

THE HOLOGRAPHIC PRINCIPLE IN BIOLOGICAL DEVELOPMENT AND QUANTUM PHYSICS

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INTRODUCTION

I would like to introduce the themes of this paper in the form of a dialogue:

Q: How should we build complex forms, such as living things?

A: Organise them as a hierarchy of stable subassemblies, or homologous organs.

Q: Surely the genes are all you need to explain living organisation?

A: But the same organ can be the result of different genes! When we look at the genes as more than simply stretches of nucleic acid, but see them switching each other on and off, then a hierarchical organisation emerges spontaneously.

Q: Anyway, hadn't Darwin explained homology?

A: No, his explanation fails, and the pre-Darwinian understanding of homology is much closer to the hierarchical approach.

Q: Isn't there a quantitative approach that explains form?

A: No, form is a qualitative distinction between an inside and an outside. Living things are autonomous forms, themselves maintaining this boundary.

Q: Is such a boundary a purely material skin?

A: A boundary can be seen as the interface between the parts inside and the rest of the universe outside, through which information flows.

Q: Can't an organism be described in isolation?

A: But then it would be a stone! An organism is a process of interaction with its environment, a process of creating and discovering.

Q: Creating and discovering? Is that a linguistic process?

A: Yes, a living thing is a focus of a linguistic process, where meanings are recognised and transformed.

Q: Eventually we will be able to reduce form to physics and chemistry, won't we?

A: Could you reduce the meaning of these words to the chemistry of the ink? The same form may be realised in many different physicochemical configurations. The Cartesian method just won't work.

Q: Do you mean to say that genetic and morphological descriptions of living things are radically different?

A: Yes, they are complementary yet incompatible. Continuity of morphological information is a kind of memory without mechanical storage. Without this holistic memory, the mechanically stored genetic information would deteriorate over time.

Q: I know that many quantitative models of morphogenesis have been proposed. So how can you say that form is qualitative?

A: Morphogenetic models exhibit bifurcation points, where the system shifts suddenly from one form to a quite different form.

Q: I feel uncomfortable with this idea of sudden jumps.

A: You feel happy about the sudden jumps in quantum physics, don't you?

Q: But how do you decide between all the different interpretations?

A: Things become a lot clearer once you understand that the most important thing is the form of the quantum system, not the energy.

Q: Isn't that a very organic way of putting things?

A: Yes, the ageing of a living system is much closer to the development of a quantum process than to anything Newton described.

Q: But how deep could the comparison be?

A: Well, certain forms of the equations for both look very similar, the same equations that describe a hologram. You can talk about a quantum process as a hierarchy of surfaces through which information flows.

Q: 'Surfaces through which information flows'—that's how you described living things and their organs, isn't it?

A: Yes, that's right! And these surfaces turn out to be holographic.

Q: Oh so that's where the holographic principle in your title comes from?

A: Yes, the holographic principle may hold the key to bringing quantum physics together with relativity. Looks like it might bring in life and non-linear systems too!

1. MORPHOLOGICAL STABILITY

The parable of the two watchmakers is first presented by Simon (1962: 470), and has been variously adapted by Koestler (1967: 45-47) and Allen and Starr (1982: 49-51). In Simon's account, the two watchmakers are named Hora and Tempus, whereas Koestler renames them Bios and Mekhos, and Allen and Starr provide a factual exemplar of the fictional Hora. Both Hora and Tempus make watches that consist of 1000 parts. However, Hora manufactures his watches in subassemblies of 10 parts each, whereas Tempus puts his watches together part by part. The workshop is a busy place, often disturbed by the telephone ringing. Hora and Tempus must leave their work to answer the telephone, in case it is a new customer on the line. Who gets his work done more quickly? Hora's subassemblies are stable in themselves. They do not fall apart when their maker leaves them to answer the phone. But for Tempus only the completed watch is stable. A disruption at any stage except the last means he will have to start from scratch again. Hora's strategy is the better one for dealing with disturbances from the environment, since his use of stable subassemblies minimises the effect of those disturbances. Watches built by Hora as a hierarchy of subassemblies will come to predominate in the market at the expense of the watches of Tempus.

Living things are not simply aggregates of parts, nor are they indecomposable wholes. They are loosely coupled, or near decomposable (see Simon, 1962, 1973; Koestler, 1967: 64-65; Allen and Starr, 1982: 70-74). Living things consist of sub-wholes, parts in relation within the whole. A kidney is defined in terms of its function within the body, but may also be transplanted from one body to another. Its function within the body is an aspect of its *partness*, the fact that it can be transplanted an aspect of its *wholeness*. Koestler (1967: 48) describes such semi-autonomous sub-wholes as *holons* (from Greek: *holos*, meaning whole, and *-on* as in electron, proton). 'The evolutionary stability of sub-assemblies—organelles, organs, organ-systems—is reflected by their remarkable degree of *autonomy* or self-government. Each of them—a piece of tissue or a whole heart—is capable of functioning *in vitro* as a quasi-independent whole, even though isolated from the organism or transplanted into another organism. Each is a *sub-whole* which, towards its subordinated parts, behaves

as a self-contained whole, and towards its superior controls as a dependent part.’
Koestler (1974: 62).

‘Among possible complex forms, hierarchies are the ones that have time to evolve’ (Simon, 1962: 473). Simon’s conclusion from the watchmaker parable has been tested recently in evolutionary computing. The final solution of a problem specified for a population of genetic algorithms emerges from a synthesis of several partial solutions, known as building blocks. Wagner (1995) draws the following lesson for the evolution of living things: ‘... a system consisting of building blocks has a much better chance to be improved by mutation and natural selection than an unstructured system ... Hence the building block hypothesis can explain why it makes sense to organize a complex organism into individualized characters called homologues.’ Living things consist of a wide variety of standard parts (Raff, 1996: 330), building blocks (Wagner, 1995) or modules (Wagner and Altenberg, 1996). ‘The most fundamental principle of evolutionary strategy, related to the watchmakers’ parable, is the *standardisation* of subassemblies ... Animals and plants are made out of homologous organelles like the mitochondria, homologous organs like the gills and lungs, homologous limbs such as arms and wings. They are the stable holons in the evolutionary flux’ (Koestler, 1967: 135, 139).

Riedl introduces a concept of morphological stability, or fixation, to account for the fact of homology: ‘Actually, every homologue is characterised by the fact that it shows adaptive freedom in only a few directions, but fixation in many others. If this were different, if every character were free to change in every direction, the living world would appear as a random chaotic mixture of patterns, as chaos, and the single relationship left among representatives would not relate to common ancestry but only to common functions, such as analogous limbs, horns, wings, jaws, and so forth’ (Riedl, 1977: 354; cf. Alberch, 1982: 315-316). Parts of organisms possess a stability, which permits us to recognise relationships between them that are not the result of shared function.

2. METABOLIC STABILITY

‘A living thing is a complex net of interactions between thousands or millions of chemical species’ (Kauffman, 1969: 437; 1970: 18). How is it possible for an organism to arrive at a stable metabolism among these chemical species? The answer lies in how the organism is able to construct a number of specialised compartments as it develops, the different cell types. It then has at its disposal a range of environments in which specialised metabolic reactions can take place. The problem of metabolic stability is a problem of cellular differentiation.

Kauffman (1969, 1970) describes cellular differentiation in terms of the Jacob-Monod theory of gene expression. Genes are modelled as binary switches, turning each other on or off. Each gene executes a certain Boolean operation on its own state, on or off, and the states of the genes connected to it in order to generate the state at the next point in time. Connections among genes are randomly assigned. Kauffman discovers how, with these model genomic networks, the behaviour of the system is related to its connectedness. With one connection the behaviour is frozen, the activities of the genetic elements are not coordinated. When the number of connections is large, chaos reigns and the array does not reach a stable pattern of activity. However, when the number of connections is poised at two, complex behaviour emerges. Here the system of elements divides into a number of functionally isolated subsystems, loosely coupled to each other, each of which settles down into a regular pattern of gene activity. Metabolic stability emerges out of randomness. Kauffman is able to introduce perturbations to test this stability, either by changing the state of a particular gene, or by altering its Boolean function. Genes will generally return to the same state cycle, or shift to a limited number of other cycles (Kauffman, 1969: 463; 1970: 34). The emergent subsystems are therefore ‘poised’, that is, they are to transform into a very limited number of other subsystems (Kauffman, 1992). This is the very nature of differentiation. Remarkably, the number of subsystems for a particular number of genes is of the same order of magnitude as the number of cell types found in organisms possessing that number of genes. Kauffman concludes that the genomes of organisms may indeed be constructed more or less randomly, and rely on the order that spontaneously emerges from such randomness for their coordination.

Kauffman (1983: 218) explains how a compartmented organisation of the genome is advantageous in evolution: ‘Selective evolution [evolution by natural selection] requires the capacity to accumulate partial successes sequentially. Were the genome organized such that a small change in connections could alter coordinated dynamical patterns of gene activities throughout the network preservation of past favourable combinations of activities would be difficult. Accumulation of partial successes requires either genuinely isolated subsystems, hard to maintain in a scrambling genome, or functionally isolated subsystems which are otherwise loosely coupled, as arise inevitably in these model genomes. Selective modification of the combinations of gene activities in one functionally isolated subsystem would not alter the dynamics of the remaining system, hence allowing piecewise evolution of favourable new cell types.’ Kauffman’s findings harmonise very well with Simon’s proposal that hierarchically organised, near-decomposable systems are the most likely to evolve. As Wagner (1995) perceives, each subsystem is a partial success, or building block, to which new improvements can be added. Kauffman’s model of cellular differentiation is discussed in the chapter on modularity in Raff (1996: chapter 10). Cell types are described as modular units of gene expression (Raff, 1996: 328).

3. THE HIERARCHY OF TYPES

‘What can be more curious than that the hand of man, formed for grasping, that of a mole for digging, the leg of the horse, the paddle of the porpoise, and the wing of the bat, should be all constructed on the same pattern, and should include the same bones, in the same relative positions’ (Darwin, 1859 [1968: 415]). The forelimbs of the different mammals are homologous and overall, the mammals, indeed all vertebrates, show the same plan of organisation, or unity of type.

The bones in the forelimbs of mammals maintain the same relative positions: ‘An organ is sooner altered, atrophied, or annihilated than transposed’ (Geoffroy Saint-Hilaire, 1818: xxx; translated in Appel, 1987: 99). The criterion for their homology is the principle of connections. Geoffroy Saint-Hilaire discovered this principle through his attempt to establish the homology of the opercular bones, the bones that cover the gill opening in fishes. By considering only their connections, he reached the conclusion that the opercular bones are located in the middle ear of mammals, as the

malleus, incus and stapes (Geoffroy Saint-Hilaire, 1818: 37). Similarly, by considering its connections to bones of the ankle, the horse's hoof is the enlarged nail of the third toe (Goodwin, 1994: 131).

The explanation of homology that Darwin proposes is that the two structures trace back to a structure in the common ancestor (see also, Ghiselin, 1976): 'If we suppose that the ancient progenitor, the archetype 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 [1968: 416]). Darwin's explanation assumes that bodily organs are replicated and handed on entire from generation to generation. But we know that this is not the case: 'Only replicators like genes pass on their own structure to their descendants directly. Morphological structures are not replicators ... The notion of continuity of descent is not problematic for genes but is less clear for organs' (Wagner, 1989b: 55, 56).

There are two possible ways of revising the Darwinian explanation of homology:

1. The homology of structures in different animals is due to the same genes handed down from the common ancestor.
2. Homologous structures form from the same cells in development.

However, counterexamples can be given to both explanations:

1. 'In the fruit fly *Drosophila* there is a particular gene which governs the formation of the eyes and there is an allelomorph (a mutant alternative) of this gene which in the homozygous state produces an eyeless condition. Now [T. H.] Morgan showed that, if a pure homozygous eyeless stock is inbred, the other genes in the gene complex, by reassortment, may come to be recombined in such a way that they will deputise for the missing normal eye-forming allelomorph, and lo and behold flies appear in the "eyeless" stock with the eyes as good as ever! These eyes must surely be regarded as homologous with the eyes of normal flies, yet their production is not controlled by the same genes' (Hardy, 1965: 212). This is the phenomenon of genetic piracy (Roth, 1988).

2. ‘... in one species of frog (*Rana fusca*) the lens of the eye can only be induced by the presence of the optic cup; in another species (*Rana esculenta*) while it can be induced by the optic cup, it is also formed in its proper place if the optic cup is removed—formed apparently in relation to the developing whole animal’ (Hardy, 1965: 213). ‘Phylogenetically homologous characters need not share common pathways of ontogenetic development’ (Wagner, 1989b: 58). Between species, the origin of cellular material, the precise sequence of events or specific inducers, have all been found to vary.

One also runs into problems applying the Darwinian criterion of homology to repeated elements in the body. Lankester (1870) claims that the fore and hind limbs of land vertebrates cannot be homologous, rather they are analogous, responding independently to the same functional requirements. Since fore and hind limbs do not trace back to the same structure in the vertebrate ancestor, then they cannot be homologous, according to Lankester. The Darwinian criterion stretches one’s credibility when one thinks of structures repeated through the body: ‘If we admit the homology between any scale x of an individual trout and any scale, say y of a salmon, and between this scale y in the salmon and scale z in the trout, then how can we logically deny that homology exists between scales x and z on the body of the same trout!’ (Hubbs, 1944: 294). Consider structures repeated across the axis of the body. Common sense tells us that our left hand is the mirror image of our right. Darwin would have us believe that left and right hands trace back to a single structure in a one-sided animal! *Reductio ad absurdum*.

The Darwinian approach assumes we have atomic parts that are passed on from generation to generation: ‘In the simplest case phylogenetic homology is a one-to-one mapping from the characters of one species onto characters of another species. A one-to-one mapping implies that in each species all characters can be recognised individually’ (Wagner, 1989b: 57). However, a living thing is not a composite of inert atoms. Its loosely coupled organisation emerges from a dynamic interplay between conflicting tendencies: ‘Every holon has the dual tendency to preserve and assert its individuality as a quasi-autonomous whole; and to function as an integrated part of an (existing or evolving) larger whole. This polarity between the self-assertive

and integrative tendencies is inherent in the concept of hierarchic order; and a universal characteristic of life. The self-assertive tendencies are the dynamic expression of holon wholeness, the integrative tendencies of its partness' (Koestler, 1967: 343).

The distinctiveness of an element, the fact that we can recognise its identity across numerous organisms, derives from its wholeness, the tendency of a holon to assert itself. If an element cannot be recognised individually, this lack of distinctiveness emphasises the partness of the holon, its tendency to integrate itself among other elements as part of a larger whole, such as a series. We may understand serial homology in this light: 'The phenomenon of serial resemblance is in fact an expression of the capacity of repeated parts to vary similarly and simultaneously. In proportion as in their variations such parts retain this capacity the relationship is preserved, and in proportion as it is lost, and the parts begin to vary independently, exhibiting differentiation, the relationship is set aside' (Bateson, 1894: 569). When elements of a series vary similarly and simultaneously they cannot be recognised as distinct. They remain parts integrated into the larger whole, the series. When elements differentiate, they become individually recognisable and thus assert themselves as wholes distinct in themselves. The first element in the vertebral series asserted itself, weakening its integration into the rest of the series, and became individualised as the axis in tetrapods. Whether an element appears as a part or a whole depends on the broader context.

All teleost fishes have a recognisable palatine bone, in the context of the palatopterygoquadrate arch, but vary in the extent to which parts of the palatine are developed. Hence, we can describe a number of states of the palatine bone, recording differences in the shape and orientation of the boss and prong, for example. States within a character represent divergent differentiations of parts within the context of whole. A character representing the presence or absence of the palatine describes the expression or suppression of the self-assertive tendency of the holon, the acquisition or loss of its individuality. For example, the prootic and epiotic of reptiles lost their separate individualities and fused to form the mammalian petrosal, which then in its turn has followed its own path of differentiation.

A good example of where members of a series have individualised is the thorax of insects (Wagner, 1986: 151; 1989a: 1162; 1989b: 63). The thorax most probably arose as a differentiation of segments 7, 8 and 9 in the annelid-like ancestors of insects. However, the thorax as an entity in itself is not homologous to the corresponding segments in centipedes, which have remained closer to the annelid form. ‘The thorax is the unit differentiated from the rest of the body in terms of appendages and internal anatomy, a condition not found in centipedes’ (Wagner, 1986: 151; 1989a: 1162; 1989b: 63). There is no direct homologue with the thorax in the segments of the centipedes—we cannot establish a one-to-one mapping. The thorax represents a new condition of form, a new autonomous whole, which serves to “individuate” the taxon Insecta (in the sense of von Baer, 1828; see Rieppel, 1994: 90).

Nelson (1989) suggests that instead of taxa being seen as groups of units, such as species or organisms, they should be seen as relationships. A taxon is a relationship inherited by organisms, and a homology, then, is a relationship inherited by parts of organisms. ‘Conceived as relationships, taxa and homologies do not literally descend from one another. Taxa come into being with organisms that literally descend’ (Nelson, 1989: 281). A taxon is not a group of organisms tracing back to an ancestral organism, but a type, a relationship inherited by organisms. Homology is not the tracing back of structures to an ancestral structure, but a relationship inherited by parts of organisms. Taxa are relationships and have homologies for their parts (Nelson, 1989: 279). Nelson’s view is much closer to the spirit of Geoffroy Saint-Hilaire. Homology is not the conservation of material structures among descendant lineages, but rather the conservation of positional relationships within the developmental process: ‘... systematics and comparative anatomy ... are possible only to the extent that ontogeny is orderly ... the concept of evolution is an extrapolation, or interpretation, of the orderliness of ontogeny.’ (Nelson, 1978: 336).

The four laws of von Baer affirm the orderliness of the developmental process (von Baer, 1828: 224; modified from the translation in Gould, 1977: 56):

1. The general features of a broad animal type appear earlier in the embryo than the special features.

2. Less general characters are developed from the most general, and so forth, until finally the most specialized appear.
3. Each embryo of a given species, instead of passing through the stages of other animals, departs more and more from them.
4. Fundamentally therefore, the embryo of a higher animal is never like the adult of a lower animal, but only like its embryo.

A human embryo has a tail and clefts in its pharynx early in its life. These homologues humans share with all animals of the chordate type, including lancelets, sea squirts, and all vertebrates. It is only within the first year that the human infant walks upright, demonstrating the homology of the human type. More general characters, which specify more inclusive types, appear earlier in development than the more special characters, which specify less inclusive types.

The human embryo shows itself to be of the metazoan type when it develops more than one cell layer. Its left-right symmetry displays the bilateral type, not the radiate type, where animals such as jellyfish have a rotational symmetry. The embryo then develops a polarity such that the anus is the first to form, not the mouth, therefore adopting the deuterostomian type, rather the prostomian, where the mouth develops first. The human body plan becomes specified in more and more detail as the embryo develops. The embryo displays in turn the homologies of each type in the hierarchy of types that it has inherited. The order of classification is the order of development.

4. BOUNDARIES AND INDICATIONS

It is a simple business to talk of tables and chairs. We attach our language to them as labels. We count them and attach numbers to them. Tables and chairs are separate from one another and external to one another. They are solid bodies. Our calculus of number and language of nouns suit solid bodies. Yet, consider living beings. Is a strawberry plant separate and external to other bodies? You may have planted a single individual, but the strawberry has sent out a long stolon, which has taken root and given rise to a series of new plants. We are able to distinguish different plants; together they remain one whole. We have distinction before we have number (see Bortoft, 1996). It is among solids that 'our action finds its fulcrum and our industry

its tools' (Bergson, 1911: ix). Our preference for a quantitative logic of solids is understandable then, but it is not nature's logic and life confounds it. Far from being illogical, life teaches a deeper, qualitative logic.

Within Bohm's metaphysics of process, characteristic forms in nature arise through the coincidence of vast processes, which extend over the whole universe. Each centre or focus of process maintains itself within its environment through self-regulation: 'Because the basic order of process is eternal change of everything, we can no longer appeal to the mechanical notion that certain basic objects, entities, etc., 'simply exist' with constant and invariable properties. Rather, the survival of any particular thing, however 'basic' it may be thought to be, demands a complex process of regulation, which provides for the stability of this thing, in the face of the eternal change in all that serves to constitute what it is' (Bohm, 1969: 42, 52).

A living thing is a distinction between inside and outside, autonomously defining its boundaries and maintaining them through a process of self-regulation. Not only is there distinction, but also indication, that one of the two distinguished states is primary, namely the inside, not the outside, the living system as opposed to its environment (Varela, 1979: 84). In his *Laws of Form*, Spencer-Brown elegantly captures an essential fact of life: '... a universe comes into being when a space is severed or taken apart. The skin of a living organism cuts off an outside from an inside. So does the circumference of a circle in a plane' (Spencer-Brown, 1969: v). In his book, he describes the calculus of indications, the qualitative logic of life.

Despite their autonomy, living things do not exist in isolation. They interact with surrounding physical systems and with fellow members of the ecological community or social group: 'No man is an island—he is a holon. A Janus-faced entity who, looking inward, see himself as a self-contained unique whole, looking outward as a dependent part' (Koestler, 1967: 56). Janus is Koestler's emblem of hierarchy, named after the Roman god of two faces, the guardian of doorways and, with the month of January, the passage of the years.

Living things exist far from thermodynamic equilibrium, and must maintain themselves through constant interaction and exchange with the environment. Homeostasis, the maintenance of stable conditions necessary for life, may be the most obvious in the higher vertebrates, the birds and mammals, but is required by all living things. Living things, then, are constantly interacting with their environment. They adapt their internal environment to suit themselves, regulating temperature, salinity and pH.

Animals are active; they are able to make choices about where they live and actively shape their external environment, whether physical or social (Bateson, 1988: 193). '[An animal] does not merely adapt to the environment, but constantly adapts the environment to itself—it eats and drinks its environment, fights and mates with it, burrows and builds in it; it does not merely respond to the environment, but asks questions by exploring it' (Koestler, 1967: 153). Indeed, all living things have the characteristic of irritability or sensitivity. They are able to choose or discriminate between aspects of the environment that are pleasant and beneficial, and those that are harmful. How a living thing influences its external environment has consequences for itself and its descendants. A plant dropping its leaves will change the pH of the soil for itself and other plants including any offspring that disperse nearby; a beaver building a dam changes the environment of the flooded valley (Bateson, 1988: 195). Living things choose which questions to put to their environment and are able to respond to their discoveries. 'Life is matter which chooses' (Margulis and Sagan, 1995).

Living things are not solid bodies, because they are never complete. They never achieve a definite state, but rather exhibit certain tendencies. Every tendency has its antagonist. The two thwart each other's aims, never allowing the other to reach completion: 'In particular, it may be said of individuality; that, while the tendency to individuate is everywhere present in the organized world, it is everywhere opposed by the tendency towards reproduction. For the individuality to be perfect, it would be necessary that no detached part of the organism could live separately. But then reproduction would be impossible. For what is reproduction, but the building up of a new organism with a detached fragment of the old? Individuality therefore harbours

its enemy at home. Its very need of perpetuating itself in time condemns it never to be complete in space' (Bergson, 1911: 13-14).

A living body defines its own boundary, marking an inside in contrast to an outside. Each organ of a living body maintains its identity in contrast to fellow organs and within the context of the system of which it is a part. There are many insides and outsides within each living body, which exist relative to one another: 'At a given level in the hierarchy, a particular system can be seen as an outside to systems below it, and as an inside to systems above it; thus, the status (i.e. the mark of distinction) of a given system changes as one passes through its level in either the upward or the downward direction' (Varela, 1979: 86).

Without the conflict of opposing tendencies, each organ of the body would solidify. Each must have its own vital tendency, its power of self-assertion, to contend with the integrative power of the whole organism: 'The organized elements composing the individual have themselves a certain individuality, and each will claim its vital principle if the individual pretends to have its own. But, on the other hand, the individual itself is not sufficiently independent, not sufficiently cut off from other things, for us to allow it a "vital principle" of its own' (Bergson, 1911: 45).

Marking a holon specifies a particular frame reference. If the boundary marked coincides with the boundary that the holon, as an autonomous unit, defines and maintains, then the observer makes a discovery about the holon, rather than merely conceiving it: 'If the scientist does, in fact, define an object holon which can be associated with a phenomenon, then in finding and observing within the inertial frame of a holon, he has achieved, for that portion of the study, a main scientific objective; in the context of his procedures he views the world in terms that are compatible with those of the holon he investigates. Subsequent observation of the holon concurs with his predictions' (Allen and Starr, 1982: 242). Systematists identify the palatine bone as a boundary that is maintained in fishes of the teleost type. The systematists' mark corresponds to a boundary that the holon itself maintains. The name palatine is an *indication* of the organic holon. The palatine boundary maintains itself in the context

of the palatopterygoquadrate arch and itself defines the context within which the boss and prong boundaries define themselves.

5. THE FLOW OF INFORMATION

Koestler (1967) describes two hierarchies in living things, motor and sensory¹. In the motor hierarchy, information in the form of a goal cascades down from the inside to the outside, triggering each holon into action as a whole. At each level of the hierarchy, the goal is spelled out in greater detail, and the action becomes increasingly particularised. To make a catch, we need only look at the ball, and not worry about the coordination of muscular contractions with each shift in the ball's position.

In the sensory hierarchy, information in the form a stimulus cascades down from outside, holons passing the stimulus up to higher levels of the hierarchy. Holons scan for relevant information, taking what is relevant and passing on a digested, generalised version to the next level. One does not remember all the frequencies and harmonics in the shout 'Catch!' but only the imperative to throw out one's hands.

Bohm distinguishes the horizontal aspect of a hierarchy—the normal functioning of the holons—from the vertical aspect—the flow of information, which serves to regulate the internal functioning of the holons. He takes the example of a government department: 'There is an upward movement in which the higher level officials are informed about what is 'essential', 'relevant', 'significant' ... Then there is a downward movement in which the higher level officials inform those lower in the hierarchy how they are to order their actions in the light of the general aims of the government, and in the light of information of all sorts coming from other departments and levels' (Bohm, 1969: 52-53).

Holons at different levels in the hierarchy pass information to one another in the form of signals: 'A signal is a string of energy or matter in transit between communicating entities ... At departure, the signal represents a freezing of the infinitely rich dynamics of the transmitting holon as expressed by the medium of energy or matter of which the

¹ Compare the flow of information through the hierarchies of Manthey (1998). Information trickles down in the form of goals and bubbles up in the form of sensations.

signal stream is made. Although meanings can change, a single meaning has no dynamics of its own, in contrast to, say, a process or a system. In capturing the dynamics of the holon, the structure of the signal is a sign of the state of the holon; and signs have no rate or dynamics' (Allen and Starr, 1982: 17-18). We have a contrast between the internal functioning of each holon, based on rate-dependent dynamics, and the rules governing the flow of information between holons, based on rate-independent constraints (Pattee, 1978). The horizontal hierarchy, describing the functioning of each holon, is based in time, whereas the vertical hierarchy of information flow is timeless (Bohm, 1969: 53-54). 'Constraints always carry information which has meaning for the entities involved in natural processes. This information is not dynamically involved in the processes occurring in time and cannot be directly altered by them, but has instead a timeless quality. Furthermore, it is not altered by the rate at which some entity interprets it' (Salthe, 1985: 71).

Holons constrain or filter information that passes through them. Higher holons provide the environment and context for all lower holons with which they communicate, because the lower holons only receive information filtered by the higher level. The information emerging from a higher holon is an integration of information from its parts. 'In summary, entities (holons) in a hierarchy may be viewed as the interface between the parts and the rest of the universe. On its journey to the outside, signal from the parts is integrated through the whole...as are signals reaching the parts from the rest of the universe' (Allen and Starr, 1982: 15). Holons are surfaces through which information enters and departs.

6. CREATION AND DISCOVERY

'No man is an island—he is a holon. A Janus-faced entity who, looking inward, see himself as a self-contained unique whole, looking outward as a dependent part' (Koestler, 1967: 56). To talk of the part looking out and the whole looking in is to describe the sensations of partness and wholeness. These sensations involve the discovery of self and other: 'On the one hand an organism tends to go out of itself, to open itself to other forms around, and on the other hand it tends to organise itself, to centre on itself' (Griffiths, 1989). Going out of oneself, opening oneself to others,

may lead to disintegration, that is, integration with one's environment. Going into oneself, entering reflection and meditation, restores balance and inner coordination. Spencer-Brown (1969) is talking about the activity of distinction. When we make a mark, we cross from inside to outside and describe the part looking in and the whole looking out. Distinction is the creative act, which brings an autonomous whole—a universe—into being.

Self-assertion and integration appear differently in motor and sensory aspects. Manifesting its self-assertive tendency in the motor aspect, the holon looks out as an autonomous individual. In the sensory aspect, the holon looks in on itself, gathering itself, collecting itself. Manifesting its integrative tendency in the motor aspect, the holon looks in on itself, the parts integrating themselves by coordinating their actions. In the sensory aspect, the holon looks out and opens itself to that beyond itself, losing itself in its environment.

	Motor	Sensory
Self-assertive	looking out – whole	looking in – whole
Integrative	looking in – part	looking out – part ²

Varela (1979: 206) describes two complementarities, which match those in the previous table, namely autonomy/control and closure/interaction. Our characterisation of the system, as autonomous or controlled, depends on the tendency we highlight, self-assertive or integrative respectively. Emphasising the self-assertive

² We can construct a similar diagram if we follow Varela's (1979: 98-99) account of the general system theory of Goguen (1971). An outward functor regards a component at a lower level as a whole system at the next: 'Generally speaking, a holon on the ln level of the hierarchy is represented on the $ln + 1$ level as a unit and triggered off as a unit' (Koestler, 1967: 72). An inward functor computes the behaviour of the whole system, viewing the result as a single object at the lower level. Each pair of outward and inward functor is adjoint. The inward functor is the overlap or intersection between objects, the categorical limit. The limit has a dual, the colimit, which is the integration of systems.

	Motor	Sensory
Self-assertive	looking out – whole outward functor	looking in – whole inward functor
Integrative	looking in – part inward functor (limit)	looking out – part outward functor (colimit)

Here the complementarity of whole/part or self-assertion/integration is equivalent to the adjointness of an outward functor and an inward functor. Motor and sensory aspects are expressed in the duality of limit and colimit.

tendency, we focus on the autonomy of the living system. Emphasising the integrative tendency, we focus on the controls and constraints imposed on the system from outside. How we represent the system, as closed or interacting, depends on whether we consider the motor or the sensory aspects. Regarding the motor activity of an organism, we represent it as a closed system, maintaining a stable behaviour and identity by coordinating its parts. Regarding the sensations of the organism, we represent it in interaction, compensating for perturbations in its environment as a dissipative, thermodynamically open system.

The terms of Peirce and Uexküll may help us to understand the four aspects. Salthe (1993: 14-15) summarises Peirce as follows. Firstness is independent being. Secondness is being relative to, reacting with another being. Thirdness is mediation, whereby a first and a second are brought into relation. Uexküll (see Salthe, 1993: 176) contrasts a being's inner life, its *Innenwelt*, with the outer world, or *Umwelt*, that two beings come to share through their interaction. Looking in, a holon has a private inner life, an *Innenwelt*. The holon looking out as a self-asserting, active whole is a first. The holon looking out as an integrating, sensing part is a second. The thirdness is the immediate environment of the holons and their system of interactions. Holons encounter one another within their environment as active first and sensing second. Through this meeting of firstness and secondness, the holons' environment becomes a world, an *Umwelt* or thirdness.

'To share in the interpretation of a world and the response to it is to communicate' (McCabe, 1987: 119). A hierarchy is a system of communication, whether we are talking of a social group, or of parts organised within a body (Allen and Starr, 1982: 37). 'All life at any level is a matter of communication. Every organism is an organism by virtue of its power of communication.' (McCabe, 1987: 118). Firstness is creation, whereas secondness is discovery. Thirdness exists in the tension between the two. Living things 'realise' meanings in their world, in the sense of 'to discover' and 'to make real' (McCabe, 1987: 120). Living things find meanings to be 'real' (discovery) and at the same time make them 'real' (creation).

Living things organise their environment by relevance to their activities and needs. The fruits of an organism's exploration turn the environment into a world. A living thing's body and senses organise its world; they make the world meaningful to it. For example, fishes live in worlds very different our own, because of their different sensory powers. Sharks respond to electricity. Electric receptors allow them to detect the currents generated by the muscles of struggling prey. Elephant snout fishes are able to create an electric field around themselves. Nearby non-conducting objects will distort the field, and the fish can sense this. Elephant snout fishes live in murky African rivers and use their electric sense to electrolocate, in the same way that bats and dolphins use high frequency sounds to echolocate.

7. FEATURES, SIMILARITIES AND HOMOLOGIES

Living things are processes of creation and discovery. Their interactions form a language that can be understood through Peirce's triad of first, second and third. The classification of living things is also a linguistic process, and Peirce's triad emerges here too.

The first stage of classification involves the collection of representative specimens of the species to be studied. In the second stage, characters are conceptualised and the character states for particular species recorded. The third stage is the generation of a classification as the most economical summary of the data and the discovery of the defining characters of taxa.

Each stage of classification involves a different kind of pattern, to be understood in the terminology of Peirce. A pattern of firstness consists of the observed features of all morphological variants of a given species, which are at this stage not yet conceptualised. A pattern of secondness is a pattern of similarity shared by a number of species. A pattern of thirdness describes the pattern of homologies inherited by organisms. Sharing is meaning in the second context, and congruence, the nested hierarchical relationship between patterns of secondness, is meaning in the third context.

Features are firsts; they exist in one species considered alone. Similarities are seconds; they relate one species to another. Homologies are thirds; they show that two species are more closely related to one another than they are to a third. The third species reveals the thirdness of the sister species; it provides the context within which the other two find their relationship.

Character concepts begin life in the first stage as features identified in single species. The second stage of character conceptualisation is the clash between firsts. Character concepts are tested against specimens of different species, and if found not to be applicable are modified or abandoned. The third stage is the clash between seconds. Similarities that are not congruent with the most economical pattern are meaningless. They are homoplasies not homologies, confusing rather than revealing thirdness in the study group. As Peirce pointed out, the three stages exist together. The choice of study species and the conceptualisation of relevant characters are made with a background of existing classifications. Classification is a process of cyclic illumination (Hennig, 1966; Kluge, 1991).

Peirce's triad of first, second and third relates to referent, sign and system of interpretance. Species patterns of features are referents. Patterns of similarity between species are signs of affinity. The types, the patterns of homology, form the system of interpretance, the context that reveals the significance of patterns of similarity: 'More or less similarity is evidence for or against homology, not of more or less homology' (Nelson, 1989: 282). Homology is not the kind or degree of similarity. Meaning in one context cannot be reduced in that way to meaning in another. At each stage meanings are transformed through the context of comparison and analysis

8. ORDER ABOVE HETEROGENEITY

Physicists and chemists are used to dealing with homogeneous matter, with molecules, atoms, and particles that, if they are of the same kind, are indistinguishable from one another. The most surprising confirmation of the homogeneity of matter is spectroscopy. The elemental composition of distant stars can be compared with that

of the Sun and the Earth. Each element has its own distinct pattern of spectral lines, which is replicated throughout the universe of stars.

The Cartesian method proceeds by reducing the complexity of large phenomena to the simplicity of the small. If phenomena are indeed homogeneous in the small, then this method works admirably and has had great success in physics and chemistry. Living things are also chemically homogeneous, in that the variety of participating atoms is small. Four elements, *C, O, H, N*, make up 99% of living tissue. The same genetic code applies to all living things, specifying the same twenty or so aminoacids. Does the unity of biochemistry assure us of the success of the Cartesian method in biology?

Our everyday experience of living things, especially one another, is that we are not at all uniform, but diverse and individual, with our own inclinations, habits and personalities. Physiological and biochemical studies of the human animal confirm this. ‘Human stomachs vary greatly in size and shape...It is evident that some stomachs hold six or eight times as much as others. It is no wonder from this standpoint that our eating ‘habits’ are not all alike...The position of the stomach in the body is also widely variable...With the tip of the breastbone (sternum) used as a point of reference, the bottom of the stomach may be anywhere from about 1 to about 9 inches below this position. It is not abnormal to have the bottom of the stomach within an inch or two of the level of the base of the sternum, because about 25 per cent of people have their stomachs in this position; neither is it abnormal to have it about 7 inches lower, because more than 10 per cent have their stomachs in this position’ (Williams, 1956; quoted by Elsasser, 1998: 62). Are there any reductionists who would claim that the stomach is not homologous in humans, because its size and its absolute position in the body vary widely? Individual chemical components of bone, that solid and functionally important material, may differ between human samples by not just a few per cent, but ten times! Earlier we saw how two structures are homologous, even if they emerge through different pathways of development, or under the control of different genes. In his *Reflections on a Theory of Organisms*, Elsasser puts it thus: ‘Under these circumstances there can be regularity in the large where there is heterogeneity in the small: “order above heterogeneity”’ (Elsasser, 1998: 4).

Tennant (1986) provides an interesting discussion of how it might be possible to define a morphological homology such as the gastrula. Is it possible to reduce the homology to a precise definition in physical and chemical terms? We might start by defining the gastrula as certain types of cells in particular topological configurations. A gastrula is thus a hollow ball of cells, where the outer layer of cells is ciliated and the inner layer is unciliated and free to divide. However, in a purely reductionist exercise each cell would have to be described in terms of particular configurations of nuclear, cytoplasmic and membranous components. Each of these components could be reduced to configurations of different sorts of molecules, and so on *ad infinitum*. We might take a different approach and describe the gastrula of each species in terms of its characteristic cell types, and the characteristic rate at which these differentiate. But even with this approach, the term would become complicated and unwieldy. Moreover, the term would lose what Tennant calls its 'open-textured meaning'. Experts teach the student to recognise a gastrula by showing him an example, probably together with a simple diagram. After some exposure, the student grasps the concept intuitively. Equipped with this knowledge, he is able to apply it even to a previously undescribed species. Any description of the gastrula purely in physical and chemical terms would have to be altered with the discovery of each new example. The term itself, nevertheless, would survive this extension unchanged. The beauty of morphological terms lies in their openness, and the problem with attempts to reduce them is that this openness is lost. Morphological homologies, such as the gastrula, describe certain orders in the large, which admit heterogeneity in the small. Tennant believes that ultimately the meaning of morphological homologies will be reduced to atoms and molecules, despite these difficulties. This belief is nothing more than an act of faith. The Cartesian method fails in the face of order above heterogeneity. There is no way, in this case, to reduce complexity to simplicity. No wonder that homology has never yielded to the Darwinian explanation.

9. GENETIC AND MORPHOLOGICAL APPROACHES

In the morphological approach to systematics, we study the outward form of organisms to generate classifications. We can also study sequences of nucleotide bases of DNA or RNA, with the aim of tracing the pathways of genetic transmission. This is the genetic approach to systematics. There is an intuitive element in

establishing characters, but this can be eliminated using suitable automations. Nucleotide sequences may be aligned by eye, gaps being inserted by inspection to produce the closest visual match between the sequences. Bishop and Thompson (1986) automate the alignment of pairs of sequences under a model of evolution that incorporates sequence substitution, deletion and insertion events. Their achievement shows that genetic data are fundamentally different from morphological data. Patterson (1988) discusses the attempts made by Jardine and Jardine (1967) to develop a mathematical means of comparing morphologies. He notes significantly that the authors quickly saw the computer program they wrote to be 'only an aid' (Jardine, 1970: 332). Patterson links the failure of their attempt to the fact that morphology exists in three dimensions, rather than one. We may link it to the fact that, unlike DNA sequences, morphologies are hierarchically organised. There are emergent properties, homologies, which are irreducible to any quantitative model of physics and chemistry.

The genetic approach deals with linear DNA sequences, which are aligned according to a dynamical model of the causal process of evolution, a process assumed to take place independently of the observer. The context of morphology, with its inherent hierarchical organisation, dictates that character concepts are the result of the interpretations made by a community of observers. The morphological approach derives its data through a process of interpretation, similar to that involved in any linguistic communication.

The structure of the DNA can be understood in terms of physical *laws*, whereas its function can only be comprehended in terms of *rules* of interpretation specific to living organisms (Pattee, 1978: 195-196). The coding relationship between DNA triplet and aminoacid is not reducible to physical laws, but rather to be understood as a property of the whole organism. The two approaches to systematics we have discussed are readily understood in these terms. The genetic approach assumes a process of evolution that, at least for the purpose of the analysis, lawfully governs all sequence alignments over the whole study group. The aim of the approach is to improve the fit between the model and the data. The aim of the morphological approach is to discover rules for the interpretation of biological structure. Thus, the

underlying aims of the two approaches can be seen to have the character of law or rule respectively. The genetic approach generates its data using a dynamical, necessarily rate-dependent model of evolution. The morphological approach derives its data through a process of interpretation and the results of the interpretation are independent of the rate at which the interpretation is carried out. The genetic approach is dynamic, the morphological approach linguistic. The two are complementary, yet incompatible in the sense of Pattee (1978).

The aim of the morphological approach is to discover the hierarchy of types, the aim of the genetic approach to discover the family tree of life. The hierarchy summarises putative homologies, in such a way that the greatest number agree (are congruent). This is a purely logical, linguistic criterion, as to the most efficient summary of symbols. The family tree expresses the most likely pathways of genetic transmission, based on a dynamic model of genetic change. The two approaches are complementary in the sense of Rieppel (1988: 159): 'Classification emphasises discontinuity and the subordinated hierarchy of types and subtypes ... By its logical construction, the hierarchy of types is static, i.e. ahistorical ... By its abstraction from specific form and function, the hierarchy of types is acausal: it abstracts from the causes (structural and functional) of similarity versus dissimilarity and change, but remains restricted to the representation of formal, i.e. topological relations of similarity.'

10. TWO PARALLEL STREAMS OF INFORMATION

Elsasser (1998) takes order above heterogeneity as the foundation of a theory of organisms. It is the first of four principles, which he puts forth. They, and their corollaries, are listed below:

1. The principle of ordered heterogeneity

'Take a cell of 1 micron³; if an atom occupies somewhat less than 1 angström³, there will be over 10¹² atoms in such a cell. Some fraction of these will be carbon atoms; given the capability of carbon atoms to form complex, three-dimensional structures, a tremendous number of such structures becomes possible ... *the number of theoretically possible structures is vastly in excess of the number of living cells that*

could possibly exist in a universe of the space-time extension determined by astronomers' (Elsasser, 1998: 30).

1a. The postulate of finiteness

'If a heterogeneous object is sufficiently complex it may and often does occur that the investigator runs out of samples of a class of objects (cells, organisms) before he has been able to determine the structure of the objects with sufficient precision. ...'*The laws of physics do not preclude unbounded repetition of an experiment, the regularities of biology (morphology) do'* (Elsasser, 1998: 41).

2. The principle of creative selection

'Our chief statement is then that a cell of certain (morphological) characteristics can exist in many more different molecular patterns than there are actual cells in the world. Hence *a choice is made in nature* among the immense number of possible patterns ... *the availability of such a choice is the basic and irreplaceable criterion of holistic or nonmechanistic biology* ... those aspects of morphology that cannot be "reduced" to mechanistic causality appear here as direct expression of a scientifically justifiable form of creativity' (Elsasser, 1998: 5).

3. The principle of holistic memory

'that the content of that which is created results from a selection, among the immense number of patterns available, of a pattern that resembles some earlier pattern of the same organism or of preceding (parental) organisms. *The main point of the third principle is that no mechanism for the transmission of information over time is specified. We therefore postulate here the transmission of information over a time-interval without an intervening device, such as computer engineers call a "storage" mechanism'* (Elsasser, 1998: 5).

3a. Homogeneous and heterogeneous replication

'If we now assume that there is a process of information transfer without intermediate storage, *we claim in effect that organisms make use of two separate and quite different processes for information transfer over time'* (Elsasser, 1998: 7). 'The molecular process underlying genetics will from now on be designated as *homogeneous*

replication, where by the term “homogeneous” we mean that in order to duplicate molecular copying in the laboratory in macroscopic terms one must have a homogeneous assembly of identical DNA molecules. The process just considered, of information transfer without intervening storage will from now on be designated as *heterogeneous reproduction*’ (Elsasser, 1998: 43).

4. The principle of operative symbolism (releasers)

‘We now interpret the discrete, genetic message as a *symbol* of the complete reproductive process. *Here a symbol is defined as an incomplete message [or releaser], from which the organism can reconstruct a structure by the process of heterogeneous reproduction such that the final structure is similar to an ancestral structure.* ... For instance, if the gene induces the appearance of an enzyme, then the enzyme is an operative component, indispensable for the reconstruction of the future message, “necessary but not sufficient” in the mathematician’s language’ (Elsasser, 1998: 45).

The autonomy of living things is a creative act, which is irreducible to underlying physics and chemistry. There is a creative selection among the immense number of possible physical configurations, so that the form established is similar to previous forms. Living things possess a memory of their type, which shapes their development. This holistic memory is not stored in the genes, but is transmitted through an alternative process of reproduction. As Wagner (1989b) said, homologues do not literally descend, yet, in some way, they are continuous from generation to generation. Van Valen (1982) proposes that homology is correspondence caused by continuity of information, but information that is not genetic but morphological. There are two kinds of information stability in living things. Genes are an information store, physically embodied in DNA molecules, and homogeneously replicated from generation to generation. Homologies are stable information memories, transferred without mechanical storage by heterogeneous reproduction. They are mnemes of Semon (1921). Genes do not bear sole responsibility for the development of living things. They are releasers of patterns of memory, Post-It notes in the realm of life. Tuning to a particular radio frequency releases a particular

pattern of sounds to be reproduced in the radio receiver. Tuning to a particular gene frequency releases a particular morphological pattern in the population.

After discussing the problems with the Darwinian explanation of homology, Hardy (1965) considers his own mnemonic theory. In addition to the genetic stream, there is a psychic stream, which is a species' experience of habit, form and development. 'There would be two parallel streams of information—the DNA code supplying the varying physical form of the organic stream to be acted on by selection—and the psychic stream of shared experience—the subconscious species "blueprint"—which together with the environment, would select those members in the population better able to carry on the race ... Such an internal conserving selective element might explain the secret of homology in face of an ever changing gene complex' (Hardy, 1965: 258, 259). Homologies are conserved morphological information, responsible for maintaining the peculiarities of individuals over their own lifetimes, the stability of species over millions of years, and the permanence of higher types, such as the mammals and the vertebrates (Elsasser, 1998: 110).

Genetic replication is simply a form of chemical copying. 'The conditions for heterogeneous reproduction are quite different. The process makes sense only if there is an immense reservoir of potential variants which differ from each other in structural or dynamical details but such that certain sets of them have a similarity in the large. This similarity in the large ... is taken in such a scheme as the very foundation of a holistic view of organisms' (Elsasser, 1998: 73). Homology is this similarity in the large, and is therefore foundation of holism in biology. Genetic replication, given that it is homogeneous, is prone to errors according to Shannon's Law: 'The latter expresses a phenomenon purely of statistics that holds in any system which obeys mechanical laws ... provided there are many equal components (atoms or molecules) present' (Elsasser, 1998: 44). Holistic memory, on the other hand, is not made up of separate parts to which the law could apply, so does not deteriorate over time. The permanence of type is an empirical fact demonstrated by the fossil record: 'species live in the average for several million years from their first appearance to their extinction. During this long time the characteristics of the species change very little, mostly in barely perceptible ways' (Elsasser, 1998: 44). Elsasser (1998: 118)

therefore declares that ‘holistic memory is a primary phenomenon of nature whose existence is postulated but cannot be deduced from any “laws”.’ It is similar to the invariance of the speed of light in special relativity. No wonder that the permanence of type has never succumbed to Darwinian explanation.

11. HIERARCHIES OF CONSTRAINT

In order to take into account how the genes are mapped onto the phenotype, population genetics has to invoke a number of postulates, for example, pleiotropy, penetrance and covariance (see Wagner, 1989, and Wagner et al., 1994, summarised in Wagner and Altenberg, 1996). Alberch (1991) regards these as ad hoc: ‘This phenomenological treatment ... prevents the possibility of studying the role of development in evolution’ (Alberch, 1991: 5). Alberch rejects a simple genotype-phenotype map, in which genes control developmental parameters, which in turn control morphology. Rather genes, through protein synthesis, lead to changes in cell properties and tissue geometry, which, through inductive relationships, lead to new patterns of gene expression. ‘The implications of this cyclical/feedback scheme drastically alter our perception of how complex morphologies evolve. Development cannot be reduced to a problem of gene expression, since gene expression itself is under epigenetic control’ (Alberch, 1991: 6). Alberch proposes that there exist certain developmental constraints, which are not determined by the genes, but rather by the non-linear character of the developmental system as a whole (see also Arnold et al., 1989).

Turning to an earlier treatment, Alberch (1982) describes the idea of developmental constraints with the aid of a thought experiment. He considers, for sake of example, that the whole diversity of a phenotype can be expressed in terms of two variables, x and y . (Alberch, 1991, considers a more realistic experiment, where there are m parameters that describe the spatial and temporal interactions that occur during development). The distribution of forms found in nature is not continuous. Instead, phenotypes cluster and certain regions of the xy space remain empty. Now let us take a population of one of the natural forms and breed the population for a large number of generations. The effect of natural selection is eliminated as far as possible, by enforcing random mating and minimising competition. The overall genetic variability

of the population can also be increased using mutagens. Score all the new phenotypes in terms of x and y , including teratologies. We will get the same phenotype clusters as before, plus new ones, which will be naturally lethal or non-functional phenotypes. 'However, there will still be states that are prohibited by developmental constraints' (Alberch, 1982: 318). The basic effect of developmental constraints on the apportionment of morphological variation is that 'a continuous distribution of genotypes can result in a discontinuous distribution of phenotypes' (Alberch, 1982: 319). Homology of structures thus emerges from the discontinuous apportionment of genotypic variation.

The theoretical framework that Alberch (1982) provides for understanding developmental constraints is that of non-linear systems: 'Developmental systems are complex non-linear dynamical systems. It is an intrinsic property of such systems that they will fall into a discrete number of stable states, i.e. we should find a discrete and bounded distribution of phenotypes. Furthermore, non-linear dynamical systems will exhibit preferred transitions of form' (Alberch, 1982: 327-328). The analysis of development as a dynamical system, in terms of some model of pattern generation, enables possible stable states of morphology to be identified and the preferred transformations between those states. Stable states of the morphogenetic system, like those of the genome, are poised. The morphogenetic process is conceived as a set of simple, locally acting assembly rules (Alberch, 1982: 321). Genetic or environmental change perturbs the values of the parameters of the developmental system, but as long as the values stay within certain limits, the morphology remains unchanged. The morphology is said to be self-regulating or canalised (Waddington, 1957). However, if a particular parameter reaches a threshold value then a sudden shift to a different stable state occurs. This effect is known in the language of non-linear systems theory as 'bifurcation'. The parameter space for a particular dynamical system is said to have 'bifurcation boundaries' at which the global behaviour of the system, such as the resulting morphology, shifts from one stable state to another. Oster and Alberch (1982) describe 'how the bifurcations in the developmental program acts as a filter, giving order to the random mutations in the genome, so as to present natural selection with a small subset of the possible phenotypes' (figure 11, legend). Thus

developmental bifurcations ‘filter random mutations, giving them a non-random character’ (p. 454).

Signals pass out from the genome and modify the environment to produce the phenotype. This is what we call development. Development is an interaction between the genetic signals and the environment. The dividing line between the phenotype and the environment is not precise: the phenotype ‘is a bit of the environment locally modified by the genetic information’ (Cairns-Smith, 1982: 80). It is possible to imagine that the phenotype, the manifestation of the effects of the genetic signals, extends into the environment beyond the bounds of the body housing the corresponding genes. This is the ‘extended phenotype’ (Dawkins, 1982).

‘Hierarchies can be profitably viewed as systems of constraint’ (Allen and Starr, 1982: 11). We can envisage the phenotype itself as a set of holons, which differ in the extent to which they filter genetic signals as they pass out into the environment. Genetic signals that pass through few phenotypic holons will be expressed relatively unfiltered. On the other hand, genetic signals that pass through many levels of the hierarchy will be significantly filtered. Continuous genetic differences between organisms in a population may be expressed as continuous phenotypic differences, if the corresponding genetic signals are relatively unfiltered, or as discontinuities, if the genetic signals are significantly filtered. The accumulation of genetic changes will cause gradual modifications of the phenotype in the first case, but sudden shifts between stable states in the second. In this way, phenotypic holons can be said to constrain the dynamics of genetic change. These constraints are properties of the developmental system: they are *developmental constraints*. Genetic signal is filtered in such a way that across individuals, and indeed across species, qualitatively different morphologies are produced.

Homologies are developmental constraints conserved among organisms. Homologies are the rules operating at the phenotypic level that constrain the dynamics of the genetic level (cf. Allen and Starr, 1982: 42). Through descent with modification, organisms accumulate inherited constraints on their genetic dynamics, or as Riedl (1977) would put it, on their adaptive freedom: ‘Structures from two individuals or

from the same individual are homologous if they share a set of developmental constraints, caused by locally acting self-regulatory mechanisms of organ differentiation. These structures are thus developmentally individualised parts of the phenotype' (Wagner, 1989b: 62). The taxon or type is the totality of constraints inherited by the organism, characterising 'a set of species sharing a common pattern of constraints and adaptive opportunities ... the key event in the origin of a taxon is a change in the pattern of constraints' (Wagner, 1986: 154-155). The thorax individuates the insect type, yet it cannot be a structure, since there is no continuity of morphological structures from one generation to the next. The thorax is relationship of developmental constraint inherited by insects, which individuates them as such. Through descent with modification, organisms accumulate inherited developmental constraints, and thus become increasingly individualised.

I have described above a 'feedback regulatory cycle' operating between genotype and phenotype, similar to that envisaged by Riedl (1977). In order to explain the stability of homologues over evolutionary time, Riedl saw the necessity of 'feedback loops of cause and effect both from the genome to the phenome and in the *reverse* direction' (Riedl, 1977: 364). The dynamics of gene frequencies may be the cause of phenotypic change, but the effects are constrained by the phenotype itself. Thus information flows both ways: from genotype to phenotype in the causal relationship enshrined in the 'central dogma' of molecular biology, and from phenotype to genotype as constraints enshrined in the systems approach (Riedl, 1977; Wagner, 1986).

12. QUANTUM FORMS

In Bohr's principle of complementarity, we must renounce full knowledge of systems that undergo discontinuous changes. We know a quantum system as either a particle or a wave, but cannot combine the two descriptions in a picture of what the system is between measurements. To extrapolate behaviour between measurements would assume that they change continuously, an assumption broken by the quantum of action. The agencies of measurement and the measured system form an indivisible and unanalysable whole. It is inherently ambiguous to talk of a particle following a defined trajectory between measurements. The holon, too, exists in an unanalysable,

ambiguous state—the Janus state—which is broken into complementary aspects when we mark the boundary of the holon. We see a holon as either part or whole, but not both; these are complementary, yet incompatible. We can say nothing of the holon before we see either part or whole, renouncing our knowledge of the living system, as it exists prior to our intervention³. Bohr's logic of generalised complementarity emerges from the laws of form.

The agencies of measurement and the measured effect have a form which is conspicuous to the human observer, but which cannot be reduced to the behaviour of individual elements of the system. In the conventional interpretation of quantum mechanics, the so-called Copenhagen interpretation, the form of the system is ascribed to some power of the observer's measurement apparatus to collapse the wave function of the elements of the system. Indeed some have suggested that this power lies not in the measuring device, but in the mind of the observer (Wigner, 1970; see also Rae, 1986, chapter 5). In both cases, we are left with the conundrum of how the wave function of the universe could collapse before the existence of observers and their measurements. Wheeler saw the universe before observers as less real, like a 'smoky dragon' (see discussion in Midgley, 1992: chapter 18.) Those who adopt a principle of complementarity tend to reject such metaphysical difficulties and take a phenomenalist stance. Phenomenalism is concerned only with the operations of measurement and leaves open the question of the underlying reality (Harré, 1972: 68-80). Different experimental arrangements can lead to the observation of the electron as a particle and as a wave, but we have no need to enquire further into the nature of the electron. A less orthodox approach is to say that when quantum situations of different forms are possible, a new universe comes into being for each form, only one being actualised in any particular universe (see DeWitt and Graham, 1973; Rae, 1986, chapter 6). These approaches show a certain discomfort with the notion of form, probably because none directly addresses the issue.

In Bohm's causal, indeed morphological interpretation of quantum theory, a quantum

³ I would like to compare the Janus particle in Etter (1998). A quantum system is a system of two linked probabilities, neither of which is itself observable. Measurement of the system amounts to disconnection of the link and the probabilities fall apart into the complementary descriptions of the Heisenberg and Schrödinger equations.

potential is postulated which is dependent on the form of the wave function not on its intensity (see Bohm and Peat, 1989: 88-97; Bohm and Hiley, 1993: 31-32). The particle's trajectory is constrained by the whole form of the quantum potential and the two are considered to belong to different orders of existence, explicate and implicate. Complementary descriptions in terms of explicate and implicate order are required for a full account of the quantum situation (Bohm, 1980: 166).

Bohm's quantum field has much in common with the idea of a morphic field suggested by Sheldrake (1990, 1995a, 1995b). Morphic fields do not consist of matter or energy, but rather shape matter and energy into particular geometrical patterns. The quantum field for a graphite diffraction grating, for example, shapes the matter and energy of electron particles passed through it into a characteristic diffraction pattern. Even in cases where particulate behaviour is observed, the wave is present, acting as before to guide the motion of the particles. This is Bohm's resolution of wave-particle duality, in terms of a "guiding wave", which is quite unlike any other wave field known to physics. The guiding wave possesses very little energy of its own yet it is able to influence the behaviour of its associated particles.

Sheldrake (1995a) discusses the multiple minimum problem in biochemistry. Proteins fold up in a matter of minutes, assuming only one of many possible minimum energy configurations. If induced to unfold, they will refold again into the normal configuration, avoiding other energetically possible but abnormal arrangements. They are able to reach the same end by a variety of different paths. The total number of possible configurations is enormous (Sheldrake, 1995a: 65). 'It is therefore conceivable that some factor other than energy 'selects' between these possibilities and thus determines the specific structure taken up by the system' (Sheldrake, 1995a: 70-71). It is the morphic field, which brings about this selection. Each morphic field is associated with a particular kind of morphic unit, which it stabilises through a rule of repetition. 'The characteristic form of a given morphic unit is determined by the forms of previous similar systems which act upon it across time and space by a process called *morphic resonance*' (Sheldrake, 1995a: 116-117). Morphic resonance is heterogeneous reproduction and the whole statement is equivalent to the principle of holistic memory. Indeed, Sheldrake (1995b) specifically

describes the action of morphic resonance as a kind of organic memory, echoing both Hardy (1965) and Elsasser (1998): ‘...natural systems, such as termite colonies, or pigeons, or orchid plants, or insulin molecules, inherit a collective memory from all previous things of their kind, however far away they were and however long ago they existed. Because of this cumulative memory, through repetition the nature of things becomes increasingly habitual. Things are as they are because they were as they were...A beech seedling, for example, as it grows into a tree takes up the characteristic shape, structure, and habits of a beech. It is able to do so because it inherits in nature from previous beeches; but this inheritance is not just a matter of chemical genes. It depends also on the transmission of habits of growth and development from countless beech trees that existed in the past’ (Sheldrake, 1995b: xvii).

13. TIME AND TIMELESS

Different physiological time scales exist in living things. A mouse, for example, lives at a much faster pace than an elephant. Indeed, physiological time scales change with age, from the fury of youth to the calm of old age. Psychological time scales can change by the emotions. Consider a wonderful play or a film where three hours feel like five minutes, or a boring speech where five minutes feel like three hours.

Bergson makes the distinction between concrete time and abstract or mathematical time (Bergson, 1911: 22). Concrete time is constant creation, where each instant is incommensurable with the last. In abstract time, all times are equivalent. If living time is concrete and embodied then the variations of psychological and physiological time make sense. From an abstract perspective, this makes no sense; in the logic of solid bodies, time does not really flow at all and certainly not at different speeds for different organisms.

The logic of solids—of bodies external to one another and separated in space and time—is the logic of the analytic mode, distinctive of mainstream science. It is a logic of abstract time. In the holistic mode, the unity of a system stands before the separation of parts: it is a unity without unification (Bortoft, 1996). This is a logic of concrete time.

Bohm (1969; Bohm and Peat, 1989) considers that there is a flow of time that is mechanical—a manifest or explicate time—but every so often there are creative periods, where new content unfolds from the implicate, hidden order. In mechanical time, there is a chain of events, where one event determines the next event. Creative change, on the other hand, is “timeless”, the origin of a whole new chain of events, incommensurable with the last.

The analytic logic of solids is a good description of the explicate order, the holistic logic that of his implicate order. Whereas for Bohm the implicate order is timeless, for Bergson this is the domain of concrete time. Whether a process appears as in time or timeless depends on whether we look from the abstract or concrete perspective:

Abstract:	time	timeless
Concrete	timeless	time
	analytic	holistic
	explicate	implicate

On the one hand, we have the natural, living process, which is creative and irreversible, to be understood in the holistic mode. On the other hand, we have an artificial or classical process, which is mechanical and reversible, understood in the analytic mode. From the abstract perspective, time is proper to the reversible, artificial process; the natural process appears timeless. From the concrete perspective, time, in its irreversibility, is proper to living things; artificial systems are timeless.

Prigogine (1980) develops a notion of concrete time for irreversible processes, which he calls age. As living things endure, so do they age. Bohm (1987) derives Prigogine’s age quantity as an enfoldment parameter. A movement of enfoldment is therefore a movement along an axis of concrete time, or ageing. Such a movement involves a number of repetitive transformations. The cogent moment of time for a living thing grows longer as it ages. So does the rhythm of its life change, solidifying as habits become entrenched.

Think of the history of an invention, such as photography, the bicycle or the motorcar. In the beginning, there are a wide variety of competing designs, which eventually give way to a small number of successful designs. These few designs form the basis of future changes, which are constrained to be much smaller in scope. It is difficult to identify the reason for the survival of the successful few. Gould (1989) describes the evolution of multicellular animals in this way. Testified in the fossils of the Burgess shale, Cambrian there were a large number of disparate body plans in the Cambrian period, which gave way to a smaller number of successful designs. For example, among twenty-five different arthropod designs, only two survived, the chelicerates and uniramians. The most beautiful, complex and common designs became extinct, whereas the rare and specialised continued.

According to Bergson, life is impelled by a creative impetus, an ascending movement, whereas matter is the reverse tendency, a descending movement (Bergson, 1911: 11-12). Matter is life unmaking itself: 'So, from an immense reservoir of life, jets must be gushing out unceasingly, of which each falling back is a world. The evolution of living species within this world represents what subsists of the primitive direction of the original jet, and of an impulsion which continues itself in a direction the inverse of materiality ... In vital activity we see, then, that which subsists of the direct movement in the inverted movement, a reality which is making itself in a reality which is unmaking itself' (Bergson, 1911: 261). The ascending movement takes life to ever more widely differing forms. The descending movement takes matter into ever more regular and repetitive forms. Matter is life grown old.

Sheldrake points out that there must have been time when there were no atoms as we know them: 'Once there were no lead atoms, or sodium atoms, or atoms of any kind at all' (Sheldrake, 1995b: 61-62). There must have been a time when matter had not solidified into patterns we know by the names of these elements. Now any atom of lead is indistinguishable from any other. However, this homogeneity is result of a large number of repetitions in the evolution of the universe: '... these particles have been replicating so long that they are pretty well determined, or fixed in the "cosmic memory"' (Bohm, in Sheldrake, 1995a: 239). In the beginning, all matter was alive, as Peirce said: 'Matter is merely mind deadened by the development of habit to the

point where the breaking up of these habits is very difficult' (quoted in Sheldrake, 1995b: 14). Let us think of the early history of the universe as a time of diversity, rather than the unity of the unified field. Two electrons would meet each other and not recognise each other, have a conversation and discover their similarities and differences.

In Elsasser's scheme, the distinction between the homogeneity of matter and the heterogeneity of life is important. We can now see this as a matter of degree rather than kind. Life is still in the vigorous blush of youth; matter has reached a calm uniformity. Elsasser does note that heterogeneous reproduction, even though it involves a creative selection of possible forms, does tend towards repetition: 'What observations show us is that the characteristics of the individual as well as of the species change only very slowly. *Thus it becomes imperative to assume that, in a first approximation, the outcome of creativity is repetition*' (Elsasser, 1998: 154). Species are indeed stable for at least one million years. The possibility of rapid, creative change remains, however. When change does occur, new species emerge very quickly: 'At certain moments in the geological record new species appear that show distinct differences from the older, related ones. This differentiation occurs in a relatively short time as the geological record goes; thereafter the new species maintains its characteristics relatively unchanged for its lifetime, that is until extinction occurs' (Elsasser, 1998: 96-97).

14. HIERARCHIES AND THE IMPLICATE ORDER

Oster and Murray (1989) describe two classes of pattern generation models, chemical prepattern and mechanochemical. From the chemical prepattern viewpoint, either simple chemical gradients are established across tissues or the pattern emerges through 'diffusion-driven instabilities' (Turing, 1952). The latter subclass includes the reaction-diffusion models studied by Prigogine, such as the 'Brusselator' (Prigogine and Lefever, 1968). The mechanical aspects of development, which shape form, are not taken into account in this approach and the identity of the 'morphogens' involved has not been ascertained. From the mechanochemical viewpoint, chemical and mechanical processes interact and are framed in terms of measurable forces and displacements. Goodwin (1990) notes the elusiveness of chemical morphogens and

summarises his own work on mechanochemical models, which involve measurable quantities such as the concentration of calcium ions and the viscoelastic strain of the cell membrane.

Both classes of models generate patterns through a combination of activation at short scales and inhibition at long scales (Oster and Murray, 1989; cf. Gierer and Meinhardt, 1972). Models in yet a third class, namely the Lotka-Volterra models of population dynamics, generate pattern in the same way and are therefore morphogenetic (Britton, 1989, 1990). Indeed, Lotka first published his model as a description of the oscillating concentrations of two reacting chemical species (Lotka, 1920). Though activation between species is significant only at short scales, an inhibitory effect will be experienced among species of widely differing scales.

An entity's scale is its position in the hierarchy. The greater an entity's scale, the greater its influence on other entities, and thus the higher its position in the hierarchy. Scale may be defined as 'the period of time or space over which signals are integrated or smoothed to give message' (Allen and Starr, 1982: 18). To illustrate their concept of scale, Allen and Starr (1982: 19) discuss May's (1973) Lotka-Volterra model of the history of resource use in a series of populations (or generations of a given population): 'May's concern is for the influence (messages) that past populations (signal) have upon resources (the holon) at time t . He integrates the signal N using a particular weighting function Q . "The function $Q(t)$ specifies how much weight to attach to the populations at various past times, in order to arrive at their present effect on resource availability." Thus the total effect of past populations on resources [the scale] at time t is

$$\left[\int_{-\infty}^t N(t') Q(t-t') dt' \right],$$

'where N = the number of individuals in the past populations.'

May's Q function is an example of a Green's function, where only temporal convolution is considered. The amount of resources available to the present population has the history of resource use of previous generations enfolded within it.

There are a number of previous populations, where contributions of different degrees of enfoldment are combined. The amount of resources available to the present population depends on the total series of generations, on the age of the population. The knock-on effect of more ancient populations on the present population will be greater than the effect of recent populations, thus more ancient populations will filter present resource use more than recent populations. Age is related to scale.

In Gourley and Britton (1996), the inhibition term uses a Green's function to describe how the whole history of predation throughout space and time influences the current behaviour of the prey population. Thus, spatial and temporal convolution are both included. Gourley and Britton (1996: 332) justify their approach as follows: 'Whilst integrodifferential systems tend to be rather complicated in appearance, all we have done essentially is to recognise that time delays should be included in the term representing intraspecific competition for resources for the prey species, and that the assumption of motion (through diffusion) means that any time delay term should be nonlocal in space as well as in time. As a consequence, we have obtained a variety of solution behaviours which reflects phenomena such as animal aggregation, population cycles and the motion of aggregations as observed in nature. We therefore claim that nonlocal effects play a very important role in pattern formation, and that our model is more realistic than the usual type of reaction-diffusion system used to model predator-prey interactions in which the species can diffuse.' The richest models use Green's functions to capture the nonlocal, holistic order of morphogenesis.

Bohm make use of Green's functions to describe the movement of unfolding and enfoldment that takes place in quantum processes (Bohm, 1980: 160; Bohm and Peat, 1989: 175-179; Bohm and Hiley, 1993: 354-355). The form of the wave function $\Psi(x', t')$ is related to its form at a later time $\Psi(x, t)$, by a Green's function $Q(x - x', t - t')$, such that

$$\Psi(x, t) = \int Q(x - x', t - t') \Psi(x', t') dx'$$

The value of the wave function $\Psi(x, t)$ is the sum of contributions over the whole range of values x' at time t' , weighted by Q . The region near x is in communication

with regions from all over space at other times, enfolding the information contributed by them. Information contributed from each region near x' will unfold into the whole space x , filtered by the factor $Q(x - x', t - t')$.

15. NESTED HOLOGRAPHIC SURFACES

Let us consider the picture of hierarchy introduced by Kron (1963), as a series of tears. Tear a system by removing a layer of components, namely the intersection network, at the interface between adjacent subsystems. Bowden (1990) shows how Kron's picture is equivalent to Huygens principle in the reinterpretation of Jessel (1962). Information about any subsystem is held in holographic form at its surface, that is, at the intersection. All that an observer needs to know about a torn subsystem is the information on the surface enclosing that subsystem. Similarly, all an observer within a torn subsystem needs to know about the outside world is on the surface. A holon is an interface between its parts and the rest of the universe, a holographic surface through which information enters and departs. The signals emerging from the internal dynamics of the torn subsystem pass through its surface. A holon is the surface screen of a subsystem, upon which an image of the dynamics unfolds. The most succinct description of a subsystem is the evolution of the image of the subsystem projected onto its surface.

Take a system and make a series of tears, disconnecting subsystems step by step. A series of tears is a series of transformations of the system matrix of the form $E' = MEM^{-1}$: 'Such a succession of transformations was referred to by David Bohm as an "ordering or enfolding", and by Jessel and Resconi as a Logical System...' (Bowden, 1998). Thus, given a frame of reference, E , the transformation or metamorphosis M turns E into a different frame of reference E' (Bohm, 1980: 165-166). Marking a holon specifies a particular frame reference. The level of the analysis given by the mark is the choice of a particular degree of tearing, a particular degree of enfolding. E' is enfolding with respect to E , and two are complementary yet incompatible, since an observer cannot adopt both scales simultaneously.

If we base the transformation M on an enfolding parameter, representing successive steps, then quantum movement emerges naturally. $E' = MEM^{-1}$ becomes equivalent to the Schrödinger's description of quantum transitions: '... Schrödinger's equation can be thought of as specifying the evolution of (a series of) tearings ...' (Bowden, 1998; after Hiley, 1995). Abstract time t in Schrödinger's equation has been replaced by an enfolding parameter (as originally proposed in Bohm, 1969). A series of such transformations, $E' = MEM^{-1}$, is an iteration over the levels of the hierarchy. According to von Baer's laws, an organism iterates through its hierarchy of types as it develops. We therefore have the identical structure of order and process in both quantum physics and biological development:

1. In quantum physics
 - a. The underlying order of the quantum process, captured by Huygens principle, is a nested hierarchy of holographic surfaces.
 - b. The movement of a quantum process, given by the Schrödinger equation, is an iteration over this hierarchy of holographic surfaces.
2. In biological development
 - a. The underlying order of the developmental process, captured in morphological classification, is a nested hierarchy of holographic surfaces.
 - b. The movement of a developmental process, given by von Baer's laws, is an iteration over this hierarchy of holographic surfaces

The movement of the morphological process, whether quantum or biological, is timeless from the abstract perspective. From the concrete perspective, it is an ageing, or enduring. A biological classification is an informative summary of morphological data, in its most economical form, namely a holographic representation. The most informative summary takes the form of a binary tree (Mickeyvich and Platnick, 1989), which is also the optimal means to store data holographically (Bowden, 1994).

The discovery of hierarchies of holographic surfaces in biological development and quantum physics makes sense in the light of a recent proposal called the holographic principle. According to this principle, the world is 'a network of holograms, each of

which contains coded within it information about the relationship between the others' (Smolin, 2000: 178). Any surface is a channel of information between observers: any surface may be treated as a holon. 'In such a world, nothing exists except processes by which information is conveyed from one part of the world to another. And the area of a screen—indeed, the area of any surface in space—is really nothing but the capacity of that surface as a channel of information. So, ... space is nothing but a way of talking about all the different channels of communication that allow information to pass from observer to observer. And geometry, as measured in terms of area and volume, is nothing but a measure of the capacity of these screens to transmit information' (Smolin, 2000: 177-178). In other words, the world is a hierarchy of holons.

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