets, or the acquisition of a particular signed language from one’s conspecifics, are widespread. These behaviours are stabilized within the species if they increase the viability and fecundity of the organisms using them.
Learned behaviours may also include the avoidance of certain types of prey or the avoidance of some highly dangerous predators on the basis of their phenotypic features. After learning from experience, from copying the behaviour of parents or peers, a bird may be able to recognize and avoid eating the bad-tasting prey, such as *H. sapho* butterflies, on the basis of their wing patterns. Or it may learn to avoid the red, yellow, and black striped markings characteristic of the many highly venomous coral snakes (e.g. the Texas coral snake *Micrurus fulvius* and the Arizona coral snake *Micruroides euryxanthus*). As discussed above, other species may exploit these learnt behaviours by mimicking the phenotypes of the model species that are already recognized by predators. The result of this on the behaviour of the birds learning to avoid the phenotypic markings of the bad-tasting butterfly or venomous snake is that both the models (e.g. *H. sapho, H. eleuchia* and the coral snakes) and mimic species (e.g. *H. cydno*, the Scarlet King snake, *Lampropeltis triangulum elapsoides*, and the Colorado Desert Shovel-nosed snake, *Chionactis occipitalis annulata*) are systematically avoided by birds that have acquired this learned recognition and avoidance behaviour (Stebbins 2003).

Lastly, organisms may also pass on environmental resources or constructed environments such as webs (spiders), dens (foxes), nests (wasps, robins), galls (mites), warrens (rabbits), dams (beavers), song dialects (whales), or libraries (humans). These may be passed vertically or horizontally, or may even be a resource acquired from different species (e.g. hermit crabs’ shells, a rattlesnake’s use of tortoise burrows, bats’ use of bears’ caves, and generations of earthworm burrows that produces the topsoil in which other organisms also live). These resources are used in the construction and reconstruction of environmental niches by organisms of a particular species in a similar way.

4.2.3.2 Generic Preformationism
The gene-centred interactionist position of the BSC, PSC, and related concepts is doubly preformationist. It relies on there being a common informational program for species specific traits contained within the genes such that development is merely the unfolding of this preformed program. And it conceives a pre-existing niche as selecting and moulding the traits of species. Rather than conceiving of a species as a group of organisms sharing a common genetic program, according to the organism-centred view a species is conceived of as sharing common generative capacities, common resources, and a common way of life within similarly constructed environments. Instead of viewing organisms as outcomes of the causal forces of its genes or its environment, (e.g. understood as either the result of factors present in a pre-formed program, a pre-existing environmental niche, or a combination of these), an organism-centred view suggests we can view organisms as well as species as both cause and effect of their own construction. Species are not strongly preformed or predetermined; but they are generically preformed.

Whereas strong preformationism considers an organism’s form to be a “mere educt,” the result of an unfolding preformed form, generic preformationism takes an organism’s form to be a “product” which is generated anew in reproduction. However, this product is not generated de novo from “crude ... unorganized matter” (Kant 1790: Ak. 424). The form of a species is “preformed virtualiter in the intrinsic purposive predispositions [Anlagen] imparted to the stock” (Kant 1790: Ak. 423). The organism is constructed in part from these generically preformed Keime and Anlagen. But, as my discussion and extension of Kant’s generic preformationism suggested, organisms also utilize resources acquired from their environment and through their interaction with other organisms (Chapter Two).

An organism-centred view of species suggests that traits are not the result of a preformed form contained in the unfolding informational program

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23 An educt is understood by Kant to be in contrast to a product. Whereas a product’s form is generated or “brought forth,” an educt already has its form. An educt’s form is simply “brought out” rather than “brought forth” (Kant 1790: Ak. 372).
of the genes. Genes are just one resource the organism uses for its self-construction, one of many resources that it acquires from heterogeneous sources by different pathways of inheritance. Environments do not shape or choose the traits of species. Resources in the environment are used in the self-construction of an organism over its lifetime. Successive generations of organisms of the same species construct themselves and their niches from similar sets of resources in similar ways.

A species, as a sequence of generically preformed ontogenies, relies on understanding each individual life cycle as contributing to it. As such, the species is a process of constant reconstruction where organisms come into being with certain resources and capacities (Keime and Anlagen). Their constructive activities shape their environment, interactions with conspecifics, and the resources and capacities of future generations of conspecifics. The tendency for like to produce like is not a necessary tendency that is set within the genes or the environment. In many cases, like does not produce like. Whether like produce like is contingent on the varying phenotypes of different life stages of organisms, whether the offspring have similar genetic, cellular, metabolic, ecological, and behavioural resources and whether these are organized in a similar way in the self-construction of the offspring as they are in the parents, grandparents, great-grandparents, etc. Organismal form and organization is the result of common generic capacities and shared resources. Understanding organic matter in terms of common generative capacities for the self-organization of organisms and species means focusing on the capacities and activities of organisms that facilitate developmental and phenotypic variation.

Generic capacities facilitate both phenotypic plasticity and stability of form across organisms of the same species. The plasticity of organisms is their ability to use the same resources in constructing different phenotypes, or in utilizing different resources in constructing similar phenotypes. The stability of organisms is their ability to develop and maintain their growth throughout their ontogeny according to a conserved body plan and the
ability of successive generations to use the same resources in constructing similar phenotypes.

Phenotypes are at once plastic and stable. Phenotypes of organisms are plastic insofar as they are responsive to the continual variation within their environment. Phenotypes of organisms are stable insofar as they may develop reliably despite changes to the organism’s resources. Organisms may change their features depending on a number of factors. These changes are attributable to the self-organizing capacities of organisms in selecting which resources, in what order, and in what combination, are utilized as causes of their own development: “the origin of species differences, and of novel phenotypes in general, involves the reorganization of ancestral phenotypes … this is developmental recombination” (West-Eberhard 2005: 6543). Organisms are able to coordinate the resources used in their own development because they are:

richly endowed with a capacity for facilitating variation, a small input of random mutation would lead to a large output of viable phenotypic variation … Instead of a brittle system, where every genetic change is either lethal or produces a rare improvement in fitness, we have a system where many genetic changes are tolerated with small phenotypic consequences and whereas others may have selective advantages, but are also tolerated because physiological adaptability suppresses lethality (Kirschner and Gerhart 2005: 226).

The organism is the author of its own variability. Its generic capacities may constrain deleterious variation or enhance variability that may be advantageous to the organism. Using these capacities, organisms may either buffer or enhance any variations to their genetic or extragenetic resources or perturbations in their environmental resources.

An organism has both constraints and de-constraints on the variability of its phenotype. Its capacity for variation allows it to maintain itself across a wide range of conditions. The organism’s potential for different developmental variations lie in its capacity to self-organize its genetic and extragenetic resources. The organism’s common stock of generic capacities (Anlagen) and resources (Keime) can be understood as its “phenotypic repertoire” (West-Eberhard 2003: 146). The organism’s generically preformed capacities include a number of highly conserved core
processes: inter-cellular signalling and cell sorting (Goodwin et al. 1993); the capacity for weak linkage, exploratory behaviour, spatial patterning, compartmentation and modularity of the body plan (cf. Kirschner and Gerhart 2005); the capacity of tissues to segment or form hollow tubes (cf. Minelli 2003); and the capacity to learn and remember (West-Eberhard 2003: Ch. 3, 7, 18). A thumbnail sketch of some of these may be useful.

The capacity for weak linkage allows organisms to utilize a small number of mechanisms relying mostly on the ability to reconfigure these as and when necessary for different functions. But because these linkages are weak, they are often retraced and duplicated by other pathways or circuits to strengthen them. The use of weak linkages means that there is higher versatility with which the organism can use to alter these pathways when necessary. If these were strong, static and unchanging linkages, the organism would be arguably less fit to adjust to different environmental situations (Kirschner and Gerhart 2005: 136-7). In the course of evolution small changes result in wide variability and novelty. Weak linkages can be formed in many kinds of interactions, such as those between cells, cell populations, tissues, organs, organ systems, and behaviours. Because these linkages are weak, individual organs, cells, tissues, or behaviours may also change independently.

The exploratory behaviour of organisms is their responsiveness to different inputs and outputs. In building such things as neural networks or circuits, the organism begins by constructing a large number of alternative pathways. The best of these alternative pathways are selected and stabilized.

The form of an organism’s body plan is generically preformed. A conserved body plan—one that is retained over a succession of individual life cycles of organisms—enables independent variation of some features without adversely affecting others. It does so by compartmentation of the body plan into semi-autonomous functional and structural parts. This modularity of the organism’s parts increases its capacity for variation as changes in one subunit do not greatly affect others and thereby reduces the possibility of lethal variations. The more modular these subunits become,
the greater the possibility of variation and specialization of these structural and functional units within the organism.

The generic capacity to learn provided certain motivating factors, such as the absence or presence of certain resources needed in the construction of a particular phenotypic trait or the performance of certain processes or behaviours (e.g. metabolism, reproduction, locomotion, speech), enables the organism to vary its phenotype over its lifetime given a range of different contexts. Organisms may learn about their resources and environment by sight, by what they hear, smell, taste, or touch. They may manipulate the objects within their immediate habitat, investigate new resources or interact with new organisms (e.g. prey, potential mates, carers, symbionts) within this habitat or search for a new one. Certain types of activities may result in some benefit or hindrance to the organism (e.g. better access to food, protection from weather, increased sociality or reproductivity). Activities that effectively increase or substantially decrease resources are remembered and repeated or avoided. Species-specific learnt behaviours may be passed from parent to offspring or among conspecifics peers by learning and copying.

These generic capacities allow organisms to vary their own development and the phenotypes they construct depending on how resources are utilized within their environment. The differences between organisms are not consequences of species-specific genes. Genes do not build species specific body plans according to a species blueprint. As the previous chapter showed, homologous genes occur in many different organisms that are used in constructing completely different structures and paralogues within the same organism can serve different purposes.

### 4.2.3.2.1 Slijper's Goat

Generic capacities provide the possible means for an organism to change its phenotype depending on the resources available to it, its stage of life, or its different ecologically-embedded conditions. Organisms of the
same species may develop similar phenotypes despite variation and environmental change.

[Organisms have the capacity to] develop functional phenotypes despite variation and environmental change via *phenotypic accommodation*—adaptive mutual adjustment among variable parts during development without genetic change ... Phenotypic accommodation occurs regardless of the cause of variation, whether genetic or environmental, normal or pathological (West-Eberhard 2003: 52).

Probably the most widely discussed, if not the most striking example of phenotypic accommodation is the bi-pedal goat studied by Slijper in the 1940s (cf. West-Eberhard 2003: 6545). Slijper’s goat started life with a congenital defect that meant it was born without forelegs. As a result, it was unable to use these in supporting its weight quadrupedally. Over time, the goat learned to walk on its two hind legs with particular skill. Its novel bipedal phenotype was not caused by any genetic mutation, but was the result of the reorganization of the goat’s own body for locomotion. The goat’s bipedal gait resulted in muscular and skeletal changes that were morphologically and functionally more similar to the development of muscularity and skeletal arrangements of other bipedal mammals, such as kangaroos and humans. Over its lifetime walking on two legs instead of four, the goat’s pelvis grew wider, its tongue grew longer, it developed increase muscle mass in its thighs and its spine grew straighter with a slight S-curve. These secondary modifications were not random but the result of developmentally flexible muscles, tendons, and bones. They were the result of the goat’s developmental self-reorganization utilizing the resources available to it.

The defect in one part of the goat’s phenotype—the absence of forelegs—led to correlated changes in its locomotive behaviour, musculature, and bone structure and density. These changes in the goat’s phenotype were not the result of billions of years of natural selection over generations of goats or written into its inherited genetic program; they were instead the result of highly organized and integrated behavioural, functional, and structural changes that occurred over the short one-year life span of the goat. The goat’s bipedal phenotype was the product of its
capacity to reorganize its mode of locomotion and in restructuring and reorganizing the resources available to it to developmentally accommodate its novel ability to walk on two legs.

4.2.3.2.2 GENERIC CAPACITIES FACILITATING STABILITY AND PLASTICITY OF PHENO TYPES WITHIN SPECIES

Although the case of the bi-pedal goat is itself exceptional, the developmental processes which lead to the extraordinary reorganization of the goat’s behaviour and development are not. Less dramatic but equally exciting examples abound. One is the reduction in spines of the three-spine stickleback *Gasterosteus aculeatus*. Marine sticklebacks have a large pelvic spine which prevents other animals in their environment from eating them. However, this spine is missing in freshwater sticklebacks who do not suffer from the same predation that befalls their fellows in the marine environment. Within the marine environment the sticklebacks have more access to calcium than the freshwater sticklebacks have. The reduced threat of predation and the reduction in calcium are two factors that partly explain the absence of the pelvic spine among the freshwater fish.

Despite the phenotypic differences between marine and freshwater sticklebacks, both share similar resources, including the gene Pitx1. Pitx1 is utilized in the reduction of limbs in some animals. But in some, (mice) mutations of Pitx1 are often lethal (cf. Shapiro et al. 2004). Pitx1 provides a resource that can partially explain the variation among sticklebacks. The protein coding region of Pitx1 was found to be identical between marine and freshwater sticklebacks; however the use of this gene is different in both. In the freshwater fishes, with no pelvic spine, Pitx1 is utilized in other areas of the fish but not in any of its appendages. This results in the loss of the pelvic spine. Loss of the pelvic spine does not result in lethality for the freshwater fish. The compartmentation of the stickleback body plan allows for a number of variations to it which include the presence or absence of the pelvic spine. This variability allows the
marine fish the ability to construct the pelvic spine using the higher levels of calcium available to it thus providing increased protection from predation. It allows the freshwater fish the option of not constructing a pelvic spine in an environment which the calcium resources available for this added bone growth are limited and the need for the protection the pelvic spine would provide from predation not required.

Sharing common generic capacities also allows organisms of the same species to dramatically change their phenotype depending on different environmental conditions or resources available. For example, water fleas (Daphnia) have inherited a generic capacity to construct large helmet-shaped structures. Although this structure protects the water flea from predators, constructing it requires a great deal of the water fleas' developmental resources. To assess whether the helmet is a worthwhile investment, the flea assesses its environment for chemical traces of its predator (Agrawal et al. 1999). If chemical traces are found in its environment, it constructs a helmet, if no traces are found, it does not.

Although West-Eberhard (2003, 2005) and Kischner and Gerhart (2005) have drawn much attention to phenotypic plasticity and developmental accommodation, these ideas are not new. Kant observed something similar among organisms:

> if [organic] beings are injured, nature aids itself, and the loss of a part that was needed to sustain adjoining ones is made up by the rest; if birth defects occur, or deformities come about during growth, certain parts, on account of their deficiencies or impediments, form in an entirely new way so as to preserve what is there (Kant 1790: Ak. 372).

If there are omissions or additions in the set of resources available for the organism, it may rely on different pathways and resources in the construction of its traits within its generically preformed capacities.

Another example of an organism that preserves a particular phenotypic feature despite omissions in the resources available was discussed in the previous chapter—the different developmental networks used by fruit flies in the construction of eyes discovered by de Beer (1971) and Tomarev, et al. (1997). Some fruit flies possess the gene “eyeless” in place of other genes that are normally used in the construction of eyes in the
wild type. Despite the omission of these genes, these fruit flies develop fully
functioning eyes. They utilize other genetic resources and alternative
developmental pathways in the construction of their eyes. Their resultant
phenotype is similar or identical to that of the wild type even though the
ontogenetic pathways and resources utilized in their construction vary. The
developmental plasticity of the fruit flies has effectively stabilized this part
of their phenotype (i.e. their eyes). The stability of this phenotypic trait is
maintained by different organisms of the same species by varying their
developmental pathways and the genetic resources they use to construct
eyes depending on those available to them.

Developmental flexibility utilizing common generic capacities in the
stabilization of certain phenotypes has also been observed in humans.
Individuals who suffer from an increase of cerebrospinal fluid in their
craniums often have brains that are severely reduced in size in comparison
to those who do not have this fluid pressure on their brain tissue. Some
sufferers’ craniums are filled 95% with cerebrospinal fluid. This severe
hydrocephaly reduces brain size to just 10% of non-hydrocephalic brains.
Although half of these individuals suffer profound mental impairment, half
have IQs over 100—some as high as 126. A “substantial proportion of
patients appear to escape functional impairment in spite of grossly
abnormal brain structure” (Lewin 1980: 1232). These individuals are
functionally indistinguishable, having the same mental capacities as those
with “full size” brains. Utilizing different developmental resources, different
paths of neurological growth and linkages, cell-cell interactions, and
variations of brain activity, these human organisms construct brains with
normal mental functioning.

Generically preformed capacities such as weak linkages, exploratory
behaviour, and a conserved compartmentalized phenotype made novel
developmental variations possible from the reduced resources available.
This developmental plasticity enabled these organisms to maintain the
stable human phenotype of normal mental functioning.

Phenotypic variations in development, structure, and behaviour may
also arise as the result of different competitive frameworks. The
development of the spadefoot toads *Spea bombifrons* and *Spea multiplicata* depends on both the diet available and the presence of the other species within the same environment. Tadpoles of both species may either be omnivorous feeding on pond detritus or carnivorous feeding exclusively on small crustaceans. Their morphology accommodates this variation in feeding behaviour—the jaws of the crustacean crunching carnivores grow larger than those of the omnivores. However, if either species detect the presence of the other within the same environment, their feeding behaviours change. *S. multiplicata* becomes exclusively carnivorous. Learning that *S. bombifrons* is sharing its environment, *S. multiplicata* increases the number of carnivore morphs and suppresses production of its own omnivore morph in successive generations. Eventually all *S. multiplicata* become carnivorous. The opposite strategy is pursued by *S. bombifrons* which becomes exclusively omnivorous, increasing generations of omnivores while suppressing its own carnivore morph (Pfennig and Murphy 2000). Learning that the other species shares its environment, each species changes both its foraging behaviour and morphology. If food in the shared environment becomes extremely scarce, the carnivorous morph of *S. multiplicata* changes its feeding behaviour once again, this time by using its muscular jaw to cannibalize the omnivore morph (Elgar and Crespi 1992).

The Galápagos finches are perhaps the most famous instance of variation instigated by differences in learnt feeding behaviours. These include, “hunting on branch surfaces, probing branches, extracting caterpillars from leaves, probing dead leaf litter, nectar feeding from flowers, and ground feeding on seeds and insects” (West-Eberhard 2003: 345). As Darwin observed, the body sizes of the finches were very similar, as were the habitats in which they hunted. Individual feeding preferences of finches are learnt early in the bird’s life. Young birds observe the behaviours of adult birds of their own and other species in exploring the various ecological opportunities for prey and copy their feeding behaviours. They begin by pecking at everything, including branches, leaves, bark, flowers, the ground, and any small moving object. This exploratory phase of learning continues 12-25 days after fledging. In this phase,
fledglings of different species associate with each other and appear to copy each other’s feeding behaviours, sometimes attempting to feed in ways that adults of the same species do not. But eventually they drop these heterospecific behaviours from their repertoires (West-Eberhard 2003: 346).

Young birds may take up to a year before eventually learning the species-specific food preferences and foraging behaviours.

These food preferences are developmentally accommodated over the growing finch’s lifetime. The form of its beak is the result of its learnt behaviours and the organism’s self-organized construction to meet its own specific foraging specialization. Large, hard seed foragers develop thick blunt beaks, larger muscles, and greater skull thickness whilst those foraging small seeds develop small fine beaks, and do not gain the thicker muscles of the hard seed foragers. The intestinal morphology and digestion of these finches also varies (Hinde 1959). These phenotypic accommodations to the learned behaviours of the finches mirror those of the bipedal goat’s—variations that arise from the organism’s self-constructed phenotype to accommodate these behaviours utilizing species specific generic capacities—not simply the result of random genetic mutations.

4.2.3.3 The Whole Life Cycle

Focusing on the adult form rather than the whole life cycle of the organism for classifying species belies an essentialist notion of organisms—the belief that organisms only fully manifest their species form or essence in adulthood. It is justified by arguing that if new generations of a species were not reproduced by the adults of the present, the species would become extinct. The gene-centred neo-Darwinian perspective of species overemphasizes the importance of phylogeny and ignores the ontogeny of organisms: “[it is] a ‘theory of adults’—one which has failed to address the diversity of ontogeny” (Buss 1987: 65).

The systematic emphasis on adult organisms and the focus on the reproductive relationships of adults within a population rather than the
organism’s whole life cycle, disregards the developmental changes (and in the case of HGT, genetic changes) to the organism over its lifetime. The continual changes over the organism’s life cycle and in each of its different developmental stages are required for the succession of the species, not just the adult stage. In focusing exclusively on the adult organism and reproductive relationships between sexually mature individuals, the so-called biological conceptions of species seems to ignore the ‘immature forms’ under which many [organisms, e.g. arthropods] spend most of their lives ... and disregard[s] ontogeny as the dynamic process leading these organisms through successive and discrete steps from birth to reproduction (André 1988: 136-37).

Species experience growth through a number of stages. During some stages, some aspects of the organism’s morphology may be similar, or homomorphic, to other stages, whereas other features in other stages may be distinct, or heteromorphic, from earlier or later stages. These stages may occur in different temporal orders in different organisms. Even the ontogenetic stages of organisms within the same species may occur in a different temporal order (these are referred to as “disharmonic”). Such disharmonic ontogenetic stages occur frequently:

while a given ontogeny, under normal conditions, tends to repeat the form-sequences of its predecessors, it is liable to changes in every part of the life cycle—positively, by equipping the larval and adult stages for the changing conditions of their various careers, or with greater efficiency for the same conditions and negatively, by abbreviating the formative processes to the uttermost (Garstang 1922: 82).

Sequential polyphenism occurs in most phyla where there are different developmental stages, e.g. embryo, larva, nymph, juvenile, chrysalis, pupa, adult. Some of these stages are quite dramatic going from caterpillar to butterfly, or metamorphosing from newt to damselfly, or from tadpole to frog. One suggestion is that because there are dramatic morphological differences between juveniles and adults of the same species, we should classify these as different species (cf. van Emden 1957). Whilst recognizing the diversity among phenotypic features over an individual organism’s life cycle, this suggestion goes too far. Classifying juveniles and
adults differently would pose a new set of metaphysical difficulties. A minimal requirement of any conception of species must be to treat an organism as a living being that may change over time but is the same individual throughout its life cycle.

Incorporating ontogeny into the conception of species as a succession of organismal life cycles, the organism-centred view considers the whole self-constructed, temporally extended life cycle of organisms rather than concentrating simply on the adult stage. This is a much different view than that proposed by the BSC. Mayr’s reliance on gene flow as facilitated by reproductive relationships of conspecifics meant that the focus of the BSC is on one stage of an organism’s life cycle—sexual maturity. The focus on sexually mature adult organisms is justified by the view that natural selection acts on adult organism’s fecundity. In focusing on adults rather than the whole life cycle it treats natural selection as something that only affects adult organisms.

But when we consider the adult stage of the organism’s development we can’t but help to also focus on the stages that came before. The adult stage of the organism has a life history. Its embryological form, juvenile structures and development, and the learned behaviours and interactions of earlier stages all contribute to the phenotypes and behaviours that are retained within its adult stage. The adult stage, like any other developmental stage is “a kind of temporal slice through the life cycle. It carries the evidence of past gene transcriptions, mechanical influences inside and outside the organism, results of past activities, nutrition or lack of it, and so on” (Oyama 2000: 161).

Incorporating ontogeny back into our concept of species first requires reintroducing the historical contingency of life stages of organisms back into the concept of an organism. Each developmental stage of an organism’s life cycle has its own ontogeny. The phylogeny of a species is then simply the history of a specific series of contingent self-constructed individual life cycles.
4.2.3.3.1 PHENOTYPIC ALTERNATIVES WITHIN SPECIES AND STAGE-SPECIFIC PHENOTYPES

Relying on the adult form as central to conceiving the characteristics and behaviours of a particular species also proves difficult because there may be multiple alternative adult phenotypes (e.g. sexually dimorphic and multiple morphological forms). These include the strikingly different morphologies and behaviours between the super fertile queen and the sterile workers of colonial insects like ants and bees. Neither the worker nor the queen may be identified as the typical morph of the species. In colonial insects, no single adult phenotype is species-typical. Nest-building, defence, food foraging, egg-laying, and larvae care are constructed and organized communally in the cooperative efforts of highly specialized morphs. Even reproduction is the product of interactions among these morphs (e.g. between a physogastric queen, workers, and soldiers in termites, cf. West-Eberhard 2003: 174).

In addition to the alternative phenotypes among adult organisms of the same species, there are also widespread morphological, physiological, and behavioural variations among the phenotypes of different stages of the same organism over its life cycle. Some of the most obvious of these are those of metamorphic species, such as the changes from larval caterpillar to pupa, chrysalis, and adult butterfly, or the hormonal and morphological changes of sexual maturation, growth, and pregnancy in mammals. Other phenotypic differences that occur within an organism’s life cycle may include the change of skin colour as camouflage (e.g. chameleons) or the seasonal whitening and moulting of fur (e.g. arctic animals such as hares and foxes). Organisms may migrate (e.g. Canadian geese, wildebeest), or hibernate underground (e.g. desert toads), or have an extended life cycle (locusts), change their sex (e.g. reef fish), change their diet (e.g. the tadpoles of spadefoot toads may be omnivorous whereas as adults they may be carnivorous or vice versa), alternate their leaf forms, seeds, and flower colour (e.g. the heterophyllous aquatic plants producing different morphologies depending on whether they are growing in an aerial or
underwater environment), or change their morphology and behaviour according to their immediate ecology (e.g. various stages of parasitic nematodes, such as *Pseudoterranova decipiens*, that begin with a free swimming larvae, attachment to tissues in the peritoneal cavity of a crustacean host, migration to the muscle tissues, which, when ingested by a predator marine mammal develops into the adult form of the nematode and produces eggs) (cf. Anderson 1996: 1-5).

Some of these alternative phenotypes are constructed by organisms using environmental cues, dependent on their own developmental growth, interactions with other conspecifics, or with heterospecifics. Both chameleons and arctic hares change their phenotypes to avoid detection by potential predators. But whilst the former may do so many times in a single day, the latter does so seasonally. Migration and hibernation are two different ways organisms change their habitats and organize their resources to meet their needs. Migrating geese travel great distances to access better fishing waters or other foraging habitats, better breeding grounds or access to mates, and warmer or cooler climates than the one that they are migrating from.

Hibernating animals such as snakes, bats, squirrels, toads, and to some lesser extent, bears, alter their metabolism, body temperature and breathing in a stage of inactivity. This period of inactivity enables the organism to conserve its energy resources especially in times of scarcity, to avoid predation or exposure during a particular season (usually winter). In some mammal species, animals gestate whilst hibernating. This provides further protection and enables parents to give birth at a time (spring) when there is more food available for them to feed their young. The Sonoran Desert toad (*Bufo alvarius*) hibernates in rodent burrows or utilizes the underground passages of other small mammals during dry periods to avoid dehydration and exposure to extreme temperatures. They emerge shortly before or just after the first rain of the summer which starts the monsoon season. Using temporary large puddles of rain water as its aquatic environment, these toads are able to both feed and reproduce (Secor 2005: 2595-608).
Other animals may change their morphologies and behaviours over a much longer life cycle. The most dramatic among these is the extended life cycles of the 13 and 17-year cicadas of the appropriately named genus *Magicicada*. These cicadas grow as nymphs, go through five stages where they moult and stay immobile before tunnelling out of their underground home after 13 or 17 years (depending on their cycle). Their emergence is synchronized with the rest of the brood in an effort to increase survival by providing an overabundance of insects to possible predators. When out of ground the cicada moults one last time becoming an adult and seeks a mate to reproduce (Williams and Simon 1995).

Changes in morphology, behaviour, and even sex are common among echinoderms, crustaceans, molluscs, and fish. Reef fish of the family, *Pseudochromidae*, can change sex depending on the sex of other fish in its school. For instance, if a small all-female schools of reef fish (called a “harem”) loses its solitary male, the largest female changes sex to become male. This fish changes its female morphology and physiology to the colouration, behaviour (including those of defence and courtship), and physiology of a male. Although able to produce sperm after ten days, its full transformation from female to male takes a minimum of eighteen days. Male to female transformations take more time to complete—a minimum of 52 days. The changes in sex of reef fish are bi-directional as the same fish may change back and forth between female and male forms throughout its lifetime depending on the sex of other conspecifics whether living in schools or not (cf. Wittenrich and Munday 2005).

At different stages in the life cycle, various organisms may display different morphologies or behaviours associated with a particular stage or in a specific environment. Among most organisms ontogeny involves constant changes. On the adult-centred view of species, development over an organism’s life cycle is understood as the processes necessary in building an adult. Species are conceived in terms of the final output of this process—the adult organism. The life cycle of an organism is treated as the means necessary for building an adult which is then the object of species classification and study. In contrast, the organism-centred perspective
conceives species in terms of a sequence of constructed and reconstructed self-organizing activities of organisms over their life cycles which include the phenotypic changes over each of their stages—not just the adult stage.

4.3 THE GENE-CENTRED VIEW OF SPECIES REVISITED

A consequence of the Buffon-inspired, organism-centred view of species discussed in this chapter is that the boundary between organism and environment is dissolved. I am not the first to suggest this dissolution. Such a dissolution has been suggested by Dawkins in his conception of the extended phenotype (Dawkins 1982, 1994). In *The Extended Phenotype*, he characterizes the development of behaviours and the construction of niches that include foraging behaviours and nest-building as simply the expression of certain genes within the organism lengthening their reach outside the boundaries of the organism's skin. Because these artefacts of organismal construction increase the organism's fitness, (and so guarantee the replication of its genes), the genes for nest-construction are reliably passed on from one generation to the next. The incorporation of this kind of niche construction within Dawkins’ extended phenotype has been highlighted by Kim Sterelny:

[the] environment ... should be seen as part of the phenotype of the engineering organism, for these are the effects through which the responsible replicators have been selected. The single best reason for taking the gene/vehicle conception of evolution to be a genuine alternative to the standard genotype/phenotype conception is the fact that the systematic, evolutionary significant phenotypic effects of genes are not confined to the body of the organism carrying them (Sterelny 2001: 335).

Retaining a gene-centred perspective, Dawkins’ view, as well as Sterelny’s, takes the constructed environmental niche to be an extension of the information contained within the organism's genes. Not only is there a blueprint for building an organism, there is also a blueprint for the construction of nests, niches, and behaviours contained in the genes. Nests, like organisms, are just vehicles for gene replication—they are extended
vehicles (Dawkins 1994). No practical distinction exists between the environment outside the genes but within the boundaries of the organism’s skin and the environment outside of it.

The extended phenotype view may dissolve the distinction between organism and environment, but it preserves the strong Weismannianism of the gene-centred view which holds that there are genes and there is everything else. Relying on a linear genetic conception of causality, Sterelny argues that epigenetic, behavioural, symbolic, and cultural channels of inheritance do not constitute unique mechanisms of inheritance (Sterelny 2001: 336). These are just genetic inheritance—the product of an extended genetic replicator. The causal importance of cultural inheritance is not as significant as that of genes. Towards the end of his arguments, he partially concedes that

cultural inheritance is a key part of the explanation of human evolution. But it is not a phenomenon of much general evolutionary significance. Genetic inheritance ... is the core inheritance mechanism (Sterelny 2001: 337).

I think this contains an element of anthropocentrism. If cultural inheritance makes such a difference in human evolution, why does it make none to the rest of the organisms in the world? (cf. Jablonka and Lamb 2005: Ch. 5). And on what basis can humans overpower the linear genetic tyranny that the rest of the inhabitants of the world are ruled by?

As a conceptual sequel to the selfish gene perspective, the extended phenotype or the extended replicator perspective has as its centre the belief that genes are the primary cause of organismal form, development, and evolution. The claim that genes are immortal replicators, that they are the most important factor in development and evolution, and the privileging of genetic inheritance over all other mechanisms of inheritance, rely on an underlying commitment to linear genetic causation. Organisms, constructed artefacts, and environmental niches are the environments within which genes compete with other genes in other organisms and environments to replicate themselves. They are the constructed vehicles of gene replication.
Although the dissolution of the boundary between the organism and the environment in Dawkins’ and Sterelny’s gene-centred view is similar to my own, it is based on a wholly distinct set of commitments. Whereas their dissolution is based on the primacy of linear genetic causation and a commitment to strong preformationism in conceiving species, I rely on circular and distributed causes and generic preformationism.

The organism-centred view of species started by accepting vertical genetic inheritance as one of many routes by which resources are acquired by organisms and passed on to subsequent generations of organisms of the same species. Genetic, epigenetic, behavioural, and cultural inheritance all provide different pathways by which resources can be acquired by successive organisms to construct themselves over their lifetimes. These routes may furnish resources from conspecifics vertically, or between either conspecifics or heterospecifics horizontally. Resources may also be acquired by means of a combination of these routes. The organism’s generic capacities and stock of genetic, extragenetic, and ecological resources enable it to construct itself according to a similar way of life using similar resources in similar environments to its parents and offspring. Self-organization and reorganization of these resources is possible through the use of the generic capacities for learning, phenotypic plasticity, and developmental accommodation. Therefore, organisms are both cause and effect of the construction of its own species. This is because an organism is both the product of a previous organism’s reproduction, the constructor of itself over its lifetime, and the producer of a succeeding organism.

In Chapters Two, Three, and Four I have used the organism-centred view to reconfigure the meaning and reference of “organism,” “trait,” “homology,” “analogy,” and “species.” I suggested that the form and organization of organisms can be understood as the result of their self-construction activities rather than the preformed information contained in their genetic program or the selective factors in their pre-existing environmental niche.

These constructive efforts (over an organism’s lifetime, within its embedded environments, in community with con- and heterospecifics, and
over successive life cycles) involve physical engagement within the world. Organisms *literally* build their bodies and their environments from diverse resources.

In the next chapter I move from the constructive activities of organisms’ physical being to the constructive activities of their psychological being. In particular, I focus on a constructive activity that is unique to human organisms—the construction of race identity. The self-construction of a psychological identity may initially appear orthogonal to the physical instantiations of organismal self-construction discussed in earlier chapters. However, I suggest the organism-centred view offers a novel perspective on this kind of self-constructive activity as well as others.
CHAPTER FIVE

Re-constructing racial identity

5.1 Race is the similarity, identity, or continuity of what?

Similarity and the continuity of similarities have informed biological research from before Cuvier and Geoffroy to the present. This has been especially true within comparative morphology and more recently within comparative genomics. But how do similarities and the continuity of similarities provide empirically useful information about the world, and which kinds of similarity are informative? Preceding chapters have discussed the structural or functional resemblance among characteristics of different organisms (homology and analogy), the correspondence of parts or characters within the same organism (serial homology), and the similarity of the behaviours, environmental niches, and modes of living among individuals of the same species (and other conserved species specific traits).

Understanding something as similar to something else means there exists some relationship, property, or structure that they both share. Therefore, it is important to understand in what ways the identification of continuity among morphological, behavioural, environmental, and genomic similarities prove scientifically informative, facilitating predictions of other shared characteristics and dispositions.

In his “Seven Strictures of Similarity,” Nelson Goodman maintains that “every two things have some property in common ... two objects are
similar when they have at least one property in common” (Goodman 1972: 443). There are an infinite number of comparisons we can make between any two things, such that any two things, no matter how different, can be understood as similar in some respect. But if everything is comparable to everything else in terms of some common feature, then saying something is similar to another is just stating what is trivially true. Pointing out that two individuals are the same in some way without qualification is stating an empty, uninformative truism. In speaking of the luggage left at an airport at check-in, Goodman suggests,

the spectator may notice shape, size, color, material, and even make of luggage; the pilot is more concerned with weight, and the passenger with destination and ownership. Which pieces of baggage are more alike than others depends not only upon what properties they share, but upon who makes the comparison, and when (Goodman 1972: 443).

Judgments and comparisons can only be made with regard to a particular set of contextually specified standards. For similarity and resemblance to be explanatory, a more specific understanding of the relation of sameness is required. Our selection of which items we choose to compare and which relations of sameness are relevant in making these comparisons are dependent on relevant conditions of our environment as well as our own interests at that time. Comparison is always “relative, variable, and culture-dependent” (Goodman 1972: 438) occurring, as it does, within the layered contexts of our situated experience.

This contextualized understanding of the similarity among different individual objects or subjects is widely criticized as both ontologically and epistemologically lacking. It does not provide a fixed theoretical foundation on which to secure either metaphysical or scientific investigations. A belief in some underlying form, structure, or essence within individual substances or subjects that determines their nature pervades philosophical and scientific theories concerning both the very nature of being and our ability to refer to it:

essence (or a natural/metaphysical defining characteristic) is discovered as part of our general epistemic activity. The Putnam, Kripke, Donnellan causal theory of reference explains how the discovery of the ‘essence’ of such a natural kind can be spread
rapidly [such as] ... Putnam’s famous example concern[ing] the discovery that the essence of water is H₂O. Once it has been established that water really is H₂O then any apparent instance of water can not be water unless it is in fact H₂O (Gillett and McMillan 2001: 137).

Setting up his causal theory of reference, Hilary Putnam uses the example of water to ask how we can know that a sample of colourless, tasteless, potable liquid is water. He argues that we know it is water when we discover its underlying structure or essence. All samples of water, whether solid, liquid, or vapour, have the same underlying structure. We grasp what water really is when we learn that its chemical composition is H₂O. Every molecule of water has two hydrogen atoms that are covalently bonded to a single oxygen atom. Given any sample of ice, turgid liquid, or vapour we can judge whether the substance is water or not by discovering if its chemical structure is H₂O or something else. Knowledge of the chemical composition of water facilitates our predicting how it will behave in various circumstances: e.g. its freezing and boiling points, its electrical properties as an insulator, its low conductivity, its density in different forms, its cohesion, surface tension, and how it reacts when mixed with other substances.

Claiming that H₂O is water’s underlying structure has been taken to be a paradigmatic case of revealing something’s essence.²⁴ The idea that the essence of chemical substances is given by its chemical composition has been extended to living beings. The essence of an organism—what makes it the organism that it is—is its underlying microstructure. For both Putnam and Saul Kripke, the sameness relation that holds between two organisms is dependent on this underlying microstructure. Kripke famously muses, “whether science can discover empirically that certain properties are necessary of cows, or of tigers, is another question, and one I answer affirmatively” (Kripke 1978: 128). With the advances in genetics and genomics research, this underlying structure is identified as the organism’s genomic complement of DNA, one that it shares with all other organisms of

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²⁴ Arguing that water’s essence is its chemical structure H₂O and using it as a template for a natural kind is dubious. Even what is considered to be pure water includes more than just H₂O, including OH⁻, H₃O⁺ and many other ions (VandeWall 2007: 906-19).
the same kind. Just as water’s chemical composition determines its dispositional properties and behaviours, organisms too have “certain essential properties [that] determine the[ir] nature ... and how they will behave in any situation” (Ellis 2001: 3). In contrast to Goodman’s characterization, the development of the characteristics, behaviours, and dispositions of organisms are determined by its DNA. The similarity between any two organisms, for instance two tigers, is the result of their chemically defined essence. This determines their nature independently of where they live, their individual ontogeny, how they were brought up (in the wild or in a zoo), or their diet. Tigers “behave as they do ... not because of any external constraints that force them to, but because this is how they are intrinsically disposed to behave in the circumstances” (Ellis 2001: 3). All tiger behaviours, physical features, relationships within other members of the pride, and interactions with other animals and humans, are understood as having a single underlying cause—their DNA.

If there can be some underlying essence (either DNA or something else), a fixed definition of what makes a tiger a tiger, analogous to the identification of water with \( \text{H}_2\text{O} \), is possible. When used as the basis by which living organisms are classified in terms of crucial similarities or relationships, it is thought to provide an immutable foundation on which to group things according to their non-accidental properties. A classification system based on underlying essences would take all (or at least most) organisms thought to be of a particular kind as sharing the same underlying microstructural properties or relationships.

As previous chapters have revealed, trying to establish the criteria for membership within one group or another on the basis of uncovering essential underlying properties or relationships of resemblance has proved an often confused and misguided project. The confusions that arise when one attempts to decide the essential elements or relationships one should use to identity different natural kinds of individuals are many. If not the most evident, the most controversial cases where these confusions occur are in the various attempts to classify human beings into races on the basis of what are purported to be their essential properties. Many properties and
relationships from a wide range of disciplines, from philosophy, biology, anthropology, and sociology to politics and religion have been suggested as the continuities and sameness relations essential to revealing an individual's race.

“Race” has been the name under which people have been grouped on the basis of their phenotypic traits, (e.g. hair texture, skin colour, nose and lip shape), religion (Muslim, Jewish, Yoruban), cultural heritage (Inuit, Mestizo, Romany), geographical origin (Pacific Islander, sub-Saharan African, Amazonian), mitochondrial DNA, y-chromosome (distant Viking, Native American ancestry), language (Welsh, Hadza, Creole), or whether one is likely to be resistant to malaria, give birth to a child with Tay-Sachs disease, or suffer from cystic fibrosis (Black, Ashkenazi Jew, or White respectively).25

Sustained attempts throughout history and across disciplines have provided scores of possible divisions of humanity into races. Darwin, writing in 1871, lists the number of races as ranging from two to a sixty-three. Writing more recently, Lucius Outlaw emphasizes the challenges faced in selecting the criteria used to identify individuals according to their race. Both highlight the lack of agreement around conceptions of race.

Man has been studied more thoroughly than any other organic being, and yet there is the greatest possible diversity amongst capable judges whether he should be classed as a single species or race, or two (Virey), three (Jacquinot), four (Kant), five (Blumenbach), six (Buffon), seven (Hunter), eight (Agassiz), eleven (Pickering), fifteen (Bory St. Vincent) ... or [as many as] sixty-three, according to Burke (Darwin 1871: 62).

there is no settled consensus among persons ... in answer to questions of whether and if so how (and if not, why not), it is possible to characterize and classify racial and ethnic groups, and thereby identify individuals with precision as members of a particular racial or ethnic group, on the basis of real, objective, shared features, in rigorous accordance to the most settled norms governing the production and validation of empirical knowledge (Outlaw 1996: 15).

25 In section 5.2.1.2 I argue that equating these biomedical factors with racial ascriptions is both highly contentious and based on some spurious metaphysical assumptions about identity.
The various conceptions of race each bring with them their own criteria for identifying races. These amount to different ontologies of race: they posit basic categories and relationships which are then used to define individuals or types of individuals. They suggest a number of categories of racial conspecificity according to which all peoples can be classified.

The perspective set out in this chapter offers an alternative to these ontologies of race. My own organism-centred perspective utilizes the metaphor of heterogeneous construction. I suggest we construe the human organism as the centre of its own racial ascription. An individual organizes and interprets his or her own morphological, cultural, and historical embeddedness, directing his or her experiences, and making historical and causal linkages among these various factors. Racial identity is reciprocal and dynamically caused by one’s own ascription and the ascription given to one by other groups and individuals. It embraces both the multiplicity and changeability caused by one’s temporal, spatial, and cultural-situatedness and how these are manifest in one’s racial identity(ies). Before articulating my own ontology of race, I begin with a condensed conceptual history. This will highlight some recurring concerns and underlying assumptions about race. Responding to these, I critically discuss six current conceptions of race.

5.1.1 Early Conceptions of Race from Bernier to Boas

One of the earliest accounts of race as a category by which humankind could be divided into different categories was written anonymously in 1684 with the title, “A New Division of the Earth” (Bernasconi and Lott 2000: viii). This monograph was later attributed to François Bernier. Bernier and other European travellers at the time were particularly struck by morphological differences among the various peoples observed on their travels across Europe, the New World, Africa, and the Far
and Near East. Given that the original depictions of indigenous peoples were reports from upper middle class gentlemen travellers, Bernier’s as well as later reports tended to read a bit like travelogues rating the attractiveness or otherwise of the inhabitants (especially the females) of various “exotic” lands they visited. Most conspicuous to these travellers were what they perceived to be the striking differences in the forms of the bodies, facial features, skin and hair colour of the inhabitants of these lands in contrast to the form and pallor of the more familiar European faces and bodies.

[In the Indies ... they are beautiful brunettes ... some are coloured of ever so little a yellow, who are very much prized, and whom I found also very much to my taste; for that shade of yellow is vivid and brilliant, and has none of that ugly and livid paleness of jaundice. Imagine to yourself a beautiful and young French girl, who is only just beginning to have the jaundice, and instead of that sick, pale visage, and those yellowish eyes ... give her a healthy face, soft, laughing, and beautiful ... amorous eyes, and you will have as near an idea of them as I can given you (Bernier 1684: 3).

Bernier believed that these morphological differences signified underlying essential differences between human beings which suggested that they could be divided into different groups or races on the basis of these differences. Although Bernier’s reliance on skin tone is of paramount importance to him and other gentlemen, the justification for this is left unstated. In “A New Division of the Earth,” Bernier proposes that the world’s human population can be divided into four or five races. Bernier draws a number of distinctions between these races on the basis of skin colour as well as the morphological features of the face. He is careful to discriminate those that are manifest within the individual arising “by accident” from those arising “by nature.” In some individuals, a dark complexion is accidental, as it is due to excessive sun exposure. If these individuals were taken out of the sun, their skin would lighten. He contrasts individuals whose skin colour is accidental and individuals whose dark skin colour remains dark regardless of sun exposure. The latter’s skin colour is a feature essential to them. Bernier’s emphasis on racial divisions is later taken up by Linnaeus (1735) and Kant (1777). Although intending
to set out a natural classification based purely on biological differences among human beings, Linnaeus’ four races (or subspecies\textsuperscript{26})—White Europeans, Yellow Asians, Black Africans, and Red Americans combine skin colour with nationality (Banton and Harwood 1975).

Following Linnaeus, Kant also sought a division of races based principally on the morphological characteristics of human bodies. He intended his concept of race to form a natural division amongst individuals, in the same way that \textit{species} and \textit{genus} do, on the basis of heritable biological variations. However, instead of focusing on describing and classifying races like Bernier and Linnaeus, Kant was keen to explain the origin\textsuperscript{27} of racial differences and their perpetuation along racial lines. In “Of the Different Human Races,” he explains that the origin of racial differences is in the “special seed or natural predisposition [and] is to be found in organic creation … that necessarily pass on the same characteristic features that they have inherited” and that produces, generation after generation, those characteristics associated with race (Kant 1777: 14). Kant is careful to note that sun exposure and diet, on their own, do not cause changes in the growth of human beings. Any changes they do cause are conceived of as Bernier did, as accidental rather than essential features. Sun and diet alone cannot cause growth or modification of a human being’s development unless an ability to change and modify is already present within the human being. “Any possible change with the potential for replicating itself must instead have been present in the reproductive power so that chance development appropriate to the circumstances might take place according to a previously determined plan” (Kant 1777: 14). In distinguishing the artificial from the essential traits of humans, it is only the latter characteristics which are the result of an inherited stock of special seeds (\textit{Keime}) and dispositions (\textit{Anlagen}). Kant’s claims broke with the

\textsuperscript{26} At this time, racial classifications were commonly used as a further taxonomic specification although they were often used interchangeably with both species and subspecies.

\textsuperscript{27} Although beyond the scope of this chapter, there were heated debates between those who argued that the races were created from one initial race (monogenesis) and those who believed they were created separately (polygenesis). Kant (1777), Blumenbach (1776), and Darwin (1871) argued for monogenesis, whereas Voltaire (1766) and others argued for polygenesis.
traditional view that the morphological differences associated with race in different groups are fixed. Instead these differences were due to “numerous seeds and predispositions [that] must lie ready in human beings either to be developed or held back in such a way that we might become fitted to a particular place in the world” (Kant 1777: 14).

Kant dismissed the idea that race was the result of the unrolling of a fully preformed form. Human beings also inherit dispositional qualities for living in particular environments which are passed on from one generation to the next. Race is instead a generically preformed property of human beings. Because humans have ranged all over the world and settled in vastly different environments from arctic to desert, they have acclimatized to a range of different conditions. They have inherited a variable set of dispositions for the purpose of facilitating a way of life within a particular climate. Humans with these climate-specific dispositions remain in the climates they were born to, thus ensuring the continuity of races over generations.

the growth of the spongy parts of the body had to increase in a hot and humid climate. This growth produced a thick, flat nose and thick, fatty lips. The skin had to be oily ... to lessen the too heavy perspiration. Besides all this, humid warmth generally promotes the strong growth of animals. In short, all of these factors account for the origin of the Negro, who is well-suited to his climate, namely, strong, fleshy, and agile (Kant 1777: 17).

As the above passages of Kant, Bernier, and Linnaeus show starkly, the importance of skin colour and morphology was believed to be self-evident, as plain as the nose on one’s face, easily judged to be narrow, broad, flat or projecting.

Influenced by both Bernier and Kant, and his studies of various human subjects at the Muséum d’Histoire Naturelle, Cuvier (1824-1847) proposed that there was an underlying nature which determined the different cultures of races. To discover what this was, Cuvier studied a variety of what he believed were racially “pure” individuals. In studying them, he hoped to uncover which morphological traits were held in common among races and which varied. One of the most famous individuals he studied was a Khoi-San woman named Saartjie (Sara) Baartman.
Originally a servant in South Africa, Baartman went to England after it was suggested that she could gain considerable wealth by exhibiting herself around Europe. In England, her exhibitors displayed her under the title, the Hottentot Venus.\textsuperscript{28} She was treated as a curiosity at the time as some of her morphological features, in particular her steatopygia (large buttocks) and sinus pudoris (elongated labia minora), as they were thought to be remarkable in comparison to those of European women (Fausto-Sterling 1995: 19-48). Although Baartman refused to display her genitals while she was alive, they were preserved and displayed along with her skeleton and brain in Paris’s Musée de l’Homme until 1974 and were only returned to South Africa to be buried along with her other remains in 2002 (Sadiah 2004: 242-51).

Cuvier’s own studies of Baartman were as a taxonomic archetype of a pure race. Through his observations of Baartman, both during her life and of her remains after her death, Cuvier concluded that there were just three pure races: Whites, Yellows and Blacks. All other races were variations or “hybrids” of these pure types (Cuvier 1812).

A common belief in the 17\textsuperscript{th} and 18\textsuperscript{th} centuries was that the morphological features so readily distinguished, and often judged lacking in comparison to those of the European travellers themselves, were taken to be external indicators of other characteristics of temperament, intellectual capacities, and vigour. The categorization of peoples on the basis of their morphological characteristics as a way to judge a whole host of non-morphological qualities was based on the assumption that these physical attributes and their temperament, behaviour, and intellectual capacities all had a common cause in their essential nature.

In his seventh chapter of \textit{The Descent of Man}, “On the Races of Man,” Darwin lists some of these morphological and intellectual capacities among human beings which he believes are of “no doubt:”

\begin{itemize}
\item the texture of the hair, the relative proportions of all parts of the body, the capacity of the lungs, the form and capacity of the skull
\end{itemize}

\textsuperscript{28} The Khoi people were called “Hottentots” by the 19\textsuperscript{th} century Europeans due the sound of the clicks in the Xhosa language they spoke (Ladefoged and Maddieson 1996).
liability to certain diseases. Their mental characteristics are likewise very distinct; chiefly as it would appear in their emotional, but partly in their intellectual faculties. Every one who has had the opportunity of comparison, must have been struck with the contrast between the taciturn, even morose, aborigines of South America and the light hearted, talkative negroes (Darwin 1871: 56).

Human variations in skin colour, anatomical form, facial features, disease susceptibility, emotional and intellectual development, and nationalities were features that were widely thought to naturally coincide. Darwin believed, like Cuvier, that these variations fell into obvious pure categories of race, and intercrosses or blends of these (Darwin 1871: 58-61). Augmenting Cuvier’s description of pure races, Darwin explained how a race can be continuous over generations if there was no (or little) blending. Human beings who live hundreds of miles apart may be of the same race because their “general resemblance [is due] to descent from a common stock” (Darwin 1871: 71).

One of the first theorists to challenge the racist assumption that one’s skin colour and morphological characteristics could be causally correlated to one’s temperament, intelligence, or emotional capacity, perpetuated in many of the early accounts of race was Franz Boas (1911, 1940). Boas’ contribution to the conceptual history of race was to create a clear division between what were considered to be the “biological” and the “cultural” characteristics of race. He argued that, apart from being based on racist assumptions, explaining one’s biological features by relying on one’s cultural features or vice versa was an ontological mistake and “any attempt to explain cultural form on a purely biological basis is doomed to failure” (Boas 1940: 165). This separation of the biological and the cultural remains in many, if not most, race concepts today. Often, theories of race are grouped as belonging to one of two different categories depending on whether they employ criteria from the putatively natural sciences or the putatively social sciences.

The preceding discussion has focused on the origins of many of the most controversial and persistent concerns for those attempting to form or re-form a conception of race: belief in race as natural kind or essence;
reliance on morphological features conceived in contrast to the (often white) observer; the cause of racial continuity among generations; the belief that raced morphological features, behavioural, and intellectual capacities are linked; the idea of racial purity; and the separation between the putatively biological and putatively cultural characteristics of race. In doing so, it serves as the contextual setting within which both the subsequent discussion of current conceptions of race as well as my own reconceptualization can be understood.

5.2 TWO CATEGORIES OF RACE CONCEPTIONS: NATURAL SCIENTIFIC AND SOCIAL SCIENTIFIC

In the following, I discuss six conceptions of race separated into the two categories to which they are usually understood to belong. The first is composed of those conceptions which have been understood to be based on (putative) natural scientific evidence. The second is composed of those based on social scientific evidence. Natural scientific conceptions have been variously identified as physical, biological, or absolutist (the latter by their detractors). The social scientific conceptions have been called anthropological, historical, and relativistic (the latter by their detractors). The natural scientific conceptions seek to order the contents of the world systematically on the basis of the physical measurements and distribution of biological variation among human bodies, whereas the social scientific conceptions focus on the phenomena of race as the product of cultural and behavioural interactions among persons.

The natural scientific category of race conceptions includes: 1) the morphological race concepts which emphasize the proportions of the face and skin colour, 2) biomedical race concepts which use recent techniques for obtaining medical information concerning such traits as whether individuals are tolerant to lactose in adulthood, are resistant to malaria, or on the basis
of chromosomal information (e.g. y-chromosome, mDNA) as evidence for a biological basis to race, and 3) population race concepts which focus on the effects of migration and mutation on different groups of people.

The social scientific category of race conceptions includes: 1) the developmental and behavioural concepts of race which hold that it is our characteristics and actions rather than our morphology which give meaning to “race,” 2) the familial concepts which hold that race is passed down directly from grandparent to parent to child, and 3) the cultural concepts, which rely on the relationships and shared history of individuals within societies and communities.

5.2.1 NATURAL SCIENTIFIC CONCEPTIONS OF RACE
5.2.1.1 MORPHOLOGICAL CONCEPTIONS OF RACE

According to a morphological conception of race, people of the same race share certain intrinsic properties. These conceptions rely on supposed correlations in morphology. For example people from continents with hotter climates are believed to have darker skin, darker eyes and darker, curlier hair; people from colder continents, lighter skin, lighter eyes, and lighter, straighter hair.

In some morphological accounts these bodily features are believed to be visual indicators of deeper unseen differences in character and behaviour. Bernier, Kant, and Darwin’s divisions of humanity into races discussed above are examples of morphological accounts of race. They connect the named divisions—Black, White, Yellow, Red—classifying human beings on the basis of their colour, facial and bodily structure, as well as the temperament and behaviour supposedly associated with these divisions. Certain behaviours and temperaments were thought essential to all
individuals whose bodily features were perceived characteristic of a particular race: thus certain behaviours became racialized stigmas such as "taciturn, even morose, aborigines of South America" (Darwin 1871: 56), or "the Black Negro, who is well-suited to his climate, namely, strong, fleshy, and agile. However because he is so amply supplied by his motherland, he is also lazy, indolent, and dawdling" (Kant 1777: 17). Approaching race morphologically means that individuals are understood to have nameable, discrete, objective, and immutable racial identities that are discoverable purely on the basis of their external physical appearance.

Morphological race groupings divide individuals into groups sharing physical bodily traits judged to be indicative of a particular race type. They take it as given that one can distinguish any Nordic person from any person from sub-Saharan Africa since the contrasts in bodily and facial features (e.g. musculature, hair texture, nose and lip shape, skin and eye colour) are so great. These accounts propose that racial difference is either entirely or mostly caused by one’s physical anatomy rather than being environmentally, behaviourally, or culturally caused. Our physical anatomy is the ultimate determiner of who we are. My race is somehow written on my body—conceived of as an essential and inescapable fact of who I am. Because our bodily and facial features are perceived as more natural and essential to us, it is believed to be more worthy of attention and provides a more justifiable basis on which to classify humanity according to what are conceived to be natural divisions.

Not all morphological conceptions presuppose that physical features can be used as indicators for behavioural, intellectual or emotional traits. A recent example of a morphological conception of race of this kind has been presented by Armand Marie Leroi. Leroi suggests that, taken as individual traits, skin colour, body, nose shape or eye colour do not tell us anything about a person’s race or country of origin. However, if we take these characteristics together we can make a number of correct predictions about a person’s other physical traits, country of origin, or even their genetic constitution. This is because

certain skin colors tend to go with certain kinds of eyes, noses, skulls and bodies. When we glance at a stranger’s face we use
those associations to infer what continent, or even what country, he or his ancestors came from—and we usually get it right. To put it more abstractly, human physical variation is correlated; and correlations contain information (Leroi 2005).

In this quote, Leroi clearly takes morphological variation to be the main determiner of one’s racial categorization. Although writing more than a century earlier, but just twenty-six years after Darwin’s “On the Races of Man,” W. E. B. Du Bois (1897) provided what can now be understood to be a particularly enduring analysis of the problem with relying on morphological features in determining an individual’s race. If we consider Du Bois’ “The Conservation of Races” we can begin to uncover the persistent morphology-centred thinking that leads to Leroi’s conception of race. Du Bois questions the appropriateness of any classification of race based on morphological indications such as skin colour, head shape, or the type or amount of facial or body hair. He argues that although there may be differences in these respects, there is so much diversity among individuals within a particular race that relying on these morphologies produces an inadequate basis for racial differences and similarities.

Du Bois argues that variations in morphological features do exist, and if they tended to co-occur with each other then we would be able to use them to classify humans into races on the basis of these. However, they do not. Variations in the colour of skin, texture of hair, shape of the head do not, pace Leroi, naturally “tend to go with each other.” They can be found separately in some individuals and in all sorts of combinations within a variety of different peoples such that any classification on the basis of them would prove useless.

All these physical characteristics are patent enough, and if they agreed with each other it would be very easy to classify mankind. Unfortunately for scientists, however, these criteria of races are most exasperatingly intermingled. Color does not agree with texture of hair, for many of the dark races have straight hair; nor does color agree with the breadth of the head, for the yellow Tartar has a broader head than the German (Du Bois 1897: 109).

Du Bois is quick to point out that any classification that takes these physical characteristics to be the basis of its racial divisions fails in its aim of being based on universally held or essential traits. Physical
characteristics such as head shape or skin colour do not determine one’s race. Although these types of physical variation are intended by morphologically based classifications to be common to all human beings of a particular race, they are only mere descriptions of observed variations among individuals by someone with certain features. Race cannot be characterized in terms of shared morphological characteristics of some group of individuals because the physical features shared do not fall into categories but are, as Du Bois describes “intermingled.” He denies that knowing that an individual has light skin and light straight hair provides enough information to allow us to make reliable predictions about her other morphological (or behavioural traits). These morphological variations (in skin colour, hair texture, and head shape etc.) do not form the basis on which we can ground generalizations or predictions because they do not necessarily coincide with one another. That is, morphological traits are nonconcordant with one another and with other supposedly racialized traits (e.g. of behaviour and intelligence).

While it is undoubtedly possible to group human beings on the basis of morphological traits, it is a mistake to think that the resultant groupings form natural or “pure” homogeneous kinds of the type Cuvier or Leroi assume. This is because there is no metaphysical basis for the belief that individuals grouped on, say, the basis of hair texture and head shape necessarily coincide with individuals grouped on the basis on, say, of skin colour and eye colour.

5.2.1.2 BIOMEDICAL CONCEPTIONS OF RACE

Du Bois and others have shown that race, if it exists at all, cannot be sufficiently based on morphological features. However, this has not dissuaded Leroi and others (cf. Sesardic 2005) who still seek to secure a natural scientific conception of race. The identification of individuals on the
basis of biomedical, genetic, or genomic data relies on the assumption that racial identity is based on unique biomedical phenotypes or genotypes. Seeming to trade on the idea that the underlying essence of water is \( \text{H}_2\text{O} \), this view holds that different kinds of human beings can be identified in terms of their similar biochemical make-up. Instead of just relying on the external similarities and variations within different peoples, the biomedical conception of race seeks evidence of biologically determined racial differences within epidemiological and genomic data.

Instead of using outwardly recognizable morphological characteristics to identify individuals as belonging to one race or another, there is now growing interest in the view that racial differences are written in our genes. There has been an increasing belief that the new genomic data sources developed in the Human Genome Project will secure a gene or set of genes that are the ineluctable determinants wholly (or mostly) responsible for who we are. Knowledge of our genetic information means that we can find out whether we have a particular gene or if we are a carrier of a particular disease. Who we are is then fully available to us when we uncover our genetic codescript. According to a Putnam-Kripke approach to essences, we now have access our own underlying microstructural essence—the definitive causal source that determines who we are. This genetic determination has been vigorously sought by those wanting to find a “Black gene,” “Native American gene,” or “Inuit gene” in order to prove or uncover their racial identity (Langdon 1995). Reliance on genes as the most important cause underlying one’s racial identity effectively essentializes these complex identities. It assumes who we really are is wholly contained within the information encoded in our complement of genes. The increasing array of genetic and medical tests being offered to us to find out more about ourselves, where we really come from, and who we really are attests to the prevalence of this view of race.

One of the minor pleasures of this discovery is a new kind of genealogy. Today it is easy to find out where your ancestors came from—or even when they came, as with so many of us, from several different places. If you want to know what fraction of your genes are African, European or East Asian, all it takes is a mouth swab, a postage stamp and $400 (Leroi 2005).
Although this way of speaking is pervasive in the various media, what does it really mean to say that a person’s race can be fractioned, as being 14% African, 12% European, 8% Iroquois, or 20% Inuit? Interpreting an individual’s racial ancestry in this way assumes race is something to be uncovered, like an essential underlying property (or oddly, a percentage of properties) of being a particular kind of human. It assumes that there are genes that can be objectively identified as indicators of one’s racial identity, and provide what fraction of one’s genes are attributable to which races.

Conceiving of race in terms of the presence or absence of certain genes, or “what fraction of your genes”, are for instance, Iroquois, also trades on the often unspoken premise that there are individuals who are (or could have been) racially pure. As I mentioned at the beginning of this chapter, the idea of pure lines was originally formulated by Cuvier (1812), and taken up by Darwin (1871). They held that there are a few pure types and all other races are merely hybrids or intermediates whose racial identity is not pure. If someone can be 8% Iroquois, then there at least seems to be the possibility that someone else might be 50%, 60%, or even 100% Iroquois. If we (as Leroi suggests, literally) buy into the idea that we can find our racial heritage in this way, then we also must believe that there is indeed the possibility that there may be an individual who is 100% Iroquois. Identifying someone as 100% Iroquois would be tantamount to identifying them as a racial archetype or type specimen to which all other individuals would then be compared as tokens which have a certain percentage similarity to that type. The purity of racial lines or of the archetypes they use as “pure” type specimens has been most aggressively pursued by those interested in establishing a genetic basis for a Jewish identity among the Falasha of Ethiopia, the Lemba in South Africa, and the right to claim Native American identity in some North Americans. For instance, both serotological and genetic data using the y-chromosome have been used to judge whether individuals are Cherokee or not (Pollitzer et al. 1962), and have also been used in determining the inclusion or exclusion of

29 More problems surrounding the idea of pure lines will be discussed towards the end of this chapter.
individuals in other Native American tribes (Harpending and Ward 1982, Dupré and Hauskeller 2007).\textsuperscript{30}

What race someone belongs to has often been understood to be a crucial property of who she is, and her identity as a person. In this respect, medical and genetic testing could be taken to justify the reality of natural racial groupings that were originally decided on the basis of morphology. There are a number of genetic variations within human beings that have been of particular interest in the search for a biological basis for race. Uncovering certain biomedical differences has proved especially compelling for those who seek biologically determined racial differences. However, deciding what kind of biomedical data is central to someone’s race has not been straightforward. This data could include autosomes, x- and y-chromosomes, introns, exons, deletions, duplications or insertions, mitochondrial DNA, or susceptibility to sickle cell anaemia, lactose tolerance or intolerance.\textsuperscript{31}

Two biomedical phenotypes that have frequently been suggested as candidates which could be used to group individuals into races are the resistance to malaria(113,773),(113,773) (often purported to be specific to a relatively high incidence of sickle cell disease among black-skinned people of African descent) and the ability to tolerate lactose (purported to be specific to white-skinned people of European descent).

Sickle cell disease is the name given to a range of disorders, including sickle cell anaemia. Sickle cell anaemia is thought to be most common to those peoples who live in hot and tropical climates which make malaria a real threat to survival. Although it can affect persons of any race, it is less frequently found in northern climates where malaria does not affect people.

\textsuperscript{30} These data have also been utilized by those interested in discovering race-related genetic diseases and prenatal testing (Hauskeller 2004: 285).
\textsuperscript{31} Genetic and biomedical research has proved important not, in the way Leroi specifies, for resolving an individual’s racial composition and therefore identity, but for improved biomedical testing for inherited diseases. Although not designed to provide any causal connection between disease and racial identity, some have seized upon these biomedical tests as providing evidence for objectively defined racial categories. It has also become increasingly popular to rely on racial categories for health policies and distribution of resources, a practice which has been called “racial profiling” (Satel 2002).
Sickle cell anaemia is caused by a single nucleotide polymorphism (SNP).\footnote{There are four bases: guanine, adenine, cytosine and thymine that combine to form nucleotide triplets that make up the rungs along the double helix of DNA.} In individuals without sickle cell anaemia, the nucleotide GAG is usually present. In individuals with sickle cell anaemia, GUG is present (Ashley-Koch et al. 2000). SNPs are common and most do not cause any deleterious consequences. However, this is not the case in this instance. This single change affects the shape of the red blood cells causing them to form long thin spikes or sickles. Because red blood cells contain haemoglobin, the protein that carries oxygen from the lungs to the rest of the body, this causes problems in sickle shaped blood cells that do not affect normal round blood cells. Not only do these sickled cells live shorter lives than non-sickled ones, which causes anaemia, they do not flow through the blood vessels as well as the normal round cells. These sickled cells have a tendency to stick together causing potentially life threatening conditions due to lack of oxygen, vascular occlusion, and stroke (Desai and Dhanani 2004).

Sickle cell disease is present in homozygotic individuals (who inherit two alleles, one from each parent). Heterozygote carriers have no anaemic symptoms, but because there is incomplete penetrance, heterozygotes posses some sickle shaped red blood cells (although not as many as homozygotes). When an heterozygote individual lives in an area where the malaria parasite is present in the gut of mosquitoes, she has a level of malarial resistance. The misshapen red blood cells of the sickle cell carrier hamper the ability of the \textit{Plasmodium falciparum}, which is the most virulent plasmodium responsible for malaria, to reproduce. When not in the gut of its mosquito host, the malarial parasite spends most of its life within the red blood cells where it multiplies. The thinner and more fragile sickle shaped red blood cells are not conducive to the life cycle of the plasmodia (Pearson 1977). This results in the resistance to malaria of those individuals with sickled red blood cells.

Although sickle cell disease is common among many West Africans, it is also found in some North and South Americans living in areas where malaria is a threat. But malaria also occurs in individuals of the Mediterranean, Southeast Asia, and the Middle and Far East. Although
people in these areas do not suffer from sickle cell anaemia they do have a resistance to malaria due to the presence of \( \alpha^- \), \( \beta^- \) and \( \delta^- \)-thalassaemia (Lau et al. 1997).

Malarial resistance is treated as a racial trait caused by sickle cell anaemia. On the basis of the racialized phenotype of malarial resistance, the grouping of individuals resistant to malaria is believed to form a racial group—black Africans and those with black African ancestry. However, if we were to classify individuals in terms of their resistance to malaria, we would actually obtain a very different grouping of individuals—one which would not align with other racial divisions (e.g. based on skin colour: black, yellow, white, red; or geography: Africans, Asians, Europeans, Americans). Individuals within populations of the Mediterranean, such as some Italians, Greeks together with some Africans, Southeast Asians, Arabians, and those of the Far East would be members of the group resistant to malaria. The Northern Europeans and the Xhosas of South Africa would be grouped together as non-malaria resistant. When speaking of malarial resistance, it is simply not explanatory to say that the reason someone has malarial resistance is because they are black. This is because the groups identified using morphological concepts of race do not overlap with those identified using this biomedical conception of race.

The second candidate criterion for grouping people into different races on the basis of biomedical traits is lactase persistence. The presence of the enzyme lactase enables individuals to digest the main carbohydrate, lactose, which occurs in milk. Nearly all infant mammals possess the enzyme lactase but later, after weaning, lose the ability to digest lactose later in life. The persistence of the lactase enzyme after weaning until adulthood arose when humans began domesticating cows, sheep, goats, camels and buffalo for their milk. Although the presence of lactase has been associated with milk drinking in Northern Europeans, it cannot be attributed to something like the presence of a racial white gene. In fact, if we group people in terms of their ability to drink milk in adulthood due to their retention of lactase from infancy, this group would include Northern Indians, some Africans such as the Fulani, and Central and Northern
Europeans; whereas those who are not able to digest lactose include Southern Europeans, East Asians, Native Americans, and some Africans (Tishkoff et al. 2007).

At least in terms of the morphological and national/geographical divisions of race, classifying peoples using both malarial resistance and lactose tolerance in adulthood as criteria results in groupings that are wildly nonconcordant. As with malarial resistance, lactose tolerance is a trait that does not align with any of the traditionally understood, morphologically defined groupings of race.

What may be more explanatory are: the ecological conditions which were conducive to mosquitoes thriving, the transfer of plasmodia among mosquitoes, or the agricultural practices and dairying within particular communities. These biomedical phenotypic traits are more likely to be endemic to social organization and agricultural practices (cf. Livingstone 1958 and Weiss et al 1984). Malarial resistance may be interesting not because it is correlated with dark skin but because the incidence of malaria occurs among certain groups who share similar agricultural methods or live near swamplands. For instance, different groups of individuals may share similar techniques in crop growth, irrigation, or fertilization. They may choose to cultivate their crops on drained swaps. These practices are conducive to the breeding activities of mosquitoes, whose larvae require an aquatic environment.

Race (morphologically construed) is not the explanans to the explanandum, why does this group of people have malarial resistance? In order to determine an individual’s race, it must first be necessary to identify a race group. Identifying a particular race group is often based on selecting individuals whose morphological traits or genes fit with those of interest to the researcher (e.g. malarial resistance or lactose tolerance). This is done by a set of factors which the classifier has pre-selected on the basis of their possible co-occurrence in commonly understood racial groupings (often known as “racial-profiling”). This means that the researcher must first have criteria other than an individual’s country of origin or distant ancestry to initially select individuals thought to be members of the same race, i.e. the
researcher’s initial recognition and attribution of the person's morphological characteristics as belonging to a particular race. If the researchers findings then suggest that the ancestry of a particular individual reveals her race, it does so by proving to be evidence in support of the researcher's initial racial ascription—not the necessary correlation of a biomedical trait, e.g. lactose tolerance with race.

Attributing causal or correlative biomedical features to one’s racial identity is at best dubious. This does not mean that there is nothing that might explain the occurrence (or origin) of these biomedical phenotypes. Following the above suggestion, what might explain these are the common agricultural practices of peoples and their shared ways of living. Human beings are not classifiable into a particular race on the basis of their propensity to a particular disease or their having a particular gene, but this information may be used by someone as contributing to their own racial identity. However, this is based on the appropriation of biomedical or genetic features into one’s psychological identity of their own racial ascription, a theme I will explore later.

5.2.1.3 Population Conceptions of Race

If environmental and geographic locations can provide information for predicting more characteristics of a person’s makeup than purely morphological or biomedical features, perhaps a better candidate by which to understand race might be found in the population conception. These accounts demarcate human beings in terms of the ecological groupings or migration of populations. Knowing the agricultural history and geography of the place from which an individual originated only provides partial information and cannot on its own explain the presence or absence of certain phenotypes such as one’s hair texture, lactose tolerance, or malarial resistance. In addition to agricultural and ecological information, the population conception relies on migrational routes from and to other geographical areas, the trade between different groups, and the political and social groupings that may have affected whether two groups living in the
same area interacted with one another, whether they were in fact adversaries who avoided each other at all costs, or were friendly, cohabitated, and intermarried with one another.

According to population conceptions of race, migration, rare genetic mutations, and genetic drift are thought to cause evolutionary differences between populations. This approach takes race to be a feature of group relationships. On this view, population differences may result due to a number of reasons. For instance, populations tend to genetically diverge when they are (reproductively or geographically) isolated from one another. This divergence halts when two previously separated populations merge and share a gene pool. Populations also change due to what is called the founder effect. The founder effect consists in the spread of genes from a small group of individuals which originate from a different geographically and genetically isolated population who relocate to a new geographical area (Cavalli-Sforza 1995). Any rare genetic mutations within the original founder population are transmitted to all subsequent generations. Consequently, there will be a higher percentage of that rare mutation within the individuals of the population founded by the small group of individuals than in other populations (including the population from which the founders emigrated from).³³

There are a number of reasons why people migrate from one area to another. Migration might occur if there is an incentive for one group to move into another area, e.g. due to better climate, more cultivatable land, to escape political unrest, or to avoid starvation. If there is another population already occupying that area then this migration affects both the newly migrated population and the resident population. This is because they now have an opportunity to exchange both culture and genes with populations from which they were previously isolated. For these reasons Cavalli-Sforza argues that these geographic expansions can be traced genetically. The high frequencies of certain genes or alleles may indicate the expansion of different groups from one area to another. He believes that population

³³ This is especially pronounced in island populations which are genetically and geographically isolated.
genetic analyses can reveal some similarities which exist among individuals of the same race and some differences between individuals of different races.

This approach focuses ostensibly on genetic markers and in tracing these in current populations to suggest the major directions of migration over hundreds of generations. Genetic data are suggestive, because both genetic and cultural factors co-evolve through the movement of people. Groups of people moved with their ideas. Cavalli-Sforza (2000) argues that the original direction of the migration of human populations expanded from southeast to northwest into previously unoccupied geographical areas. These migration patterns suggest the spread of farming technologies and linguistic usage.

This population conception of race relies on gene frequencies and genealogical inferences using both haplotype data from mtDNA, the y-chromosome, and low recombination autosomal genes as well as archaeological evidence. It tracks migration events and interprets the pattern of migration and evolutionary adaptations as specifying certain population groupings. This provides information about the movements of raced populations from one country to another.

This conception of race is based on a similar set of assumptions to the standard Mayrian biological species concept (discussed in Chapter Four). Just as the similarity among members of the same species are thought to be ensured by the reproductive isolation of the population and the lack of gene flow between members of different species, the cohesion of raced populations is preserved in like fashion. Within members of the same race population, cohesion is thought to be ensured by forming reproductive relationships only with members of the same population. Different raced populations are believed to be isolated from one another due to such factors as geographical distance, political isolation due to fighting, religious strictures against marriage of those outside the population, or other considerations which make marriages and sexual relationships between members of the same population statistically more likely than with those of different populations. All of these are barriers to matings between members of different populations. This is thought to ensure the preservation of race-specific
traits within the population that may be preserved generation after
generation.

Whether a population concept of race accurately demarcates
humankind into races on the basis of such empirical evidence may be in
doubt if,

[there has] always been a very large amount of migration and
intergroup mating ... in the history of the human species but
[which] is now more widespread than ever. The result [would be]
that individuals identified by themselves or others as belonging to
one ‘race,’ based on the small number of visible characters used in
classical race definitions, are likely to have ancestry that is a
mixture of these groups (Lewontin 2005).

Reproductive isolation may be explained on a small scale with regard to
cultural and religious practices, however; according to Lewontin, intergroup
mating has been and continues to be generally pervasive among different
racial groups. Although there may be definite differences between
individuals of various populations, an overwhelming 85% of genetic
variation in humans is actually within populations, not between them
(Lewontin 1972, 2005). The majority of biological diversity (and genetic
variation) occurs within rather than between what have been commonly
understood as races.

Understanding race in terms of the genetic differences between racial
populations assumes that there is significant genetic as well as geographic
isolation between groups which prevents intermixing; however, this rarely
exists. The reason why certain genes (rare mutations) are present in high
percentages within a population may be explained by population changes
such as the founder effect. But this is not the only explanation. The
population conception, like Mayr’s BSC, takes race populations to be defined
as isolated interbreeding groups which share a gene pool. But as Lewontin
argues, in terms of racial populations, this isolation is an illusion.

Proponents of the morphological, biomedical, and populational
conceptions of race seek to equate different biological variations with race.
What is not in dispute is that variations exist and racial classifications have
been based upon them. What *is* in dispute is whether the variations
identified by these natural scientific conceptions of race alone can identify
the kinds of things that are important in both recognizing and understanding an individual's racial identity.

5.2.2 SOCIAL SCIENTIFIC CONCEPTIONS OF RACE

5.2.2.1 THE DEVELOPMENTAL AND BEHAVIOURAL CONCEPTIONS OF RACE

An alternative to conceiving of race in terms of morphological, biomedical, or population genetic features are those explored by Boas (1911) and Appiah (2004). Boas formulated his conception of race as an alternative to what he took to be the deeply flawed assumption common to many scientific conceptions of race, that

when we try to judge the ... races of man, we make the silent assumption that [race] is something permanent and stationary, that it depends upon heredity, and that, as compared to it, environmental, modifying influences are, comparatively speaking, of slight importance (Boas 1911: 84).

Boas argued that understanding races as unchanging stable types was both theoretically and empirically disputable. By focusing his research on the differences in body morphology of families who emigrated from Europe to America in the early 1900s, Boas found that newly emigrated Europeans' height and the shape of their heads was dramatically different as compared to the height and head shape of their first and second generation born American descendants. Of the families he studied in New York, he observed of the East European Jews that

the head of the European-born is shorter [and wider] than the head of the American-born ... At the same time the American-born is taller. All these differences seem to increase with the time elapsed between the emigration of the parents and the birth of the child, and are much more marked in the second generation of American-born individuals. Among the long-headed Sicilians similar observations have been made ... [and] the people of Bohemia and Hungary (Boas 1911: 86).

The racialized characteristics of individuals which were seemingly fixed in one country changed when families immigrated to the New World.
Boas concluded from these studies that race types were inherently unstable and plastic. The individual development of morphological characteristics among these families was found to be considerably influenced by the different geographical, ecological, and social environments in which they lived showing considerable modification and plasticity of their “racial features” and “racial types” (Boas 1911).

More recent studies have shown similar results to those of Boas. The plasticity of one's own racialized features and ascribed racial classification can change in as little as a few years if one moves to a different country, or different community within the same country, with a different set of beliefs concerning the assessment of morphological, religious, linguistic, or behavioural features than one's own. These changes may even affect the racial ascription of individuals after a matter of months. For example, a recent study showed that there were differences between the ascribed races on the birth and death certificates of babies who had died aged one year. The study found that 37% of the infants who were born Native American died a different race (Hahn et al. 1992). According to the developmental reading of race, because human beings develop differently, individuals—even at their birth or in the year afterwards (as the above case illustrates)—already have a history of development which contributes to their racial ascriptions (Dent 1990: 694).

Opposing what he believed to be the main failure of previous notions of race, Boas’ critique of the assumption of the fixity of race was a significant theoretical influence in Appiah’s own understanding of race. Insofar as the meaning of our actions is constantly being shaped over our lifetime by our own understanding of them, Appiah argues that racial behaviour can be understood as intentional under a description. Our behaviour is understood by us (or by others) as behaviour appropriate to a person of a specific race: “what I do intentionally is dependent on what I think I am doing” (Appiah 2004: 65). His notion of race employs a joint understanding of behaviour. One’s behaviour can be understood as being both self-directed and other-directed. A person understands her behaviour as self-directed when she understands her own behaviour as different or
similar in relation to another person or to a group. She ascribes to her own behaviour a particular understanding of conformity or difference to various groups she perceives racially. She may judge herself similar to a group with which she identifies herself racially. Her behaviour is self-ascriptive when she chooses to act in a way that she believes is consistent with a group she wishes to belong to. For instance, she may dress, speak, and conduct herself in a way that she believes is indicative of that group. All of these decisions can contribute to one’s intentional ascription of race and be used to direct one’s future behaviours.

Behaviour is other-directed when individuals, groups, or nations make decisions about what group an individual belongs on the basis of her appearance and behaviour. This conception of race claims that we utilize information about how certain kinds of people act to direct our own behaviour and interactions with them in a variety of situations. It can include societal conventions, legal precedents, and political or class based discriminations among races. Actions towards individuals judged to belong to a certain race are shaped by the expectations a group or individual has of others’ behaviour as well as the individual’s own behaviour, and interactions with different kinds of people based on these conceptions of different racial identities.

Appiah (2004) argues that this behavioural conception of race is not biological, but it is objective. Its objectivity is not based on biological differences but instead on how one person’s actions are directed by his or her identification of another person’s race. Race may not be a real biological notion, but racial conceptions have real behavioural effects. The way individuals identify other individuals on the basis of their race forms the guidelines of their behaviour and treatment of others as well as their expectations of the behaviour of others.

Boas and Appiah’s conceptions imply that the persistent argument for a fixed, essential biological basis for racial classifications misjudges both the basis for racial groupings as well as what is required for them to be objective. These “biological” features are inextricably linked to an individual’s development within a set of political, societal, class, linguistic,
and economic practices. Discriminatory practices based on these perceived differences among raced individuals have lead to gross inequities where some are systematically privileged while others are oppressed. Recognizing these constraints is surely necessary if we wish to understand the use and abuse of race-based classifications. For Appiah, distinguishing individuals on the basis of their skin colour may be a significant characteristic just because there is a history of oppression that has made it one of the key differences perceived and utilized by those seeking to oppress or privilege one group over others. The Jim Crow laws in the Southern United States that relied on the “common report” of (usually whites) in determining the race of infants (Omi and Winant 1994: 181), the history of oppression in the United States, the caste system in India, apartheid in South Africa, the ethnic cleansing of Russian pogroms, genocide in Rwanda, as well as the continued use of skin colour as a discriminating marker attest to the objective reality of it for sociologically and politically defined race categories.

I am sympathetic to the view that race is contingent on our interactions and behaviours with others. However, as I will show towards the end of this chapter, I do not think the contingency of our racial ascriptions is limited to our actions but depends on a panoply of developmental, behavioural, physical, familial, and cultural features.

5.2.2.2 Familial Conceptions of Race

Rather than relying on explicitly raced genetic or morphological features of individuals, the familial notion takes human beings as forming kinds based on whether they have descended from a common ancestral lineage or whether they share the same genealogical tree. Human beings belong to the same racial kind if they are descended from the same unbroken sequence of ancestors. This account of race originates with Darwin’s own understanding in The Descent of Man (1871).

According to the widely adopted familial conception of race, “[we] assign people to races in a way that is governed by the rule: if your parents
are of the same race, you’re of the same race as your parents” (Appiah 2006: 364). This conception of race rests on the naïve assumption that raciality is somehow biologically encoded and reliably transmitted from one generation to the next; racial traits are passed down from great-grandparent to grandparent to parent to child.

The most infamous of the familial conceptions of race were those collectively referred to as the “one-drop rules.” These were a number of laws which were first enacted during slavery34 and were common in the Southern United States. Although now officially rejected as unconstitutional, the one-drop rule is still used colloquially as an objective measure by those seeking to racialize both others and themselves on the basis of family ties or ancestry (Coolidge 1998). One-drop rules held that if you had as little as one black ancestor in your extended family tree, you were black. In some states this was set as a fractional notion, such that if one of your great, great-grandparents (one-sixteenth of your ancestry), or in some states, one of your great, great, great-grandparents (one-thirtysecond of your ancestry) was considered black then you were black. These laws attempted to purify what was seen as a gradual dilution of the white race by multiracial individuals, previously classified as “mulattoes.” This division was not between individuals commonly ascribed as black or white on the basis of their skin colour. In practice these laws took the form of witch-hunt like searches for any distant black ancestors of individuals living as, and accepted as, white. These laws were upheld in some states as late as 1982 (Omi and Winant 1994). Although originally aimed at black and white races, the absolute intolerance to those of “mixed race” was not limited to those of black and white ancestry.35 Madison Grant warns of the waning of his own white race in *The Passing of the Great Race*,

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34 The first law was established in North Carolina in 1802: Gobu v. Gobu, 1 N.C. 188.
35 This intolerance to individuals of multiraciality was not restricted to the U.S. Early in the 20th century, laws were enacted in Australia to ensure the protection of the purity of the aboriginal people. These laws forced the removal of the light-skinned children born of aboriginal and white parents (labelled by the government as “half-castes”) from their aboriginal families and taken by force to government-run camps where they were trained to eventually “integrate” within the white
The cross between a white man and an Indian is an Indian; the cross between a white man and a negro is a negro; the cross between a white man and a Hindu is a Hindu; and the cross between any of the three European races and a Jew is a Jew (Grant 1916: 18).

Although the naïve and popular variations of familial conceptions of race may seem more harmless than the notoriously racist one-drop rules, these familial conceptions all envisage race as an objective essential set of characteristics that are passed on through pure lines of inheritance. In doing so they marginalize all individuals of whose ancestry does not conform to the continuous “pure” lines of inheritance or are easily classified with the neatly defined categories of Black, White, Red, and Yellow.

Familial conceptions of race can sometimes employ the use of racialized notions of morphology and the necessary continuity of inheritance in defining what “pure” and “mixed” racial lineages are. Many of these rely on a gene-centred view of racial inheritance which takes an individual to inherit all of her genes that code for her racial traits from her parents. This would mean that she is of the same race as her parents are, if they are of the same race as each other. Familial conceptions often assume that there exists some genealogically passed on essence or material identity, frequently construed in terms of the same genes or traits. This presupposes that “one’s own genes ... remain the same over many generations—otherwise they could not be linked to particular diseases, ancestries or traits” (Hauskeller 2004: 291). We have these same traits, same genes, and same talents and behaviours as our ancestors because we believe that they are reliably inherited through a pure, unbroken genealogical lineage of ancestors.

This account is inaccurate in many ways. The genes we inherit from our parents are neither materially nor logically identical with our own. Not only are the genes not identical across generations, they are also non-identical within the trillions of cells of one’s body throughout one’s ontogeny.

community rather than “diluting” the aboriginal population (cf. Pilkington-Garimara 1996).

36 These individuals are often lumped together under the names “mongrel” and “mixed race,” phrases that betray reliance on the assumption that there can (and should) be unmixed, pure lines.
Not all cells have identical genomes due to mutation in cell division and differentiation. The DNA may be the same sequence in all cells but the methylation of the genome in each cell type, the specific cell products, proteins, and daughter cells may differ (cf. Hauskeller 2004: 294).

The one-drop rules suggest race may not be easily recognized in the faces or in the skin colour of some individuals. They imply that it may be “hidden.” An individual’s ancestry may suggest that she is not as she appears to be. This may occur if her morphologically ascribed characteristics and the commonly ascribed race attributed to her by those within different communities are challenged with what is thought to be essential information about her identity. For example, before the repeal of the last one-drop rule in 1982, a woman named Susie Phipps who, “having lived her whole life thinking that she was white, suddenly discover[ed] that by legal definition she [was] not … but if she [was] not white, of what race [was] she? The state claim[ed] that she [was] black, based on its rules of classification” (Omi and Winant 2004: 182).

Familial conceptions of race take race to be an essential quality—perhaps unseen, but potentially discoverable. A person’s race can be assessed purely given her immediate or, in the case of the one-drop rules, distant ancestry. Rather than anything else the presence of one of 32 great, great, great-grandparents is thought to definitively determine what race Phipps “really” was. This takes an individual’s racial identity as essentially fixed and unchangeable. Her race is determined only on the basis of her ancestral relationships. It restricts her history to the history of her racial relatedness to her distant and close ancestors.

In the remaining sections I argue that the familial view of race, like the morphological, biomedical, and populational views, assumes that race is something that is preformed prior to one’s life in the world. A person’s racial identity is determined prior to and irrespective of her experiences and relationships with other human beings during her lifetime. It is a fixed feature of human beings. And as such it is unaffected by her life activities. It can be determined before she is even born simply by examining the family trees of both her parents.
5.2.2.3 Cultural Conceptions of Race

In contradistinction to both the fixed notions of the natural scientific and familial conceptions of race, Du Bois defines “race” as a vast family37 of human beings, generally of common blood and language, always of common history, traditions and impulses, who are both voluntarily and involuntarily striving together for the accomplishment of certain more or less vividly conceived ideals of life (Du Bois 1897: 110).

In formulating his conception of race in this way, Du Bois seeks a social scientific rather than a natural scientific approach to race.

What does Du Bois mean when he writes that two people are members of the same race if they belong to the same “vast family,” are “of generally common blood,” and share a “common history”? Relying on the notion of “common blood” and “common history,” makes Du Bois appear to support a biologically based or familial notion of race. Although the idea of a common blood or a “blood quantum” is used by some Native Americans to determine their belonging to a particular tribe38, common blood has most frequently been understood to be isomorphic to “gene,” as it has been, and continues to be typically defined in many Western cultures as being an objective fact of nature ensuring one’s linear descent and the essential test for group inclusion.

Common history and vast family are often used interchangeably with common ancestry or a group of individuals sharing the same lineage or family tree. Usage of these restrictively defined notions of family is not consistent with Du Bois’ own particular use of these phrases. His explicit aim to present a sociohistoric conception of race by utilizing the notion of common blood emphasizes at once the physical and psychological continuity

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37 Du Bois’ specific use of “vast family” should not be confused with the familial conceptions of race just discussed. The distinction between these two conceptions will shortly be made explicit.

38 On the basis of such a claim, an individual may receive a “Certificate of Degree of Indian Blood” or “Certificate of Degree of Alaska Native Blood” issued by the American Bureau of Indian Affairs (cf. Schneider 1968 and Dupré and Hauskeller 2007).
among individuals of the same race. His broad use of these notions set the starting points for many later attempts to clarify a conception of race.

Even though he is explicit in his aim to secure a sociohistoric conception of race, it is hard to resist interpreting Du Bois’ use of common blood, common history, and vast family as together implying a thoroughly natural scientific notion of common ancestry and genetic inheritance. But this tendency seems to be motivated by the persistent assumption discussed at length in previous chapters, that biological inheritance is narrowly construed in terms of genetic inheritance. However, there are many different routes by which human features are passed on besides our genetic inheritance. Following Du Bois, Bernard Boxill characterizes race as follows:

a group of people have a common history if they have inherited their common way of life from a long series of ancestors who faced common problems together and passed on this way of handling these problems—their way of life—to their descendants, usually with adjustments and emendations (Boxill 1996: 60).

Instead of being limited to the vertical inheritance of genetic material from parent to offspring, features such as “a common way of life” and a “way of handling these problems” are both vertically passed on in the non-genetic “inheritance” of teaching and mirroring behaviours of tutors, mentors, community leaders, political groups, religious congregations, youth groups, printed media, or artists to individuals from infancy to senility, as well as being horizontally passed between peers. The vertical inheritance of a certain genetic complement and the development of a similar visage to one’s parents constitute only some of the features that can be inherited. Earlier generations pass on their stock of knowledge, way of handling problems, learned behaviours, techniques and insight, to later generations. This stock of knowledge is constantly being augmented, updated, and reinterpreted with the experiences of each new generation. These updates are passed horizontally between contemporaries, but also reciprocally, both from older to younger and from younger to older generations.

Even the notion of “common blood” and “vast family” need not identify individuals that are genetically related to one another. The meanings of
“ancestry” and “descendent” ultimately rely on how we understand family groupings. How someone defines “family”—in terms of genetic, developmental, or cultural relationships—depends on one’s own embedded life history, i.e. the situation one grew up in, one’s religion, current economic situation, sexual orientation, community identity, life history, the others within one’s community, and how ones’ peers form their family units. A wide variety of family groupings demarcated in a number of different ways depending on one’s cultural heritage are possible. “Family” may include a much broader unit than the nuclear family or direct descendents. These may include the children of friends or siblings in the mother or father’s care, neighbours, adopted or fostered children, community elders, half-siblings, partners, previous wives and husbands, or be structured according to matrilineal or patrilineal rules of inheritance.

Common blood and common history need not be coincident with a restrictive understanding of biologically or genetically determined common ancestry. This is because “having a common ancestry is neither necessary nor sufficient for a group of people to have a common history. What is essential is that the group inherit a common way of life that has developed over generations” (Boxill 1996: 62). This means that if an adopted child is taught by its adoptive parents their customs, behaviours, and language and has the same common way of life as them, then the child shares a common history and is part of the same vast family and is of the same (metaphorically understood) common blood as the parents (regardless of whether they are the same morphologically defined race).

The reason why this seems such a controversial conception of race is because it comes up against the morphological, ancestral, and genomic conceptions of race so pervasive within a Western, Anglo-American way of thinking of race as an unfolding of a particular set of characteristics encoded in one’s biological inheritance reliably transmitted from parent to offspring. Our individual morphological and behavioural differences are often reported as being down to our genetics. This way of speaking has buoyed a strong belief that our “biology” or our “genes” determine our racial characteristics (Dupré forthcoming). This understanding of race appears to be a sort of
Putnam-Kripke approach to races as natural kinds that defines races in terms of fixed underlying biological essences that are shared by all human beings of the same race. This underlying essence has been thought responsible for everything from a human being’s racial morphology and biomedical phenotypes to the biological variation among different populations and the kinship relations in his genealogical tree.

5.3 Pitfalls of Essentialist and Preformationist Views of Race

The belief in race as a natural kind or essence pervades many of the conceptions of race from Bernier’s to those of the present, and it is apparent in several of the above accounts. Essentialist views attribute morphological, behavioural, and biomedical characteristics as all having a common cause—an essence which determines all our racial features. Underlying this strongly essentialized view of race is an assumption that an individual’s racial essence is preformed prior to his life activities in the world. Although perhaps more obvious in some race conceptions than in others, the understanding of race as a preformed static essence transmitted from one generation to the next clearly underlies morphological, biomedical, and familial conceptions, and in part, populational conceptions. This underlying belief in preformationism conceives of an individual’s racial characteristics as determined by his essential racial nature prior to his birth. In the familial and morphological conceptions, it suggests that we inherit our racial characteristics completely from our parents, and they from theirs. Our racial genealogical inheritance then forms our complete racial inheritance and identity. In the genetic, biomedical and populational conceptions, an individual’s racial inheritance is understood to be passed on to him from his ancestors, encoded in the informational script within his genes. Racial traits—like all other traits, are simply the result of this preformed essence or code unfolding over time. These racial essences are immutable qualities that are ontologically distinct from an individual’s ecologically embedded lived experiences.
Conceiving of race as preformed in these ways effectively alienates us from our racial identity. It does so by alienating us from our own life activities and locating the source of our racial identity outside our influence and control. But relying on race as a preformed immutable set of characteristics cannot explain the changeability of one’s own self-determination or those attributed to us by others. These racial ascriptions depend on a sequence of historical events, a diverse set of environmentally situated factors, and the set of characteristics a person uses in judging one’s own or another’s race and cannot be defined once and for all. This makes race a highly unpredictable and unstable category to use in making generalizations on the basis of physical characteristics, biomedical features, or familial relatedness. Racial generalizations defined at one point in time or place may appear to be fixed, but may not remain fixed at another time and place.

Preformationist views of race take race to be a fixed essence, a stable set of objective characteristics or relationships. It thereby provides stable and objective descriptions by which the natural divisions of humanity can be delineated. But because these natural divisions were founded on the basis of, for instance, a set of morphological features shared by a particular race, one has already reified the natural racial division used to distinguish individuals on the basis of these physical variations. Alfred North Whitehead calls this type of reification “misplaced concreteness” (Whitehead 1929: 11). It arises when we assume that our categories of thought coincide with morphological characteristics and other datum of empirical scientific research.

Our tendency to believe that our conceptual categories are concrete proves unsurprising to those who believe that we have a general tendency to essentialize the differences we observe.

Few candidates for laws of nature can be stated by reference to the colours, tastes, smells or touches or objects. It is hard for us to accept that the colour of objects, which play so important a role in our visual experiments and our recognition of everyday objects, turn out neither to play an important part in the behaviour of matter nor to be correlated with properties that do (Appiah 1993: 38-9).
The assumption of essential racial types as preformed identities underlies the belief that morphological and genetic differences are continuous over generations and can be naturally demarcated along genealogical lines. Although our desire to classify may be ineluctable, this desire does not guarantee our perception that there are distinct human morphologies, genotypes, and ancestries that can be easily grouped within fixed racial types actually corresponds to any ontological divisions in the world.

5.4 A NATURAL CONSTRUCTION OF RACE

In the remaining sections, I draw from elements of all the conceptions discussed in the foregoing (but without their preformationist or essentialist assumptions), and offer my own conception in terms of one’s natural self-construction. Specifically, this account derives from Du Bois’ view of race as a group of people with a common history who handle common problems and Boas’ conception of persons as ecologically situated. Employing Taylor’s metaphor of heterogeneous construction I show how racial identities can be the products of a human-organism’s natural self-construction from her diverse environments. The constructive endeavour captures the causal reciprocity between an individual’s experiences of her racial identity as an embedded subject (with her own particular physical characteristics and multiplicity of cultural resources and relationships) and her experience as the object of other individuals’ racial ascription.

This natural constructive approach to race conceives of a human being as an agent who self-constructs, organizes, and interprets her own racial identity utilizing a diverse set of dynamic relationships, embedded environments, and histories which she links together to form her racial identity(ies). My approach to race is a consequence of viewing racial identity from an organism-centred perspective. It takes the human organism to be the centre of his or her constructive process of racial ascription. The agent determines what aspects of her environments contribute to her racial identity. Her race is not transmitted pre-formed,
either from her ancestral relationship or contained in her genes, but she may choose to use these as contributing factors in constructing her racial identity. How she links together her genes, outward morphologies, ancestral and familial relationships, cultural, national, and political environments form her racial identity. This identity may vary over her lifetime and depends on whether she relocates herself within a different set of environments and how she interprets and reinterprets both the cultural and personal historical events of which she feels a part. This is because how we identify our whole selves at any given time or place, or individual features of ourselves, is contingent on our own life history and the common history with which we identify at any particular time and place.

This view takes race as a continual process: “what is essential about races is not their state of being but that of becoming” (Dobzhansky 1937: 61). Taking Dobzhansky’s notion of race as becoming to reveal the phenomenological nature of an individual’s race ascriptions, I argue that the best way to understand the changing identity of individuals can be found in our continually changing situatedness within different environments. One’s racial identity comes from the meanings one attributes to one’s bodily features as well as one’s way of living within different environments.

Interpreting race as a continual interactive process of self-organization and self-ascription rather than something that is fixed means understanding individuals’ racial identity in terms of the links they forge between themselves and others and the meaning they attribute to their political, cultural, religious, class, and ecological affiliations. An individual may change aspects of her racial identity over time, or she may find that the race attributed to her by others changes depending on the racial categories of different environments she becomes embedded within, e.g. if she moves to another country or community. In this sense one’s racial construction does not stop. What changes when one moves from one country to another is not just the politics, social groups, religious affiliations, or currency. It is the individual’s whole phenomenology of racialized traits which changes—different cultures have different experiences of skin colour, face shape, and religious affiliation. These are perceived, understood, and believed to be
indicative of race in different ways by different groups. A particular group may favour certain physical features over others. What is accepted or desirable to those within the group might include some things which may be highly plastic. They may depend on time of life, hairstyle, lightening or tanning of the skin, application of make-up, weight gain or loss, style of dress, employment or marital status, sexuality, gender identity, religious beliefs, or cultural traditions.

An individual both sees herself, and is seen by others, as being a member of a number of different groups. Her racial identity, like her other identities, may be modified. She may also choose not to identify herself with any racial group at all. It is important to note that while my constructive approach provides an account of the dynamic process of racial ascription, it does not suggest that individuals are impelled to interpret any of their characteristics, relationships, or environments in terms of race. Race is not an inevitable source of identity. Just as an individual may choose to interpret all or some of these factors as constitutive of her racial identity, she may also choose not to identify herself in terms of race at all. The features mentioned in the foregoing count as sources of racial identification only if the individual chooses to use them as such in the construction of her identity in terms of a particular race or races.

5.5 THE DYNAMISM AND DISSONANCE OF RACIAL IDENTITIES

Racial identity is an intersubjective process of recognition, reciprocality, and exchange between oneself and other human beings. Our own self-ascribed racial identities and those ascribed to us by others may fluctuate depending on the constant flux of our environments. This dynamic conception of race relies on the reciprocality between the identity we ascribe to ourselves and the identity that others ascribe to us. As such, the causes of an individual’s racial identity can be understood as necessarily reciprocal—a dynamic product of one’s own self-ascription, the acceptance and recognition of this ascription by the race(s) with which one identifies,
and the ascription of an identity by others that is consistent with one’s own. Adopting the neo-Kantian vernacular of past chapters, we might say that an individual is at once both cause and effect, subject and object, of her own racial identity.

One may respond that although my conception of race works well when one’s self-ascription matches with that ascribed by others, it fails when these ascriptions are inconsistent with one another. This leads me to ask what happens when there is dissonance between an individual’s own ascription of her racial identity and that ascribed to her by others. In response to this, I highlight the importance of the role of others’ recognition of one’s racial identification and how reliance on the notion of “pure races” misrepresents the racial identity of those who identify with more than one race.

I begin with a series of examples. In her travels an individual may find that although she is considered white at home, on holiday she is considered brown, and when abroad, black, depending on where, when and by whom her race is being judged. Not all of these racial ascriptions may match her own. This is not just a theoretical example, as it has been the experience of many Latin Americans and South Asians travelling abroad. Whereas in New England, light skinned Latin Americans and South Asians are considered white or “nearly-white,” these same individuals are considered brown in the American South, and black in the United Kingdom (Alcoff 1995 makes a similar point). Variation in these racial ascriptions across different communities and countries may either be based on the identification of different features as definitive of one’s race or they may be different interpretations of the same features.

During the 16th and 17th centuries, the immigration, political, economic, and cultural relations between the Europe, the United States, and Latin and South America facilitated travel, emigration, employment, and marriages between individuals of different races and ethnicities. In Latin America this resulted in a largely multiracial society where the majority of individuals were born to parents of different races. To identify individuals within this society, a racial classification system was established in the 17th
century called “casta.” According to the casta system, there were numerous mixes that could be arranged in terms of their social standing within society. This system involved the fine-grained racial categorization of multiracial combinations that included the Moor (Spanish, African Black, Spanish White), Zambos (Amerindian and African Black), Mulatto (European White and African Black), Cholito (Spanish White, South Indian, African Black), Mestizo (European White born in Europe, Amerindian), and Castizos (White European born in Latin America, Amerindian, White European born in Europe), among many others (Andrews 2004, Cummins 2006). This classification system of multiracial classes was used formally until the second half of the 19th century.

Although no longer a government approved system of class and political privilege and oppression, individuals within Latin America and South America still refer to themselves utilizing a modified version of some of the racial classifications. Although some classifications still retain their class distinctions, others are used generally to refer broadly to individuals of all multiracial groups. The name “mestizo” is now understood in Latin America and Brazil to be synonymous with any mixture of races or multiraciality. A “mestizo identity” is shared by the majority of individuals living in Latin America and has been spoken about with pride by the Mexican philosopher Jose Vasconcelos, who

envisaged una raza mestiza, una mezcla de razas afines, una raza de color—la primera raza sintesis del globo.39 [Vasconcelos] called it a cosmic race, la raza cosmica, a fifth race embracing the four major races of the world. Opposite to the theory of the pure Aryan ... his theory is one of inclusivity (Anzaldúa 1987: 77).

This acceptance of multiraciality as a common mestiza race is arguably unique to Latin America and South America.40 It contrasts with the notions of racial purity that underlie the racial divisions in the majority of countries outside of Latin and South America (Rodriguez 1992: 24-25). The reliance

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39 This translates to “a racially mixed race, a mixture of [related or] compatible races, a race of colour—the first race synthesis of the globe” (Yahoo! Babel Fish translator 2008).
40 However analogous terms are used by Filipinos: “sanglay,” “pinoy” “tsinoy,” and “mistisong,” which all originally referred to individuals born of Chinese Christian fathers and Filipino mothers. Like mestizo, “mistisong” is now used to describe individuals of multiraciality of Filipino and any other race(s) (Tan 2001).
on racial purity is revealed when one analyses the underlying assumptions of the morphological, genetic, and familial accounts of race. Among many of these, the notion of racial purity or pure lineages of ancestry remains—if not as an actualized ideal, then as a theoretical ideal used to understand race. This notion of racially pure lineages or individuals is particularly ill-suited for understanding the majority of individuals living in much of North, Central and South America, the United Kingdom, Europe, and Australasia.

The reliance on race defined in terms of racial purity necessarily denies racial identity to those who are racially “mixed.” Within these societies, multiracial individuals “face an unresolvable status ambiguity. They are rejected by the dominant race as impure and therefore inferior, but also disliked by the oppressed race for their privileges of closer association with the dominant [race]” (Alcoff 1995: 141-2). They are treated as either having no race at all, as racially impure or sullied, or as symbols of racial and cultural dilution. By denying an individual this recognition, he is prevented from the possibility of acceptance within the group he may identify. Without this recognition, the construction of his identity is one-sided. It is the frustrated construction of an identity which is unreciprocated. This leads to feelings of alienation. The result of his unreciprocated racial identity is that he lacks the recognition necessary for understanding his own identity. This lack can affect his self-knowledge since it frustrates his own subjective experience.

A multiracial individual may choose to overcome the feeling of being alienated from the community he is living in and partially identifies with. For instance, an individual who racially identifies himself as both black and white may gain recognition of at least part of his racial identity if he accepts the identity within the white community, where he is recognized, or “passes,” for white. However, in passing for white his racial identification is still frustrated. Part of his identity is “hidden” when he passes for white within the white community. Although he is recognized as white in the community with which he partially identifies, this may be insufficient for his self-understanding. For instance, the lack of recognition and acceptance from the black community may frustrate part of his racial awareness when
this is denied to him. Although accepted by one community, he may continue to feel alienated—both from the community that does not recognize him and from himself.

To deny recognition of this hidden identity is to deny the individual the bonds of “human solidarity built as shared emotions, collective effervescences, becom(ing) stamped into the shared meanings, norms and feelings that constitute the glue of collective identity” (Moss 2008). This alienation from one’s racial identity can be understood in terms of Moss’s notion of the “pain of detachment” (Moss 2008).

This alienation can happen either as a result of the non-recognition or rejection by a group with which one identifies, or the divided nature of one’s own internal identity within a society that demands only unified racially pure identities. This causes a crisis of identity or the feeling of pain from being detached from either part of one’s own multiracial identity or from one’s identified racial group. Identification with groups of individuals like us can provide both the necessary recognition we need for our own self identification as well as facilitate a sense of community which is vital in avoiding feelings of alienation.

Seeking to reformulate a conception of race that encompasses the multifarious nature of racial identities, the heterogeneous construction of race is presented as a reciprocally self-organized notion of one’s racial identity. Unlike preformationist and essentialist notions of race, it does not presuppose that an unambiguous racial self already exists or even that racial self-determination is a prescriptive ideal. My account embraces rather than ignores the internal heterogeneity of individuals and their disparate relationships, environments, morphologies, and familial lineages. All can be possible factors by which the individual decides his racial identity. The flexibility and the stability of one’s own racial ascriptions can be understood in terms of the ways in which individuals use the cultural, ecological, politically embedded environments to reciprocally ascribe racial identity.

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41 Moss does not apply the “pain of detachment” to race but I have tried to show how my novel application of it is justified in the present chapter.
In attempting to subvert the racist conceptions of race of his contemporaries, Boas formulated a conception of race which separated the biological from the cultural characteristics used to identify an individual’s race (Boas 1940). The legacy of this dualism is evident in the dichotomous notions of race set out in the second section of this chapter. The putative “scientific” or “biological” conceptions, such as those based on morphological features or one’s genetic complement, are considered as being ontologically distinct from the putative “social scientific” conceptions based on behaviour, familial relatedness, or culture. Whereas those characteristics construed as “biological” are believed to be transmitted from parent to offspring through the genetic information contained within the genes, the sociological or cultural characteristics are thought to be passed on as the result of non-genetic processes such as learning or imitation.

Approaching race using a dualism of biology on one hand and culture on the other, although perhaps necessary for avoiding racist theorizing in Boas’ time, may now only be a barrier to understanding race. My final suggestion for a reconstruction of the conception of race from an organism-centred perspective is dissolve the dualism that separates the biological from cultural factors used to understand race. In doing so, I follow Ingold’s (2001, 2004) suggestion that we treat humans as organism-persons that are at once biological and cultural, body and mind embedded within environments. He argues that the problem Boas wanted to avoid and what we should continue to avoid is to equate biology with genetics; “the source of the problem is not the conflation of the cultural with the biological, but the reduction of the biological to the genetic” (Ingold 2004: 217).

Taking the dissolution of this dichotomous thinking seriously means that far from being separate and unconnected, our genetic, morphological, biomedical, national, cultural, behavioural, familial, and cultural traits are all different facets of ourselves as multiply embedded organism-persons.
The biological and cultural are simply different aspects of our biological personhood and not two sets of ontologically distinct characteristics.
CHAPTER SIX

Conclusion

The overarching aim of this dissertation has been to criticize and reconfigure the ontological framework within which discussions of the organization, ontogeny, and evolution of organic form have been conducted. I did so by defending what I called an organism-centred perspective. The claim that the organism takes priority in our understanding of both ontogeny and evolution is a central tenet of many versions of the developmental systems perspective. DSP has typically been used in criticizing gene-centred conceptions of inheritance, development, and evolution. In this respect my thesis follows closely Moss’s own deconstructive and reconstructive project (cf. Moss 2001, 2003, 2006).

There have been, though, very few applications of DSP, however formulated, to the concepts of homology, species, and race.42

I began my reconfiguration by introducing the popular gene-centred, selectionist, and interactionist perspectives of biological organization. These

42 I have not come across any philosophical applications of DSP to homology. Only Lewontin and Moss have explicitly applied DSP to the conception of species, and have done so only in passing. Many applications of DSP have criticized gene-centred views of adaptation and inheritance, views that relate to our understanding of species and homology, but have not dealt with them in their own right. As for race, only Ingold (2001: 259 and only very briefly) has even mentioned applying a philosophical perspective of developmental systems to its understanding.
are typically understood using the metaphors of the internal unfolding of information contained within the genes, the moulding of a naturally selective environment, or an interaction between the two. Understanding organismal development using these metaphors rests on viewing organic causation as concentrated within discrete sources of causal power—wholly preformed within the information encoded in the genetic blueprint and/or within the selective information of the environment. These strongly preformationist views conceive organisms as passive recipients of their own organizational form from either the active design specifications unfolding in the informational genetic code or genome, or shaped by certain selective factors.

Instead of this linear view of causation, I offered a view of organic causation that characterized its direction as mosaic and circular. The causes of organic organization are distributed across temporally and spatially diverse resources rather than localized. This view took inspiration from Kant’s conception of organisms as natural purposes, at once both cause and effect of their own self-organization and Taylor’s metaphor of organic construction from heterogeneous resources. This Kant and Taylor inspired view of organic causation was shown to be a consequence of the ontological centrality of the organism from an organism-centred perspective (as opposed to a gene- or selectionist-centred perspective). I argued that the causal importance of genetic and environmental factors does not come from pre-existing information either within the genetic code or the selecting factors within the environment but rather from the organism’s generic germs and capacities which enable its use of these features as resources in its own construction.

I fleshed out what this ontological centrality meant in Chapter Two by utilizing both Buffon and Kant’s views of organismal organization. For Buffon, organisms organize themselves throughout their lives through the joint action of their organic molecules and the internal shaping of their *moule intérieur*. In so far as Kant’s generic preformationism relied on both generically preformed parts, (the *Keime*), as well as capacities, (the
Anlagen), his view of the organization of organisms can be understood as picking up where Buffon left off.

The focal point of the second chapter was Kant’s regulative principles (i.e. God, the thinking subject, and mechanism, (cf. Kant 1781/1787: A334/B391, A646/B674 and McFarland 1970: 26-30), their use in understanding organisms as self-directed natural purposes, and various criticisms and amendments to these regulative principles provided by those studying physiology, comparative morphology, embryology, and cytology. In assessing and extending Kant’s view in light of the recent contributions by Oyama, Taylor, and Moss, I suggested that these three regulative principles of reason needed to be augmented by a further regulative idea: natural self-construction. Denuded of Kant’s transcendental idealism, these regulative ideas become facts about the biological world itself, rather than facts about the preconditions of all experience.

This extends our metaphysics by enabling us to conceive of causality not solely linearly or even reciprocally (as Kant did) but as arising from heterogeneous sources which are organized as causes by the organism itself. Using heterogeneous construction we can understand that each causal step and each causal link in the journey to any particular goal state, for the sake of which the organism aims, is determined and orchestrated by the organism itself. This means that philosophers of biology can reconceive what count as causes of the construction of organism-environment complexes. They can do so by identifying the contingent linkages that particular complexes make over space and time among a wide range of distributed resources (including genes, cells, tissues, behaviours, trees, rocks, nests, and other organisms).

In setting up my organism-centred view I diverged from a strictly Kantian approach to organismal organization. My organism-centred perspective extends the resources available to the organism in self-construction. These include not just the organism’s internal stock of Keime and Anlagen but also the so-called external resources within its habitat, through its behaviours and interactions with parents, littermates,
predators, or prey—in sum, its spatiotemporally extended situatedness throughout the course of its lifetime.

I then turned my attention to reconsidering some categories and concepts from this organism-centred perspective. In Chapter Three, I began by critically assessing various conceptions of traits, homology, and analogy.

I discussed de Beer's (1971) empirical work and his claim that homology at one level does not guarantee homology at another level of biological organization. I then showed how morphological traits that are homologous may be the outcomes of different developmental pathways and different genes (that are themselves not homologous to each other). Reflecting on de Beer's work, I questioned how the concept of historical continuity could explain the ubiquity of developmentally plastic pathways and whether this affected what we mean when we talk about the concept of homology.

In opposition to the neo-Darwinian view of homology I suggested that the biological organization of organisms does not have one cause—it does not arise simply from the vertically transferred genes passed down from parent to offspring. Challenging the general acceptance of homology as exclusively determined by unbroken ancestry to a common ancestor, I showed through a number of examples that many traits are in fact the result of different recombined elements which have been inherited from more than one ancestral trait, although these are not considered to be completely homologous. The bulk of the third chapter centred on cashing out West-Eberhard and Minelli's proposal that in order for our conception of homology to reflect this mixed ancestry, it should be extended to include complete, partial, combinatorial, and mixed homologies and analogies. I illustrated how this can be understood from my organism-centred perspective. Reconceiving homology and analogy from this perspective meant recognizing traits as being constructed heterogeneously from multiple resources. I argued that trait construction occurs within a confined possibility space, partially restricted by an organism’s “degree of partness” and its body plan. These constraints enable it to make changes to certain features while keeping the rest of its body stable.
The fact that traits are heterogeneously constructed by organisms was used to challenge the traditional view that homologues and analogues arise from two completely separate and non-interacting processes: shared ancestry and convergent evolution respectively. This duality is exemplified in the standard dichotomous thinking in the philosophy of biology which takes similar traits to be either completely homologous or false homologies. I argued that if an organism's traits are self-constructed from multiple interacting resources under similar constraints this sharp distinction is not possible. According to the organism-centred perspective, mosaic traits are the result of a combination of different structures and processes. These may be partially homologous and partially analogous to another mosaic trait in another organism which is generated by some but not all similar processes or structures. As an alternative to the standard all-or-nothing approach to homology, my organism-centred view extended both the meaning and reference of “trait” and “homology” by including the similarity of structures, behaviours, and of developmental processes of organisms in terms of their complete, partial, or mixed homology (and/or analogy).

Reconsidering homology according to this organism-centred perspective is controversial. It challenges one of the main premises of evolutionary biology on which the understanding of the conceptions of homology and species are based. This is the assumption that the ontogeny of an individual's life cycle is ontologically distinct from the evolution of the species to which it belongs. Or more to the point, phylogenetic lines of descent are ontologically separate from individual ontogenetic life cycles.

In addition to providing a reconception of traits and homology according to the organism-centred perspective, I also sought to tackle the ontological distinction between the evolutionarily significant genetic resources from which organisms are believed to directly inherit unbroken from their ancestor-descendant lineage and those evolutionarily insignificant extragenetic resources from which organisms are thought to acquire by indirect or broken inheritance. In Chapter Four, this began with my opposition to the received notion of species—Mayr's notion of a species.
as a protected gene pool maintained by a stable environment. Mayr's BSC focuses on the gene flow between sexually mature adults.

Rather than strictly defining species in terms of unbroken linear (vertical) inheritance of genetic material, I proposed an organism-centred view of species that combined Buffon's historical-ecological view of species with Taylor's metaphor of the heterogeneous construction of organisms. The adult form of organisms typically used by the BSC to classify them as belonging to a particular species was shown to be just one of many temporal slices throughout an organism's life cycle.

I argued that species should be reconceived in terms of a Buffonian view that took them to be collections of organisms sharing similar resources, a similar habitus, similar capacities for sustaining themselves, and repeated generative processes. As such, they are a recurrent succession of self-constructed and reconstructed life cycles embedded within particular temporal periods and particular spatial-ecological contexts. They are both cause and effect of the evolution of the species to which they belong.

I also considered other means of inheritance besides vertical genetic inheritance from parent to offspring such as hybridization, horizontal gene transfer, maternal oviposition, and niche construction. These revealed that the BSC's reliance on a gene-centred view that holds species to be maintained by the inheritance of species-specific genes and a common gene pool is not justified. I suggested that a common gene pool may be just one of many resources organisms of a particular species use in their construction and reconstruction over each generation. To illustrate how this might be understood, I presented a series of examples of developmental plasticity and the heteromorphism among organisms of the same species at different stages in their life cycle. These were used to show how the underlying adult-centred view of species taken by the BSC and other conceptions of species artificially restricts what count as species typical organisms.

I began Chapter Five by outlining the origins of some of the most controversial and persistent concerns for those attempting to form or re-form a conception of race. These included the belief in race as natural kind or essence, reliance on morphological features conceived in contrast to the
(often white) observer, the cause of racial continuity among generations, the belief that raced morphological features, behavioural, and intellectual capacities are linked, the idea of racial purity, and the separation between the putatively biological and putatively cultural characteristics of race. In critically discussing six current conceptions of race, I highlighted two underlying assumptions. Firstly, many are based on an essentialist-preformationist understanding of race that holds an individual’s racial characteristics to be determined by their essential racial nature prior to their birth. Racial traits—like all other traits—are simply the result of this preformed essence or code unfolding over time. Secondly, racial essences are immutable and ontologically distinct from an individual’s ecologically embedded lived experience during their lifetime. By conceiving race as preformed in this way individuals are effectively alienated from their own racial identity by alienating them from their own life activities and locating the source of their racial identity outside their influence and control. This experience of alienation was expanded later in the chapter with insights from both Alcoff and Moss. I emphasized both the external sense of alienation of being rejected by the racial group with which one identifies as well as the internal sense of alienation that can occur in multiracial individuals.

My own organism-centred perspective of race took Du Bois’ sociohistorical notion of race and combined it with Taylor’s metaphor of heterogeneous construction. The human organism is at the centre of its own racial ascription as situated within a common history. This approach took the human organism as organizing and interpreting its own morphological, cultural and historical embeddedness, directing its experiences, and making historical and causal linkages among these various factors. Following my organism-centred redescription of racial identity, I showed race to be reciprocally and dynamically caused by one’s own ascription and the ascription given to one by other groups and individuals. I endeavoured to capture the causal reciprocity between an individual’s experiences of their racial identity as an embedded subject (with their own particular physical characteristics and a multiplicity of cultural resources and relationships)
and their experience as the object of others’ racial ascriptions. I was also careful to note that race is not an inevitable source of identity. Just as an individual may choose to interpret all or some of these factors as constitutive of their racial identity, they may also choose not to identify themselves in terms of race at all. Human organisms are agents who may self-construct, organize and interpret their own racial identities utilizing a diverse set of dynamic relationships, embedded environments and histories which they link together to form their racial identities.

A number of opponent positions have recurred in this thesis. The most prominent of these have been the commitments to preformationism and the numerous dualisms that separate features of organisms considered ontologically distinct. In addition to these was the pervasive underlying assumption that there is something analogous to water's supposed chemical essence, \( \text{H}_2\text{O} \), or a privileged set of criteria that can be used to identify organic beings once and for all, rather than viewing these as providing us with valuable snapshots of organic being at a particular time and place but not exhaustive of their traits and behaviours. If the arguments in this dissertation have been successful, I will have created the conceptual space necessary for a new ontology of nature.

**Implications for further philosophical research**

As preceding chapters have demonstrated, the concepts of homology, species, and race are reconceptualized when viewed from a revised organism-centred perspective. But these are just three of many concepts whose reconfiguration is possible when viewed from this new vantage point. Others ripe for revision include the longstanding dualist conception of gender and sex; the conception of the individuality of organisms; the categories of *healthy* organism, *normal* development; and the dualism of innate abilities and learned behaviours within the philosophy of psychology. Below, I briefly sketch how my organism-centred view might be used to
reconfigure these conceptions, beginning with the dualist conception of gender and sex.

Whether sex and gender are separate categories of being human has been hotly discussed ever since Gayle Rubin (1975) suggested that the former is distinguishable in terms of a biological body type and the latter in terms of a cultural understanding of masculinity and femininity. This distinction is widely considered to be between sex—conceived of as something that is beyond our control (a determined essential or predetermined aspect of our identity) and gender—conceived of as something that is within our control (expressed over our lifetime within our culture and interactions with others). Like the other dualisms discussed throughout this thesis—the natural and social scientific, germ and soma, nature and nurture, mind and body—this dualism maintains that gender and sex are ontologically distinct categories. This duality takes the shape of one’s body and the constitution of one’s genetic complement to unambiguously pre-determine one’s sex prior to one’s life in the world. One’s sexed identity is therefore ascribed for us—written in our genes and moulded in the form of our bodies. This preformed “biological” sexed identity is conceived of as distinct from and separate to our “sociological” gendered identity. Gendered identity develops over one’s lifetime within one’s culture(s) and understanding of one’s self-ascribed femininity or masculinity.

This dualist way of thinking is aimed at thwarting the possibility that the sexual dimorphisms in human bodies (e.g. whether bodies have uteruses or penises, ovaries or testes, breasts or beards) are external markers for internal emotional or intellectual capacities. Separating sex from gender is believed to successfully separate what is biologically essential and preformed from what is the product of our cultural, political and ontogenetic activities. Although arguably politically valuable at the time, this dualist thinking now seems to obscure rather than reveal the nature of sexed and gendered identity.

Understood from an organism-centred perspective, our sex/gender identity can be conceived of in a similar way to our race identity. The
conceptions of sex and gender may continue to be used. But instead of being ontologically separate from one another, they may be reconceived as two aspects of our situated, embedded experiences in the world. These identities are grounded in our embedded spatial and temporal position. Both sex and gender, like race, have histories. These histories may include economic, political, religious, and cultural traditions that structure the meanings of sex and gender as well the development and experiences of an individual’s life history. Using insights from Du Bois, we can regard ourselves as male, female, and intersex, or feminine, masculine, and multigendered in terms of a common history and similar problems we share with others of our sex or gender when we identify ourselves in these terms. This history may change depending on where we live as well as how we live and who we live with. From an organism-centred perspective, neither gender nor sex is preformed. They are no more determined by our genes or morphological features than race is. The meaning one ascribes to one’s sex and gender is a function of one’s expressed behaviour, actions and interactions with other individuals within different embedded environments. Like race, our sex/gender identities are aspects of our heterogeneously self-constructed organism-personhood. We construct ourselves and our identities from distributed causal sources. These might include our chromosomal complement (xx, xy, x0, xxy), whether we are insensitive to androgens, how much oestrogen and testosterone we produce, our susceptibility to breast or prostate cancer, our distribution of body fat, the form of our primary and secondary sex characteristics, whether we see ourselves or are seen by others as sexually ambiguous, or have been surgically altered, our contribution to reproduction, our sexual activities, the culture in which we live, our vocation and avocations, how we dress, keep our hair, eat, behave, talk, whether we wear makeup and how, our preference of sexual partners, and what roles we occupy with regard to our immediate and extended families, at home, in the workplace, and within society.

Another concept that may be reconsidered using the organism-centred perspective is the notion of biological individuality within philosophy of biology. The individuality of organisms has been variously
conceived in terms of a single genetic lineage—a unified group of diverse cells determined by the unfolding of the information contained in the genotype present in the fertilized ovum or as a functional whole or as a developmental unit (Wilson 2000). In each of these characterizations, biological individuals have tended to be construed as closed systems that are impervious to external inputs. However, this conception jars with the multitude of viruses, bacteria, parasites, biofilms, horizontally transferred gene segments and other “non-indigenous” cell types or molecular fragments found within a single organism. Reconceived from an organism-centred view, an individual’s multicellularity is not simply determined as a functional or developmental program contained within the zygote. It is the constructed product of numerous dynamic interactions, including genes, the properties and behaviours of cells, cell-cell communication, and feedback loops between different organs and organ systems within the organism as well as its interactions with chemical, physical, and biological processes throughout its lifetime. The unity of organismal individuality is therefore contingent on a series of events—it has a history. Understood according to the organism-centred view, an organism’s individuality is not the result of its genetic, functional, or developmental program prior to its life within the world. It is the result of orchestrated ontogenetically extended self-organizing and self-constructing capacities. Organismal individuality is the result of a spatiotemporally embedded organic agency.

Thirdly, the organism-centred view could be used to reconfigure the ontological categories of healthy or diseased organisms and normal or abnormal development. This would be an extension of my brief discussion in Chapter Two of teratological development. This view would be an alternative to the view that normal development and normal function are biologically determined and scientifically discoverable objective categories (Boorse 1997). As such biological normality is believed to be firmly based in biological and biomedical science (Wachbriot 1994).

But what is normal? And how is this quantified? It seems odd that “normal” would refer to variation that is statistically most common (as it is often defined), as variation is widely regarded as necessary for evolution.
Accounts of normal development, normal form, and normal function seem to assume that biological normality is a fixed quality of organisms—a natural kind of biological variation. I think this view of biological normality rests on the assumption that there is an invariant species-specific program of development that normal individuals follow. This would mean that organisms are normal because they are the result of a well-run species specific genetic or developmental program. And they are abnormal because the program went wrong.

On an organism-centred view, normal function, normal development and normal form are perhaps better understood as normative categories that can only be defined within a particular embedded ecology and may change throughout an organism’s lifetime. If one wants to retain a conception of normality, one might consider assessments of normality to be assessments of the mode of organismal self-construction. This would include the resources it utilizes as well as the series of temporally extended environments, (e.g. that may be dependent on its embryological environment, maturation and care received by its parents, stages of ontogeny, or migrations) over its lifetime. An organism’s functioning, form, and development only make sense in light of the organism’s lived experiences and its capacities for sustaining itself within a particular ecology. Teratological, chimeric, and ectopic development of seemingly well-functioning tissues, organs, and organisms as well as phenotypic plasticity are phenomena that could be relied upon in exploring what the categories of normal and healthy mean and their underlying assumptions.

Lastly, this perspective provides another route into the recent ecologically situated view of cognitive capacities that is increasingly popular in philosophy of psychology (cf. Wheeler 2005). It does so in two ways. Firstly, it reinforces the radical externalism that claims that the mind literally extends outside the boundary of the skull. By utilizing various different resources in carrying out cognitive tasks, these resources are incorporated into the mind. Secondly, it provides support to recent criticisms of the innate/acquired distinction (cf. Griffiths 2002). This distinction is important to philosophers discussing the nativism/empiricism
debate. The idea that biological development consists in heterogeneous construction over a life cycle, a process that can avail itself of multiple resources, can be extended to cognitive development. Indeed cognitive resources would be called upon in some cases of biological development. Recognizing this might lead us to suspect that there will be no way of apportioning causal responsibility to that which is innate and that which is non-innate.

Mindedness, like the other conceptions discussed above, can be understood according to my Kant and Taylor inspired organism-centred view as a phenotypic feature of human beings that is at once both cause and effect of its own construction. This view would probably result in a view resembling Michael Wheeler’s (2005) account of situated cognition. But whereas Wheeler arrives at his view by utilizing Heideggerian phenomenology, the view I have sketched above utilizes Kantian ideas of reciprocal causation and Taylorian ideas of heterogeneous self-construction.

The above constitutes no more than an extremely rough sketch of lines of thought suggested by the organism-centred view defended in the proceeding chapters.

In this dissertation I hope to have provided reason to believe that the organism-centred perspective is a fruitful one and motivation for applying it to other concepts.
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