

THE REALITY OF SPECIES

Rohan Collier

Thesis submitted for the Doctorate in Philosophy
degree, Bedford College, University of London.
July 1985.

ProQuest Number: 10098511

All rights reserved

INFORMATION TO ALL USERS

The quality of this reproduction is dependent upon the quality of the copy submitted.

In the unlikely event that the author did not send a complete manuscript and there are missing pages, these will be noted. Also, if material had to be removed, a note will indicate the deletion.



ProQuest 10098511

Published by ProQuest LLC(2016). Copyright of the Dissertation is held by the Author.

All rights reserved.

This work is protected against unauthorized copying under Title 17, United States Code.
Microform Edition © ProQuest LLC.

ProQuest LLC
789 East Eisenhower Parkway
P.O. Box 1346
Ann Arbor, MI 48106-1346

ACKNOWLEDGEMENT

I wish to thank David Wiggins who has spent a considerable amount of his time helping and encouraging me in my work for this thesis.

ABSTRACT

This thesis examines the nature of biological species, and argues that species are real. The thesis starts with a descriptive account of species drawn from biology. This includes taxonomic views, theories of speciation and theories in ecology. In this chapter a particular definition of species, 'the biospecies', is reached. The thesis continues in Chapter Two with a philosophical account of species, which aims at reaching an understanding of the kind of entities species are. The chapter concludes that species are natural kinds, but not as traditionally construed. Chapter Three looks closely at the use biologists make of species terms, and argues that biological theories are committed to such terms. That species terms cannot be dispensed with in biological statements indicates that species are real. If species are real, they are entities for which questions of identity make sense. Chapter Four reviews different criteria for the individuation and identity of species. All the criteria are found to suffer from problems of vagueness. In view of the difficulty of providing criteria for species identity, the thesis turns in the fifth chapter to two biological views - numerical taxonomy and neo-Darwinism- which claim that biological theories can dispense with species terms. But a look at these reductive theories shows that one loses a certain measure of explanation if species are dispensed with. In the light of the failure of the reductive theories, a fresh attempt is made in Chapter Six at giving a criterion for species sameness. This last chapter also serves as a general conclusion to the thesis.

TABLE OF CONTENTS

<u>Introduction</u>	P. 8
1. The problem of the reality of species	P. 8
2. Structure of the thesis	P. 14
<u>Chapter One A scientific account of species.</u>	P. 21
<u>Part I Taxonomy</u>	P. 22
1. Morphological classifications	P. 23
2. Cladistic classifications	P. 34
3. Biological classifications and the biospecies	P. 40
<u>Part II Theories of speciation</u>	P. 50
1. Geographical isolation	P. 51
2. Genetic isolation	P. 56
3. Ecological isolation	P. 57
4. Ethological isolation	P. 58
<u>Part III Concepts in ecology</u>	P. 62
1. The ecosystem	P. 63
2. The niche	P. 65
3. Adaptation	P. 68
4. Species-specific relationships	P. 74
<u>Chapter Two A philosophical account of species</u>	P. 85
<u>Part I Different possibilities for species</u> <u>as entities</u>	P. 85
1. Classes	P. 85
2. Individuals	P. 86
3. Natural kinds. The received view	P. 92
4. Natural Kinds. An ammended view	P.101
<u>Part II Species and properties</u>	P.108
1. Essential features	P.108
2. Distinguishing characteristics	P.110
<u>Chapter Three The reality of species</u>	P.118
1. A reality sustained by diversity	P.119
2. Models and theorems in biology	P.126
3. The use biologists make of species terms	P.136
4. Vagueness. An objection to the reality of species	P.140

<u>Chapter Four Individuation and Identity of species</u>	P.146
1. Phenotypes and genotypes	P.148
2. Reproductive isolation	P.149
3. Gene pools	P.157
<u>Chapter Five Two reductive theories</u>	P.163
<u>Part I Numerical Taxonomy</u>	P.164
1. A nominalistic approach	P.164
2. Critique of numerical taxonomy	P.169
<u>Part II Neo-Darwinism</u>	P.174
1. The selfish gene	P.174
2. The unit of natural selection	P.178
<u>Chapter Six A criterion for species sameness.</u>	P.200
1. A non-reductive approach	P.201
2. A new criterion for species identity	P.204
3. Conclusion	P.214
<u>Appendix Different levels of reality in biology</u> . .	P.217
<u>Bibliography</u>	P.245

LIST OF TABLES AND ILLUSTRATIONSTablesChapter Three

Table 1. Derivation of the Hardy Weinburg theorem .	P.123
Table 2. Factors in the winter moth life table . . .	P.133
Table 3. Model of the interaction between the winter moth and its parasites	P.133

IllustrationsChapter One

Figure 1. Phyletic diagram	P. 36
Figure 2. Cladogram	P. 36
Figure 3. Cladistic classification	P. 38
Figure 4. Geographical isolation	P. 53
Figure 5. Darwin's finches	P. 55
Figure 6. Ecological isolation	P. 59
Figure 7. Energy flow diagram in an ecosystem . .	P. 64
Figure 8. The partridge's niche	P. 64
Figure 9. The thrush's niche	P. 67
Figure 10. Adaptation of the moth <u>Biston betularia</u> .	P. 69
Figure 11. <u>Biston betularia</u> , the typical form and the carbonarian form	P. 70
Figure 12. Meadow sage and bees	P. 78

Chapter Three

Figure 13. Matrix of possible genotypes for two genes A and a	P.122
Figure 14. Predator/prey relationship	P.128
Figure 15. Predator/prey interaction as predicted by the Lotka-Volterra equations	P.129
Figure 16. Predator/prey oscillation	P.130

Chapter Four

Figure 17. Circumpolar ring-species of gulls . . .	P.154
--	-------

Appendix

Figure 18. Schematic view of a generalized cell . . .	P.221
Figure 19. Human chromosomes	P.223
Figure 20. Mitosis	P.224
Figure 21. Meiosis	P.226
Figure 22. DNA molecule	P.229
Figure 23. DNA replicator	P.231
Figure 24. DNA, chemical structure	P.232
Figure 25. The genetic code	P.233
Figure 26. mRNA and tRNA	P.234
Figure 27. Building a chain of amino acids	P.235
Figure 28. A protein	P.236
Figure 29. Multiple alleles	P.238
Figure 30. Chromosomes crossing over	P.238
Figure 31/32. Chromosome mutation	P.241

INTRODUCTION

This thesis investigates the concept of biological species and aims at showing that when living organisms are classified into species, the classifications are not artificial but natural. They reflect the natural order of the world. In other words the aim of the thesis is to show that species are real. Before outlining the overall argument, it will be useful to see how the reality of biological species has been put in question.

1. The problem of the reality of species

One may wonder why the reality of species should be a problem. As it happens, it was not a problem until the last century. Indeed, in the 17th and 18th centuries, naturalists such as Ray, Paley and Linnaeus believed species were real - species consisted of organisms conforming to a type created by God. Species for these naturalists were as they are described in the Bible, distinct types of individuals able to reproduce only after their kind. In practice when biologists tried to identify which organisms belonged to which species, the criterion used was that if two individual organisms could be successfully mated then they were said to belong to the same species. This 17th and 18th century view assumed that species were fixed, and that God had created each species and fitted it to an environment which was stable. Any variation

between individuals was confined within well-defined limits. Before the 19th century, therefore, species were seen as real and unchanging, and explanations for the origin of species were nearly always given in terms of creation. It is true that there were a few naturalists such as Buffon and Lamarck, who had thought that species could undergo transformation and that these transformations could give rise to new species. But they were in a minority. Surprisingly, they would still be in a minority today, but for a different reason. They would be in a minority, not because of their evolutionary views, but because they explained change in finalistic terms which would not be acceptable to modern biologists.

Concepts of species changed in the 19th century with Darwin. Darwin was impressed by Lyell's successes with geological explanations which were given in terms of natural laws alone (without recourse to a divinity or to any concept of purpose). Most science had already been influenced in this way by Cartesian philosophy. Descartes was the first to attempt a complete physico-chemical account of life (excluding the mind). He had not, however, attempted an explanation of how organisms had evolved in the first place. This is what Darwin wanted to do. Before Lyell it was thought that the earth had had a relatively short history. But Lyell showed how extremely ancient the earth in fact was: "the belief that species were

immutable productions was almost unavoidable as long as the history of the world was thought to be of short duration" (1). Darwin, therefore, hoped to give biological evolution a mechanistic explanation instead of a vitalistic or finalistic one. But in fact a mechanical account of how evolution by natural selection operates was not found until much later, when Mendel put forward his genetic theory.

As the species concept changed, so did explanations given for biological phenomena. One major puzzle for biologists had always been the great variety of organisms existing in the world. Darwin did not accept the creationists' explanation of this, namely that God created every possible creature to diffuse every possible happiness (this is the view that Charles Bonnet holds in Contemplation de la Nature 1764). On the contrary, Darwin believed that organisms had evolved into increasingly complex forms, developing all possible means of survival and occupying all possible niches, by a process of natural selection. The characteristics of organisms were the result of chance, Darwin argued, and there was as much evidence in nature of randomness as there was of design.

Why for example create the upland geese with webbed feet, if they never swim? Webbed feet do not in themselves contribute to a creature's well-being. For Darwin creationism did not offer any adequate account of such cases, the explanation must be sought

elsewhere. He therefore proposed that the geese's webbed feet were something left over from the past. His claim was, in other words, that an organisms' characteristics bore the mark of their origins. In this way Darwin introduced a historical dimension into biology: the explanation for the immense variety of organisms was to be found in their past.

That things in nature point to the past did not fit the creationists' view, and of course they rejected Darwin's theory of evolution. But surprisingly, Darwin's contemporaries among physical scientists were also opposed to his view, and they were not impressed by Darwin's efforts to explain biological phenomena in terms of natural laws. The reason for this was that the physics of that time suggested a very static view of the world, in which a finite number of fixed elements (coupled with definite natural laws) made up the fabric of the universe. Evolving species did not fit into that picture any more than it did into the creationist's one. Kelvin, Joule and Maxwell for example all opposed the idea of evolution, although they were no doubt motivated by their Christian beliefs as much as by their scientific views. It seems therefore that scientists in Darwin's day, whether biologists or physicists, opposed the idea that species evolved and supported the idea that species were fixed and real.

At the time Darwin developed his views, Linnaean

hierarchical classifications were widely accepted. Darwin did not oppose these but gave new meaning to the classification by showing that the relationships between species, genera and families were grounded in natural laws : organisms bore the similarities they did because they had developed out of common ancestors. But whereas Linnaeus treated species as real, Darwin did not. This was because there were aspects of evolutionary theory which weakened the hold of the idea that species were real, quite independently of the fact that the reality of species had been associated with creationism. The main point against reality was the mechanism postulated for evolutionary change, which depended for its operation on variability and natural selection. This mechanism only works because individuals vary and are unique, and because some individuals have selective advantages over others and therefore survive. It follows from this that species are neither uniform nor fixed. It was this which led Darwin to believe that species were not real: "we shall have to treat species in the same manner those naturalists treat genera, who admit that genera are merely artificial combinations made for convenience"(2).

Since then, the view that species are not real has been held by many biologists, and even quite recently Haldane claimed that "the concept of a species is a concession to linguistic habits"(3).

After Darwin, it was for a long time as if the belief that species were real belonged necessarily to creationists, evolutionists believing species to be arbitrary classifications of the mind. Paradoxically though, most biologists today claim that species are real entities. Is this a legitimate shift within evolutionism? Creationism is no longer a credible scientific explanation for the origin of species. Almost all contemporary biologists are evolutionists. Why do contemporary biologists believe species are real, when evolutionary theory once appeared to give good grounds for seeing species as not real? In other words, what motivates biologists to see species as real? These questions give rise to the central question of this thesis: what is the importance of species (as real entities) to biology?

Biological sciences can, very broadly, be said to answer questions on how organisms evolve, how they relate to the environment and how they relate to each other. Within these questions biologists ask more specific questions, concerning particular types of organisms, such as: 'why has this kind of organism evolved in this particular fashion?' or 'why does it inhabit this particular environment?' or 'why does it relate in this particular way to this other kind of organism?' The biological explanations given to answer such questions will be looked at in this thesis. This will enable us to shed some light on the question of

the reality of species.

I aim to show that there are good grounds for seeing species as real entities in nature. In doing this, I also aim to give an account of the way in which the analysis of good biological explanations furnishes an answer to the reality question. The overall claim will be that if good explanations given for important questions (questions we cannot lightly dismiss) necessarily include an assumption about the reality of species, then there are good grounds for accepting this assumption. To see how an argument for this claim will be developed, it will be helpful now to reveal the intended plan of the thesis.

2. Structure of the thesis

Before engaging on arguments for the reality of species and before attempting to analyse the way in which biology assumes this reality, I start by giving a purely descriptive account of what constitutes a species. This is important because it lays down the ground upon which the ensuing arguments are based.

Chapter One surveys current biological knowledge concerning species. The first part of the chapter compares differing definitions taxonomists have given of species, and tries to determine which seems the most fruitful. The traditional taxonomic view seems inadequate. This view uses morphological criteria for classifying organisms into species according to type

specimens. This approach is rejected on the ground that it misrepresents the way organisms are grouped in nature. Indeed in nature organisms do not conform to a standard type. I also hope to show, in this first part of Chapter One, that the more recent biospecies classification is the most acceptable. The biospecies definition of species sees the species primarily as a group of genotypes making up a gene pool (an interbreeding group). The problems engendered by the biospecies definition are considered, but I am not persuaded these are serious enough for the biospecies concept to be abandoned. The second part of Chapter One looks at theories of speciation. The third part of Chapter One is on Ecology. Chapter One ends with the conclusion that theories of speciation and theories in Ecology are equally committed to a biospecies concept of species.

Chapter Two lays the ground for arguments for the reality of species and looks at the philosophical problems about species. If species are real we want to know what sort of entities they are. Several possibilities are considered. I start by rejecting the position held by David Hull and others, that a species is the sum total of all its individual members - a spatiotemporal whole. I then consider the possibility that species are natural kinds, and this view is looked at in some detail. What makes a natural kind the kind it is is its nature. Philosophers from Aristotle to

Kripke have seen the nature of any natural kind in terms of some microstructure, and this element has been extended to species seen as natural kinds. It would mean that something in each and every individual making up a species accounted for its belonging to that species. (This 'something' could be an essence.) However, such a view is untenable in the face of present day biological knowledge. The immense variety among organisms of one species is such that individuals within the same species do not have a set of identical characteristics at any level - not even the microscopic level. Nevertheless, I argue in this chapter, species do have a nature which explains the groupings we find in the world, and this is a nature that scientists discover. Scientific explanations need not necessarily be given in terms of microstructure. The last part of the chapter looks at the kinds of things one does say of species and the properties that are attributable to species.

Whereas Chapters One and Two were concerned with outlining the sort of entities species are, the rest of the thesis (chapters Three to Six) concentrates on the central argument of the thesis, supporting the reality of species. Chapter Three looks closely at the use biologists make of species terms. It looks at the way in which biological theories need species to explain the things they do explain. It also looks at what would happen to these theories if one got rid of the

species terms. I take the view that if true statements of biological sciences are committed to species terms, then species are real. Most of the chapter is devoted to examples where we find essential use of species terms. Ecology is particularly rich in such examples, because here many species-specific relationships can only be explained and predicted by theoretical models using species terms. I consider several of these and argue that one could not say the things that these theories do say without using species terms.

Having argued that species are real, it seems appropriate for me to say something of their identity, and Chapter Four turns to some of the questions in this area. Species are natural kinds, but as shown in Chapter Two, there are no characteristics which could be said to belong to all and every individual making up a species. Yet, if species are real, there must be some way of grouping together all members of a species. Chapter Four, therefore, investigates different possibilities for the individuation and identity of species. We see that the criteria for sorting individuals exhaustively into species all fail because of the inherent vagueness infecting the boundaries of species. Indeed, any criterion for species' identity which relies on the properties of individuals within the species is bound to fail. For this reason the properties of populations which make up the species are also considered. However the problem of individuation

and identity is not solved by the end of the chapter and the question is left in suspense for the space of the next chapter.

The difficulty of individuating species, considered in the light of the claim 'no entity without identity', calls for a review of certain modern views which deny reality to species. The fifth chapter, therefore, examines two reductive views. In spite of the fact that most contemporary biologists assumes that species are real, there are some well known biologists who maintain that they are not. These include numerical taxonomists and neo-Darwinians who both claim species are arbitrary and do not play any essential role in nature (or in scientific theory). Numerical taxonomists deny that species are real on the grounds that organisms are unique and cannot be classified into any finite number of groups. Numerical taxonomists do classify organisms into species, but see these as arbitrary groupings based simply on calculated similarities between individuals. The methods used by numerical taxonomists for classification purposes are very successful, but they do not of themselves imply that species are not real (in spite of the belief to the contrary held by numerical taxonomists). The arguments underlying this nominalistic view are shown in this chapter to be in fact weak philosophical ones. In addition they are not even related in the right way to the scientific methods used by numerical

taxonomists. The second reductive attempt is neo-Darwinism. One of the main claims made by neo-Darwinians is that the unit of natural selection is the gene. It is this aspect of neo-Darwinism which is of interest here, in as much as it implies that it is never species which are selected but always genes. I try to show that the arguments for a reduction from species, groups or individuals to genes do not hold. Indeed certain cases of natural selection cannot be accounted for without reference to species. Some examples of group selection which are not reducible to gene selection are given to illustrate this point.

In the light of the failure of the reductive theories, the sixth and final chapter returns to the question of the individuation and identity of species, and attempts a new approach to the question. The criterion proposed is not formulated in terms of any constitutive property of species. Roughly speaking, the criterion I propose is that groups of individuals should be seen as representing different species as opposed to one species just if the scientific outcome of such identifications are significant. That is to say, the criterion given here seeks to exploit the explanatory advantages that accrue in, for example assigning populations to different species, as opposed to different races within one species. Finally some suggestions are made concerning the implications this criterion has regarding the nature of species.

At the end of the thesis there is an appendix. This covers basic biological knowledge referred to in the thesis, and is meant mainly for reference purposes. The appendix also gives an idea of the different levels of explanation in biology.

References

- (1) Charles Darwin - The Origin of Species, first edition (1959), Chapter XIV, p. 481.
- (2) Ibid., p. 485.
- (3) Quoted by S.J. Gould in "Species are not Specious", New Scientist, 2nd August, 1979.

CHAPTER ONEA SCIENTIFIC ACCOUNT OF SPECIES

This chapter is largely descriptive. It aims to reach an understanding of the way in which biologists see species (irrespective, for the moment, of whether they consider species to be artificial or natural groupings). The main concern is with species as a determinable notion and not with particular determinate species - which is to say, that therefore this chapter concentrates on what species in general are rather than on why any particular species is what it is. In this chapter I hope to arrive at an understanding of species which will accomodate the aspects of living organisms already mentioned in the introduction. This includes change over time and variety at any one point in time. In order to achieve this understanding I shall consider three areas of biological science. This chapter is accordingly divided into three parts. Part I is on Taxonomy, and deals with the way in which organisms are classified. Part II reviews theories of speciation, which explain the way in which new types of organisms arise. And Part III looks at concepts in Ecology, and the way in which different types of organisms relate to each other and to the environment. Factual examples taken from the present chapter will be used to

illustrate points made in the other chapters of this thesis.

PART I. TAXONOMY

Taxonomy is the classification of organisms into species, species into genera, genera into families. Species, genera and families are all different taxonomic categories (see Appendix for more detail). Only that aspect of taxonomy which deals with the species category concerns us here.

Much taxonomy has stemmed from a desire to collect and classify organisms without any wish to find explanations or justifications for such classifications. But there are different ways of arriving at a classification and these different methods reflect different beliefs, in particular about the species concept. This is true even when different methods result in the same classifications or groupings. Indeed organisms are on the whole grouped into the same distinct species whatever method is used. Three different views on classification will be considered here: the first view is found in morphological classification, the second in cladistic classification and the third in biological classification (postponing a fourth view, *numerical taxonomy*, until the fifth chapter).

There is in the minds of philosophers another

classification which I shall not discuss here for the simple reason that it does not exist in biology. This is a classification of organisms according to their microstructure (genes or whatever).

1. Morphological Classifications

These classify according to phenotype (appearance). The method followed is sometimes referred to as typology since organisms are classified according to type specimens. For instance, this is a tiger if it looks like a standard or typical tiger. On this conception a species is therefore a type.

What justification can be given for classifying according to type specimens? Before Darwin the justification was that God had created organisms according to type. After Darwin some scientists in the 19th century like Agassiz, did not accept evolution and continued to hold this view. For Agassiz species have no reality in the world, the type itself exists but only as a thought in God's mind. Agassiz like all creationists believed that in the world there are representatives or copies of the type (God's thoughts made incarnate), and anything which does not approximate to the type is not of that species. New organisms only emerge with successive creations following God's plan. For Agassiz the aim of taxonomy is to uncover this plan: the biological world has a

rational basis which should appear in the relationships between species displayed in taxonomic classifications.

Virtually no biologist today holds this creationist's view. One exception however, is W.R. Thompson (1), a Canadian Entomologist, who believes that Darwin's theory has little evidence to support it and much against it. He points out that species appear suddenly in the geological strata, and that this is not the exception but the rule. There is a conspicuous lack of the interim species that would be needed to support evolutionary theory. Species, Thompson says (quoting Aristotle and St. Thomas), are like numbers. One cannot connect the numbers 2 and 3 by any intermediary, the transition from one number to the next is abrupt and not gradual. We shall come back to this question of saltation (jumps or discontinuity in evolution) later in the thesis. Thompson, following Agassiz, also holds the creationist's belief that characteristics of living organisms show finality, purpose and therefore design. But in this he is like other upholders of the argument from design, confusing function with purpose. The eye may function in such a way that we can use it to see, just as a stone may function as a dam if it falls in a stream. This, however, does not mean that its purpose is to be a dam any more than the eye's purpose is sight. Neither needs to have been designed in order to have a function. Functions can result from chance.

Although Thompson is an exception and creationism is not a serious scientific theory, morphological classifications are still more common in taxonomy today than any other forms of classification. The justification for classifying according to type-specimen is, of course, no longer given in terms of God's creation. The evolutionist's justification is merely that it is the most practical system of classification. A set of characters is chosen to be representative of a species. This set of characters becomes the 'type' for that species. The choice of a type is not directed by biological principles, but is arrived at by comparing the overall resemblances between organisms. No biological explanation is offered for this classification.

Morphological classifications present many difficulties:

(i) There are no rules or clear principles governing which characters are to be chosen as important in representing the type, because there are no biological principles to guide choice. There is also no criterion of what does or does not constitute a species if types are not seen as real in the sense in which they were for creationists, but rather as arbitrary conveniences.

(ii) More specific problems arise with difficult cases such as sibling species, where one has two groups of organisms which are manifestly distinct species

(they never mix, even when living in the same locality) and yet which 'look alike'. Sibling species are separate groups of organisms possessed of remarkable phenotypic resemblance. On the morphological criterion these groups should be classified as one species. Yet they cannot be one species because they only share looks, and in all other respects they are biologically different. For example, Drosophila pseudoobscura and D. persimilis do not interbreed, they differ in their chromosomes and in their ecology; and so they constitute two different groups, even though they have a similar morphology and live together (2). Criteria other than phenotypic resemblance have to be used to determine the distinctiveness of the group. Different species of European leaf warbler (Phylloscopus) are also impossible to distinguish visually, but they are readily identifiable by their different songs. At this point someone may say : why not group sibling species as one species using only morphological criteria for distinguishing species? However, finding other criteria which enables biologists to distinguish sibling species has led to many important advances in science. Preventive medicine is one example which I shall return to later in the thesis (Chapter Three).

(iii) There is third problem and this is the most serious one. Even if one could decide upon a type to represent a species, putting aside the problem of sibling species, such variation exists in nature that

no two individuals within any one species are exactly alike. In other words there are in fact different 'looks' within the same species. So not only is resemblance insufficient, it is not even necessary. If one chooses as the 'type' an adult, how does one classify larvae? Moths and their caterpillars are the same species. In many organisms males and females are quite different in appearance. For example, the females of very many different species of ducks are more similar to each other than to the males of their own species. It would be nonsensical to group all the females into one separate species. Within some species there are castes of individuals looking very different from each other such as the queen bee, the drones and the workers, but there is no genetic difference between the queen and her workers (3). Although castes of this kind are rare in organisms other than insects there is at least one mammalian case - the naked mole rat (Heterocephalus glaber) from Africa. In each population there is one large queen rat, two castes of small worker rats and one caste of male non-worker rats - for mating (4). In all these cases the individuals do not look alike and yet they all belong to the same species. Many errors in classifying organisms have occurred as a result of this. Linnaeus who followed a morphological system of classification, often unintentionally described males, females, young and adults as different species (5).

One of the most outstanding features of living organisms is their uniqueness. This third problem concerning morphological classifications needs emphasizing because it is pertinent to many points made elsewhere in this thesis. Before turning to the section on cladistic classification I intend, therefore, to spend the rest of this section outlining the importance of variety. (Cloning - where there is no variety, as individuals are all identical with a common ancestor - is an exception but clones are very rare.)

Typologists have attempted to account for variety. Since Aristotle variation from type has been held to result from some external interference with nature's programme; the environment somehow causing the natural intended development of an organism to change course. This hypothesis has had to account for the whole range of variations from small aberrations to monsters. But in truth variety is an important and not an incidental feature of organisms. In Drosophila it has been found that there is such immense variety in natural populations that there appear to be few characters that cannot be selected for (6). Variety has been at the basis of all domestic breeding and crop development. Natural variation has made it possible to breed cattle with greater milk yield, higher butterfat percentage, higher conception rate and so forth. Farmers select phenotypes and since most phenotypic characteristics

have some genetic basis, those selected tend to be passed on. (I.e. cows who yield milk with high butterfat percentage tend to have calves which will grow into cows who yield milk with high butterfat percentages and so on.) Another way of putting this would be to say that these variations are genetic since they breed true. Variations which were not directly caused by genes would not be passed on to future generations. Breeding by farmers merely illustrates the fact that for them at least variability has never been seen as an abnormality. On the contrary it is an important aspect of what a species is.

Variation that is not purely phenotypic, geographical or due to mutations is called polymorphism. Polymorphism refers to the genetic or chromosomal variation that exists within a species in a balanced state (7). On the whole when a population is not undergoing speciation, variation is constant from generation to generation. This is the Hardy Weinburg principle (this principle will be explained in greater detail in Chapter Three). Blood groups in man for example represent a polymorphism : the proportion of people with each blood group remains the same from one generation to the next.

It is therefore not true, within sexual species at least, that organisms approximate to a type. Variation exists at the phenotypic and genotypic levels. It is an essential part of what constitutes a species. No

one type within a species is a better or more typical representative of the species than any other. Which blood group could be said to be more typically human?

So far we have seen that variation does exist, now I wish to look at its role in maintaining a species. Variety is important for survival. If it were not for variety species could not adapt to environmental changes. Environmental change triggers selection for new phenotypes. This can be illustrated by an example: following industrialization, the peppered moth like many other species developed different colours, thus avoiding being conspicuous to predators against soot covered backgrounds. Such changes in phenotype are possible only because of the variety already available in the population, upon which the forces of natural selection can act : "For a species to remain in existence in the face of a constantly changing environment it must have sufficient heritable variation of the right kind to change adaptively" (8). Failing this it could become extinct. It is sexual reproduction which ensures that variety is maintained and that different combination of genes are tried out (9). In this respect sexual organisms have a definite advantage over nonsexual ones. Of course too much variation could prevent a species from being well adapted to its environment and from being able to reproduce successfully. (This is what would happen where genes were no longer compatible.)

Potential variation is not always actualized, indeed much variation is hidden in the genes and cannot be known to exist from looking at the phenotype alone. Much of this variation only comes to light in breeding programmes or at times of natural selection. Gene frequencies within a population are, to a large extent, dependent on natural selection. Genes which confer an advantage on the species are more frequent.

In sexual species all individuals carry two alleles (genes) for each phenotypic characteristic. A heterozygote carries two different alleles (an allele is a length of DNA coding for a particular characteristic or phenotypic trait - for more detail on genes see the Appendix), each allele coding for the same trait. A homozygote carries two similar alleles, for example blue eyes and blue eyes. Heterozygotes, therefore store more variation than homozygotes. A human individual may for example have one allele coding for brown eyes (inherited from his father) and one allele coding for blue eyes (inherited from his mother). On the whole only one allele expresses itself : the dominant one, brown eyes in this case. The other allele (the recessive one) may however be passed on to the individual's offspring. Variability is therefore preserved from generation to generation. All this means is that there is more variety within a population than can be seen by looking at the phenotype alone. It is possible for a

population to be composed entirely of brown eyed individuals and yet carry alleles for blue eyes. Hidden variations can be drawn upon in times of selection pressure.

Even without selection pressures, there can be a benefit to having hidden variation, this is what is sometimes called heterozygous advantage. In West Africa, for example, many people are heterozygote for the gene coding for haemoglobin (the oxygen carrying substance in red blood cells). Heterozygotes for this gene are rare outside Africa. Why? Research showed that one allele is the normal one for that trait (leading to the production of normal red blood cells), the other is a lethal one producing sickle cells (cells that collapse, becoming sickle shaped instead of round). Any individual who is homozygous for this second allele, and has two alleles coding for sickle cells, dies of anaemia before reaching puberty. But it also happens that a lethal form of cerebral malaria is endemic in the West coast of Africa. The malarial parasites reproduce in red blood cells. Those people who have the sickle cell trait but are heterozygotes (so are alive and healthy, the sickle cell being lethal only in homozygotes) have red blood cells which tend to collapse and therefore which do not last long enough for the parasite to reproduce itself. These people are at an advantage over homozygotes for normal red blood cells since the latter run the risk of dying of

malaria. In other words, both homozygotes (those with 2 alleles coding for normal red blood cells and those with 2 alleles coding for sickle cells), have high death rates compared with the heterozygotes (10). (In this situation both alleles are active and play a role expressed in the phenotype, the haemoglobin. To this extent it is unlike the case of a brown eyed heterozygote with a recessive blue-eyed allele which does not play any role.)

This was an example of polymorphism conferring advantage in heterozygotes at the chromosomal level. A good example of polymorphism at the phenotypical level conferring survival advantages to a group of individuals is found in the snail Cepaea nemoralis. Within a population there are brown, yellow and pink snails with and without bands of dark colours of varying widths. Why such variety here? These snails are eaten by predators hunting by sight. The banded ones are better camouflaged in hedgegrows, the unbanded ones are better camouflaged in woods or on open ground. So long as there is a variety of forms, some will survive (those which best match their habitat). Selection pressures maintain this variety (11).

We have just seen that variety is advantageous for species to maintain themselves. Variety is also drawn upon in the formation of new species. Since new species develop out of racial difference, the kind of variety which may lead to speciation can be found in

the differences between races. One of the most variable species within the British Isles is the field mouse Apodimus sylvaticus. This is surprising because its form is constant from China to Britain. But it is not constant in Britain where each island along the western coast has its own variety. Mice must have colonised these islands at different times. Each occupation of an island was probably made by a small number of individuals carrying their own selection of genes (travelling probably on the boats of Viking invaders, they tend to resemble Norwegian mice more than those of mainland Britain). Each race therefore developed its own form since it had just a small amount of variation within the colonising population and was isolated from the rest of the mainland population (12). In time these races could develop into distinct species.

In conclusion to this section we can say that although morphological classifications are frequently used, there is no future in the idea that the species is a group of individuals conforming to a type (where the type is a perfectly defined ideal to which the actual individuals conform to a greater or lesser degree).

2. Cladistic Classifications

Most methods of classification take two factors into account when deciding how to group organisms into

species, genera or families. One factor is the phylogenetic branching (which groups of organisms split off from which other groups and when they split off), the other factor is the amount of change or variation a group of organisms undergoes after splitting. Cladists avoid the problems encountered by morphological classifications by taking account only of the first factor. An added advantage of cladistic classifications is that they appear more natural since they are based on actual relationships between groups. Their classifications are based on relationship alone, and no amount of variation after splitting makes any difference to whether a group of organisms is classified as one species or another. This has important consequences for assigning organisms to species, genera or families and also important consequences for the concept of species itself. Cladists proceed by building a cladogram (a phyletic diagram) which shows which organisms gave rise to which, this is similar to the usual phyletic diagram used by other schools of taxonomy. (See, for example, the 4 different groups of imaginary organisms A, B, C, D in Figure 1). Cladists then translate this into a classification ignoring any change species may undergo in between splitting (see Figure 2).

A different taxonomic group emerges from each branching point. In Figure 2, there are 3 taxonomic

Figure 1 Phyletic diagram:

C and D are said to be more closely related than B and C, and so C and D are placed in the same taxonomic category (same genus or family) and B in a separate one. It could be that the organisms at C resemble those at B more than those at D morphologically or genetically; this would be the case if D had resulted from rapid evolutionary change after the splitting. Normally taxonomists would then place B and C in the same taxonomic category and D in a different one. Ranking (placing species in taxonomic categories) is usually done according to overall differences, but cladistics is

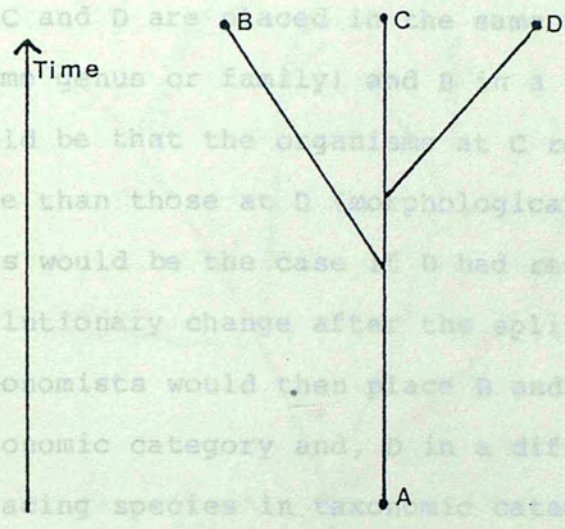
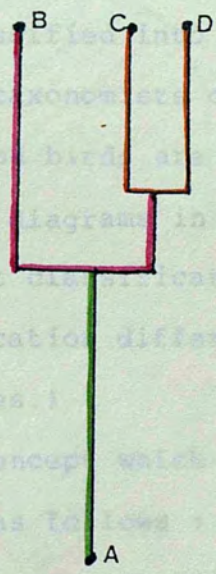


Figure 2 Cladogram:

ing to time of origin. This leads to different taxonomic groupings. One actual source of difference in ranking is that for cladists birds and crocodiles are classified in one taxonomic category, whereas for other taxonomists crocodiles belong to the reptile category and birds are in a category of their own. The phyletic diagram in Figure 1 illustrates these two different classifications. (In the cladistic classification different groups represent different categories.)



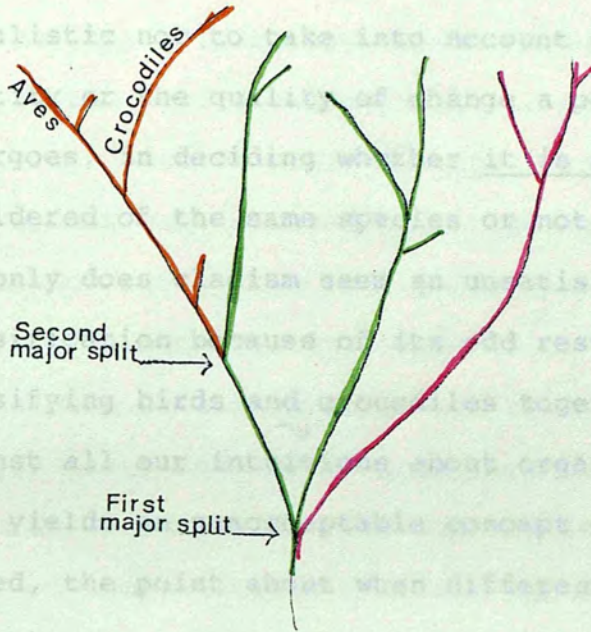
The species concept which results from cladistic classification is as follows: a species comprises all those organisms between two branching points in the cladogram (phyletic diagram). Any organism or species

A different taxonomic group emerges from each branching point. In Figure 2, there are 3 taxonomic groups each represented by a different colour. C and D are said to be more closely related than B and C, and so C and D are placed in the same taxonomic category (same genus or family) and B in a separate one. It could be that the organisms at C resembles those at B more than those at D (morphologically or genetically), this would be the case if D had resulted from rapid evolutionary change after the splitting. Normally taxonomists would then place B and C in the same taxonomic category and, D in a different one. Ranking (placing species in taxonomic categories) is usually done according to overall differences, for cladists it is done only according to time of origin. This leads to different taxonomic groupings. One actual example of difference in ranking is that for cladist birds and crocodiles are classified into one taxonomic category, whereas for other taxonomists crocodiles belong to the reptile category and birds are in a category of their own. The phyletic diagrams in Figure 3 illustrate these two different classifications. (In the cladistic classification different colours represent different categories.)

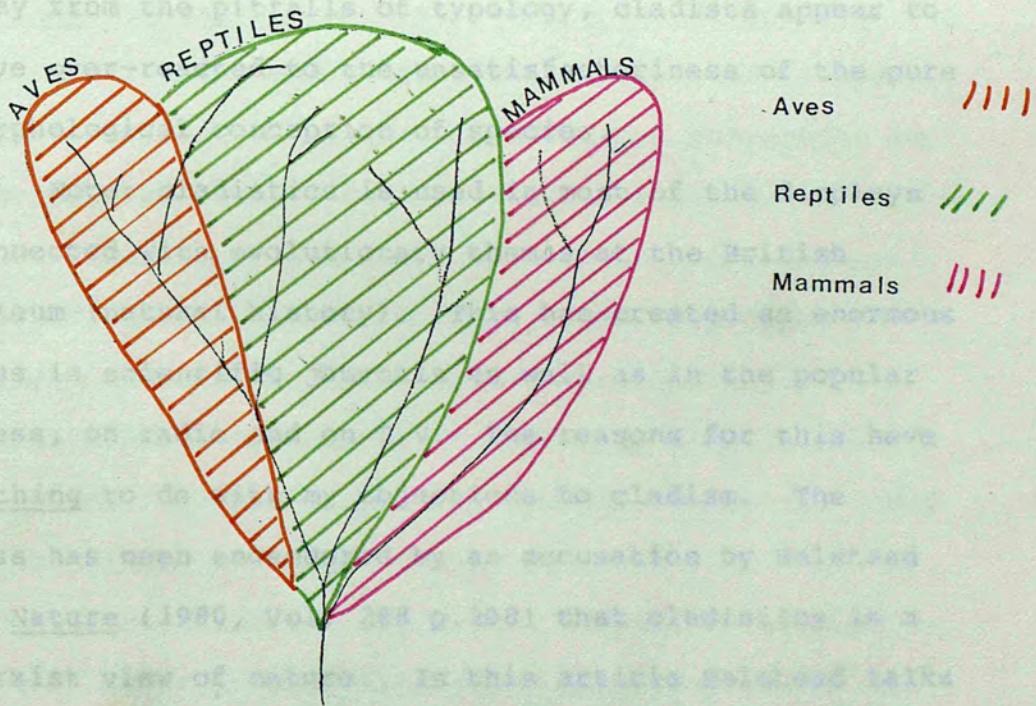
The species concept which results from cladistic classification is as follows : a species comprises all those organisms between two branching points on the cladogram (phyletic diagram). Any question of species

identity is irrelevant to cladists, species are given a purely formal definition, a species is those organisms between branching points

Figure 3 Cladistic classification:



Other classification:



identity is irrelevant to cladists, species are given a purely formal definition : a species is those organisms between branching points.

The gravest objection to cladism is that it seems unrealistic not to take into account either the quantity or the quality of change a population undergoes, in deciding whether it is still to be considered of the same species or not. For this reason not only does cladism seem an unsatisfactory method of classification because of its odd results (e.g. classifying birds and crocodiles together which goes against all our intuitions about organisms), but it also yields an unacceptable concept of species. Indeed, the point about when differentiation starts is not the same as the point concerning what a species is. Cladists seem to confuse the two. In an effort to get away from the pitfalls of typology, cladists appear to have over-reacted to the unsatisfactoriness of the pure morphological conception of species.

Note: cladistics is used in most of the displays connected with evolutionary themes at the British Museum (natural history). This has created an enormous fuss in scientific journals as well as in the popular press, on radio and on T.V. The reasons for this have nothing to do with my objections to cladism. The fuss has been engendered by an accusation by Halstead in Nature (1980, Vol. 288 p.208) that cladistics is a Marxist view of nature. In this article Halstead talks

of change - the emergence of new species - being gradual (as it is for many evolutionists), or sudden (as it is for cladists). For Halstead sudden change is revolutionary change. The fear that all this aroused was that the British Museum was presenting a Marxist view to the public under the guise of scientific authority. But as Gould (Nature Vol. 289 p.742) and many others have pointed out, cladism is not a Marxist plot. Not every view that holds that change occurs suddenly is necessarily committed to Marxism. Furthermore saltation (the view that evolutionary changes occur in jumps and not gradually) is not a view which is exclusive to cladism. It is doubtful whether views of these sorts are in any way derived from Marxist philosophy.

3. Biological Classifications and the Biospecies

A different and I think better reaction to the unsatisfactoriness of the morphological conception is what Mayr and others have called the biological classification. This takes both phylogeny and genetic knowledge into account, it also takes account of variety and change. To engage in biological classification as so conceived is to aim at grouping organisms into taxa reflecting natural groupings found in the living world.

Although the variety within a species is often just as great as the variety between species, the gap

between individuals has a different physiological basis from the gap between species. There is a relationship among organisms of one species quite different from the relationship between organisms from different species, and the relationship is much more than mere resemblance. In sexual species, this relationship is reflected in the fact that individuals of one species, however different morphologically, can interbreed in the wild (producing viable offspring); individuals from different species, however similar morphologically, cannot. So, in sexual species at least one criterion for sameness of species is interbreeding. Individuals within a species can interbreed because their genes (chromosomes) are sufficiently similar to be recombined during reproduction (see the Appendix for mechanisms of reproduction). The genetic make up of a species is part of the explanation of why a species is what it is, however varied its members may be. Biologists such as Mayr and Dobzhansky prefer the term gene pool to genotype since there is no type at the genetic level (14). This means that members of a species are more than a mere collection of individuals resembling each other. They are linked together by natural bonds. They form populations cohesively held together. In summary, the definition of a species adopted here is : a species is composed of populations which are reproductive communities, genetic units and ecological units (15). This is called the biospecies.

Since this concept is the one I shall favour throughout the thesis I now want to look at it in greater detail. The gene pool is the integrated collection of genes that make up the genetic component of a species : "all genetic information distributed among an interbreeding group of individuals collectively forms a gene pool, which is temporarily dispersed and held as a set of particular genotypes" (16), and it is "the entire effective population that is the temporary incarnation and visible manifestation of the gene pool" (17) (attempts to give formal conditions for the membership of gene pools will be explored in Chapter Four.) The gene pool explains both variation and inheritance, why individuals are like their parents yet different from each other. Seeing the species in this way explains how it can evolve and yet maintain its identity. It can evolve and maintain its identity because of the relationship and bonds between the individuals. As we have already said, in a given environment the amount of variation within a species remains constant (in the absence of migration, mutation and selection) (18).

A species is to a large extent a unique genetic response to a particular environment (19). The populations of a species form particular genetic and ecological groups. It is in this sense that the species concept is biological - it uses concepts which have no meaning outside the biological world (20).

The morphological species concept on the other hand has no specifically biological implications and "provides no guarantee that the species groups which it yields will be uniform with respect to biologically significant relationships" (21).

The genetic differences between species are often reflected in the morphological differences between them. Therefore biological species are usually morphological species. The genetic make up explains morphology, and on the whole similar phenotypes will result from similar genotypes, though the correlation sometimes comes apart. In addition to this we have already seen that there is more genetic information than can be seen expressed in the phenotype, so that although it is true that genes are only manifest when expressed phenotypically, a hidden gene may have a part to play. If one were to adopt the purely morphological criterion for species one would lose some of the information needed to group organisms into kinds. One would also be left with the need to explain why morphology is indicative of a species in the biological acceptance. Morphology does not have the same theoretical input as genetics. Nevertheless reference to morphology itself is necessary for any explanation of what a species is and how it relates to the environment, since the environment and selection pressures in particular can only act on the phenotype, which is the principal expression of the genes. The

genotype is more basic than the phenotype, but phenotypic terms are needed in a comprehensive account of what a species is.

The biospecies classification, taking into account general factors concerning species (gene pool, ecology and so on) seems to me the most satisfactory. However, many criticisms have been levelled against it and now I shall look at them in some detail.

(i) The gene pools for the vast majority of species are as yet unknown. Although this is the reason that many biologists give for rejecting the biospecies concept and preferring the morphological one, this is not a theoretical problem. It is at most a practical one.

(ii) It is often impossible to tell whether a population is an interbreeding group or not. Again this is a practical difficulty and not a theoretical one.

(iii) Species are not always reproductively isolated. Some species hybridize occasionally (eg. horse, donkey), some do frequently, and some species are progressively fusing through hybridization. For example, Pinus muricata and Pinus nemorata in California have been hybridizing since the Pleistocene, slowly forming one new species (22), this process is called secondary speciation (or introgression). Hybrids are much commoner in plants, no doubt because plants have simpler reproductive

systems : "the ability of a species to tolerate the presence of foreign genes is thus a function of the degree of complexity and integration attained by a system of genic determinants" (23). Grant adds here, by way of illustration, that one can build a good bicycle from old bicycle parts but not a good watch from old watch pieces. It is also possible that natural selection may favour hybrids in plants as a means of introducing new genetic forms into a species with simple genetic systems.

(iv) A fourth objection frequently raised against the biological species concept is that, because of hybridization, boundaries between species are vague. This is thought to imply that species in the natural world do not form sharply discrete units and fit badly therefore into the biological conception of species. It is said that this phenomenon undermines the strict individuation of gene-pools and therefore of species. The question of vagueness and of hybrids will be considered in Chapters Two and Three.

(v) A final objection is that some organisms do not reproduce sexually and therefore do not share a gene pool, although they do constitute a collection of genes. In these cases there is no reshuffling of genes at reproduction, although many asexual plant species do have mechanisms for exchanging genetic material prior to reproduction (for example, oats, wheat and barley have such mechanisms).

Among the different kingdoms of the living world, only half the species of protozoa are sexual (the asexual ones reproduce by fission). Many plants reproduce asexually (by bulbs or runners), nevertheless there are good biological species to be found in all major plant groups. In animals asexual reproduction is rare. When it does occur there is often an alternation of generations, one generation being sexual, the other asexual, thus providing some source of genetic variation in each alternate generation. This is the case for some jelly fish, the Medusa for example is the sexual swimming phase of the stationary non-sexual polyp. Other species form huge aggregates where some members are asexual, others sexual. The Portuguese man of war is a colony of polyps all attached to a large gas filled bag keeping them afloat. Each polyp plays a different role in the colony. Some have mouths for feeding, some have stings for defence, some have sexual organs for reproduction. All this gives us an idea of the range of asexual species, but generally asexuality is rare.

Asexual species are rarer than sexual ones because they are less able to adapt to new environments. They often represent "blind alleys" (24) from an evolutionary point of view. New genotypes cannot arise from re-combinations as in sexuality, but only from mutations or by polyploidy. Polyploidy is the doubling of chromosome numbers, and this can lead to the

formation of new species (for all these sources of variation see the Appendix). Although asexual species may seem a serious problem for the biospecies concept, they do form populations with recognisable genetic and ecological structures. It is also worth noting that in both plants and animals non sexual species have often been derived from sexual species, which suggests that sexual species are more basic. A study of their genes shows that "in most cases remnants of an organisation into biological species clearly persists" (25). For example plants often have flowers which are not used for reproduction, but were at one time. Sometimes they have remnants of flowers (26). In this case one could say that the biospecies is still applicable in as much as these species are derived from true sexual ones. One solution to the problem posed by asexual species would be to say that asexual organisms are not of a species. Under this view asexual species could be seen as one large organism or a clone (all the individuals in the species being descended from one individual zygote). Clones show little variation since they lack the import of new genes. V. Grant would prefer to call these species "binoms" since "clones" gives the idea of all individuals being exact copies of each other (which they are not necessarily in asexual species). Binom on the other hand suggests a whole polymorphic complex descended from one ancestor. One such example is the common bramble, Rubus fruticosus. It reproduces by

apomixis, i.e. seeds and fruit developing without fertilization. 2,000 different kinds of blackberry have been named as separate species (having slightly different morphological characters, different leaves, prickles, fruit). But it may be more reasonable to call them one large aggregate. This, however, still seems unsatisfactory since we want the individual instances (individual plants) to be organisms too. As Mayr says, this "overlooks the fact that the word species has not only the biological meaning of a reproductively isolated population but also the purely formal meaning 'kind of'" (27). If one accepts the biospecies concept, how is one to classify asexual organisms? Where there are sexual generations, or remnants of a gene pool, one can still see such groupings as true biological species; otherwise groupings must be made morphologically.

These are the five main criticisms of the biospecies concept and I shall return to some of them in the course of the thesis. At this point it will suffice to state my opinion that they do not show that the biospecies conception is inferior to the cladistic and morphological conceptions. The biospecies conception enables one to understand how species are related to each other genealogically: related species have a similar genetic make up (28). More importantly the biospecies enables one to see variation and change as essential to what a species is. This helps

understand domestic breeding as well as normal adaptations to new environments. Breeding is no more than the selection of some genotypes from the original population with a view to their adaptation to the specialised environment of the farmer (29).

Some have felt the temptation to see the question of species as an artificial or idle problem, answerable to nothing but a self-contained interest in classifying things for the sake of classifying them. I cannot hope to refute such a deeply mistaken view in one stroke. In advance of the conclusion of this thesis, I would simply point - for the benefit of those of a crudely instrumental attitude to theoretical questions - to the practical importance of correct classification for agricultural purposes. One may, for example, need to tell two similar sorts of beetle apart (one harmful the other beneficial) if one wants to use an insecticide. It may also be of practical importance in matters of public health, eg. in the identification of parasites and vector borne diseases. Here the biological species concept gives a more correct means of determining what is and what is not a separate species (that is to say when two populations should be seen as of different species). It would indeed have been impossible following the pure morphological concept to distinguish between the six sibling species of mosquito Anopheles maculipennis of which only three are vectors of human malaria (30). Programmes for the control of malaria

would not have succeeded if these had not been seen as different species. They are different species according to the biological species concept because their populations form different breeding units and different ecological units. Here good biological classification has made for insightful intervention into the workings of nature.

Finally good biological taxonomy (good in the sense of helping us to understand what species are and not merely how to identify them) has been the starting point for an increase in our scientific knowledge of the process of speciation (31).

PART II. THEORIES OF SPECIATION

Speciation is the process which leads to the formation of new types of organisms. Speciation can occur by phyletic evolution, that is to say through change over time. It can also occur by the splitting of one species into two groups followed by the divergence of each group. In practice, two forms are said to belong to different species if they are morphologically and genetically so distinct that they cannot interbreed (or even if they can still mate, fail to produce fertile offspring). If one observes that two populations for one reason or another do not in fact interbreed in their normal environment, then again however morphologically or genetically similar they may

be, they are said to be of different species (32).

Speciation is brought about in several ways. It can only be identified once the process is complete, but it is the initial step that is crucial in establishing a new species. Although the initial step is crucial - e.g. one population's becoming isolated geographically after a volcanic eruption - it is what happens to the group after this that determines whether it becomes a new species or not. All mechanisms of speciation are isolation mechanisms of some kind. Isolation gives new genes a chance to get established. Whereas they might have been swamped in a large group of organisms, they can have some impact in a small group of organisms. As new traits are selected, a group of organisms that finds itself in isolation or in a new environment, will fail to maintain its genetic and phenotypic identity. There are four isolating mechanisms :

1. Geographical Isolation

If a population becomes geographically isolated from the rest of the species, then it is highly likely that in the course of time it will be reproductively isolated. Following the accumulation of new genetic variations (eg. through mutations), it may become a new species. This sort of speciation is found where there are geographical barriers enabling small isolated colonies to develop their own gene pools. Islands

furnish a good example of such developments. First one has islands with populations showing merely racial differences. These populations are not fully separate species and can still interbreed. This is the case of the British field mouse mentioned earlier. And secondly there are cases where the races are closer to speciation, as for example with the plant Nigella degenii in the Aegean area. This species is divided into subspecies which interbreed but at a lower than normal rate of fertility (See Figure 4).

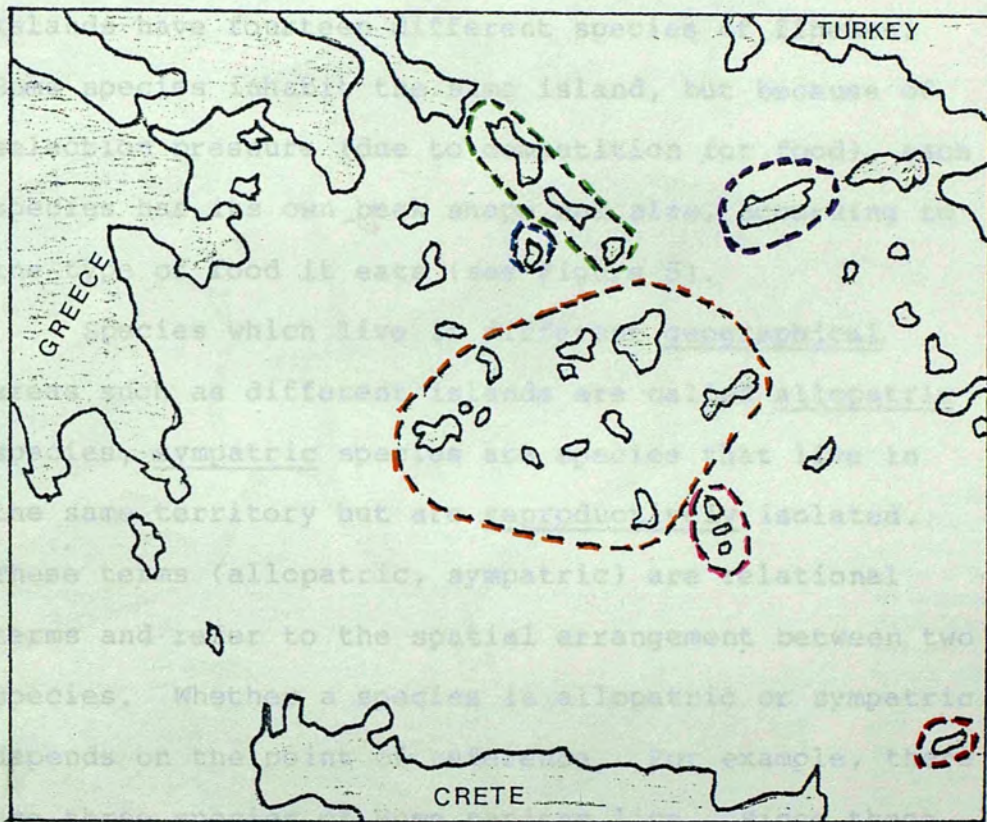
(This figure is taken from V. Grant, Organismic evolution, p.167.)

Finally, one finds complete isolation and consequential diversification. An example is furnished

by the animals of the Galapagos Islands, Darwin's

Figure 4 Geographical isolation (Nigella degenii)

by the animals of the Galapagos Islands, Darwin's
presumably they are descendants from the finches which
originally came to the Galapagos Islands and then
diversified as a result of geographical isolation. The



Scale 0 10 20 miles

N. d. barbra ———

N. d. jenny ———

N. d. degenii ———

N. d. minor ———

N. icarica } species closely related

N. carpatha } to N. degenii

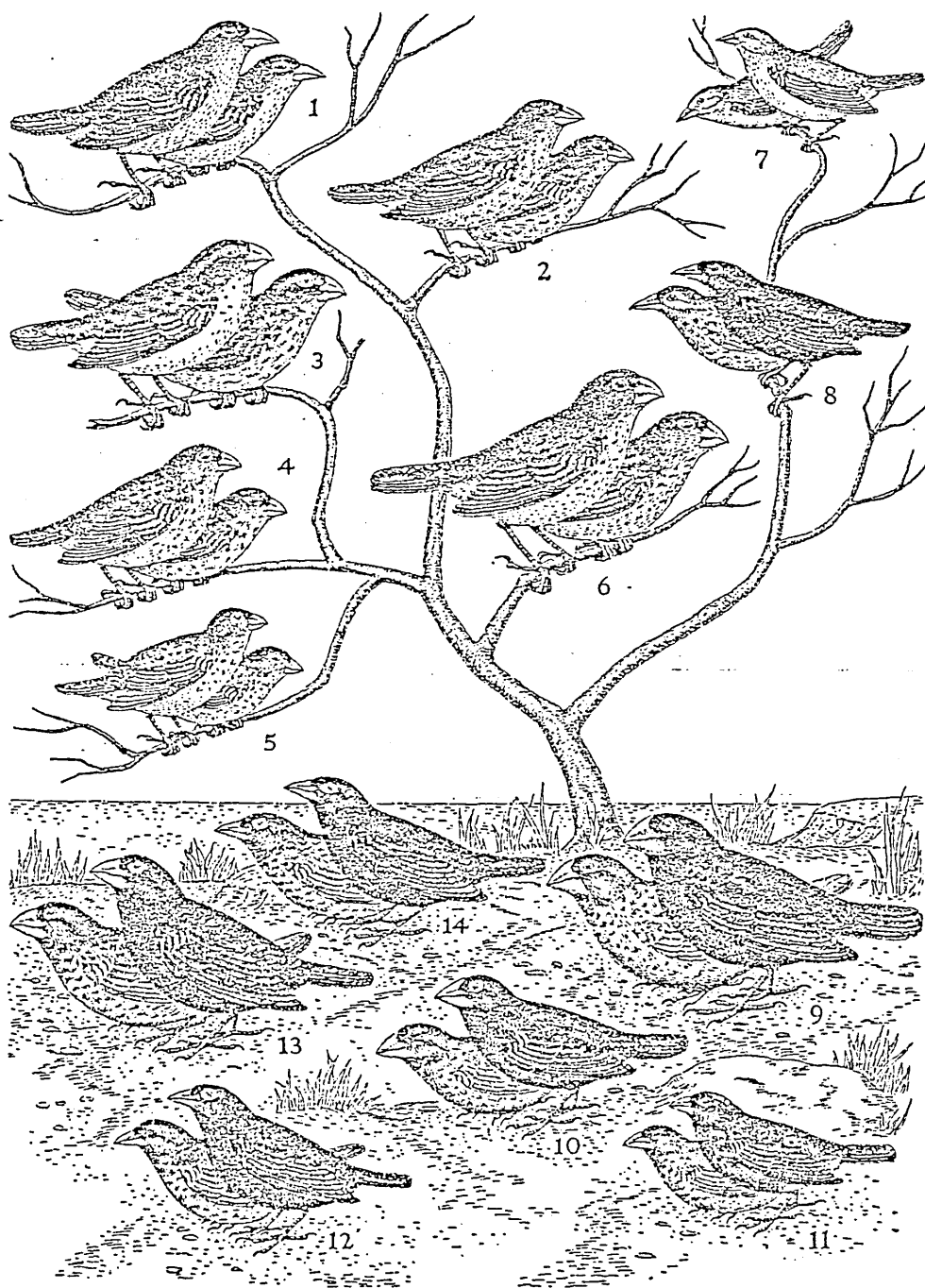
(N. arvenos proper in the

rest of Europe)

Finally, one finds complete isolation and consequential diversification. An example is furnished by the animals of the Galapagos Islands. Darwin's finches resemble those of mainland South America, and presumably they are descendants from the finches which originally came to the Galapagos Islands and then diversified as a result of geographical isolation. The Islands have fourteen different species of finches. Some species inhabit the same island, but because of selection pressure (due to competition for food), each species has its own beak shape and size, according to the type of food it eats (see Figure 5).

Species which live in different geographical areas such as different islands are called allopatric species, sympatric species are species that live in the same territory but are reproductively isolated. These terms (allopatric, sympatric) are relational terms and refer to the spatial arrangement between two species. Whether a species is allopatric or sympatric depends on the point of reference. For example, there are three species of Homo sapiens lice. Since these can live on the same members of the species in all parts of the world, they are sympatric. But if instead of taking the world as a point of reference, we take a human being, then the three species are allopatric since one species inhabits the axillae (Phthirus pubis), one the head hairs (Pediculus capitis) and the third the body (Pediculus humanus) (33).

Figure 5 Darwin's finches



Darwin's finches: an illustration of natural selection. The fourteen species of Darwin's finches are arranged to suggest the evolutionary tree of their development, divided broadly into ground finches (*geospiza*), the earliest form, and tree finches. Of the tree species, 1 is woodpecker-like, 2 inhabits mangrove swamps, 3, 4 and 5 are insect-eating, 6 is vegetarian, 7 is a single species of warbler-finch, 8 is an isolated species of Cocos Island finch. Of the ground finches, 9, 10 and 11 are seed-eaters, 12 is sharp-beaked, 13 and 14 are cactus-eaters (from *Scientific American*, April 1953. Courtesy of David Lack and *Scientific American*).

Darwin's finches comprise some allopatric species and some sympatric (those which inhabit the same island, but have diversified into different species through competition for food). The deer family (fallow deer, roe deer, red deer, moose, reindeer) is another example of reproductively isolated species living in the same regions. They are sympatric species. It is not known what gave rise to such breeding barriers between the different deer species, but the outcome has been different species with no genetic exchange (34).

2. Genetic Isolation

Many biologists believe that most speciation has taken place not on islands but on continents. It may be, therefore, that genetic mechanisms have sometimes been the initiating factor in speciation (35). We know that variation accumulates within a species before there is geographical isolation. It must therefore be possible for genetic differences to arise between two groups without physical isolation.

The phenomenon of polyploidy affords a different sort of case of speciation following genetic differentiation. Polyploids are common in plants but rare in animals. When the chromosomes from the parents are doubled the offspring are tetraploid and have four sets of chromosomes instead of two. When they are trebled the offspring are hexaploid with six sets of chromosomes. When they are quadrupled the offspring

are octaploid with eight sets of chromosomes. So long as the numbers are even the new organisms can reproduce. Polyploids are separate from their ancestors because any hybrids between them and organisms similar to their ancestors would be sterile. The reason for this is that the hybrid would have an uneven number of chromosomes (36). A diploid parent and a tetraploid parent for instance would contribute each 1+2 chromosomes to their offspring (a total of 3). New polyploid species have their own morphology. They usually have, for example, larger cells which result in thicker petals or leaves. They also have their own physiology and their own ecology. Polyploids are very common in the wild amongst ferns where 95% of fern species are polyploids. This sort of speciation is also extensively exploited in crop development: cotton, bread wheat, tobacco are usually polyploids (37).

3. Ecological Isolation


New species may evolve when a population develops new environmental habits. For example Pinus radiata and Pinus attenuata are seasonally isolated. One sheds its pollen in February and the other in April. This has meant that they are effectively isolated reproductively, and so represent two different species. The same isolation is found in the sibling species of flies mentioned earlier : Drosophila pseudoobscura and Drosophila persimilis. They share the same

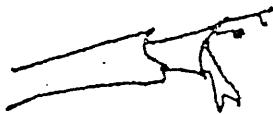
breeding season but one is sexually active at night and the other by day (38). Other species have different ecological requirements which can result in a mechanical isolation. For example, Salvia mellifera and Salvia apiana are pollinated by different bees. A species of large bees pollinates Salvia apiana and a species of small bees pollinates Salvia mellifera. Small bees cannot, for mechanical reasons, pollinate Salvia apiana. Apart from this there is very little difference between the two species of Salvia. Occasionally these two species do form hybrids when they are accidentally pollinated by medium sized bees (39) (see Figure 6).

4. Ethological Isolation

Two species may be isolated because they have different behavioural patterns. The members of a species often recognize each other because of certain

Figure 6 Ecological isolation

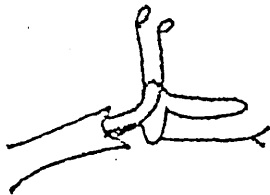
Scale : 1cm 



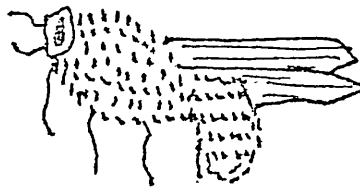
Salvia mellifera



Anthophora



Salvia apiana



Xylocopa brasilianorum

(Carpenter bee)

This figure is taken from V. Grant Organismic Evolution, p.180.

behavioural patterns. If one group for example developed new courtship patterns, it would not be recognized by other members of that species. Bufo viridis are a group of green toads which call to each other. They have developed into different species following a division into different breeding groups, each group with a different voice (40). Something similar has isolated two species of wolf spider, Schizoloza ocreata and Schizoloza rovneri, in the United States. Both species of male approach their mates by making noises. Schizoloza ocreata by tapping their legs and clicking, and Schizoloza rovneri by press-ups on the legs and rapid clicking. If females are rendered insensitive to the noises, they mate with either species of male and produce fertile offspring (41).

It is important to note that some species are distinguished by behavioural patterns which are learned and not innate. For example, different species of gulls in Britain have different sequences of calls and displays in courtship. These are learned and not innate. The Herring gull and the Lesser black backed gull in Britain are interfertile. But they do not breed. The barrier is behavioural and learned. Mate selection by the female depends on ring colour around the male's eyes, which are different for each species. Young chicks learn these colours when newly hatched (by the process of 'imprinting'). If they are hatched in

the other species' nest, they will recognize them as potential mates when they grow up instead of individuals from their own species.

Competition leads to speciation, different groups occupying the same area (sympatric groups) may diversify slightly thus avoiding competing for scarce resources. This speciation can be maintained by different forms of behaviour.

All these forms of isolation lead to speciation and also serve to keep species separate. They all result in a failure to mate, or in a failure to fertilize (if for example gametes are incompatible), or in a failure of the offspring to survive. This later case would include zygote mortality, hybrid unviability, hybrid sterility and even reduced fertility for hybrids (these would be found in species in the process of speciation). Usually several isolating mechanisms operate at the same time to keep species apart.

The above examples illustrate how reproductive organisms form units in which each organism recognizes its own kind. If this were not so they would not mate. Indeed in the case of the spiders mentioned above, if the female does not recognize the male's noise she mistakes the male for food and eats him. The problem of recognition is acute in some species such as the Angler Fish who live in semi-permanent darkness where it would be difficult to

find let alone recognize ones mate. These fish have resorted to being attached together from birth. The male is a third to half an inch long and the female reaches two feet. They attach after hatching and their union is so perfect it is difficult to tell exactly where the female ends and the male begins. Even their two blood streams connect, the male drawing his food from the female's blood (42).

All the various types of speciation reviewed here, illustrate the need to see species as unique genetic systems. The examples also point to the dynamic nature of species. The biospecies concept is the best means we have to do full justice to those considerations simultaneously.

PART III. CONCEPTS IN ECOLOGY

Ecology is the study of the interaction of organisms with each other and with the non-living world. It is not simply the study of some kind of fixed balance of nature. Indeed organisms change the world they live in. Plants for example change the nature of the soil they grow on. Grazing cows maintain the grass in a field, preventing it from returning to scrubland. The relationship between living and non-living things is an active one. Since the environment itself also changes independently from the species living in it, evolution is not the adaptation

of species to something fixed, but the repeated adaptation of species, constantly keeping pace with the changes in their environment: "Natural selection over the long run does not seem to improve a species' chances of survival but simply enables it to "track" or keep up with the constantly changing environment" (43). To continue the description of what constitutes a species, I shall look at four different concepts in Ecology: the ecosystem, the niche, adaptation and species-specific relationships. All these will emphasize the close relationship species have with their environment and the need to take this into account when deciding on the definition of species.

1. The ecosystem

A basic concept in ecology is the ecosystem. The ecosystem is defined by the workings of climate, soil, bacteria, fungi, plants and animals within a particular area. It embraces both the abiotic environment (organic and inorganic) and the biotic environment. The biotic environment is divided into producers (organisms which convert energy from the sun), consumers (organisms which get their energy by eating plants or animals), and decomposers (organisms such as bacteria which recycle nutrients). Figure 7 shows the energy flowing through a community of organism in an ecosystem.

Figure 7 Energy flow diagram

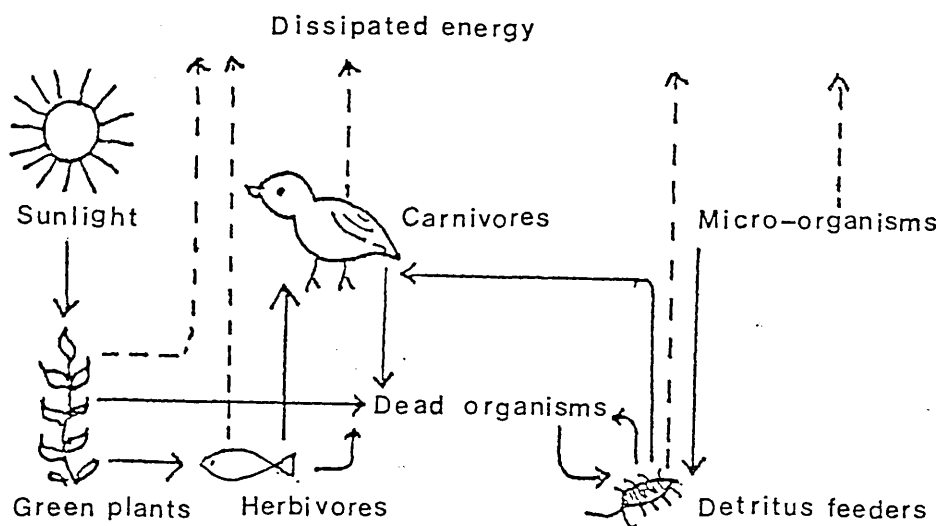
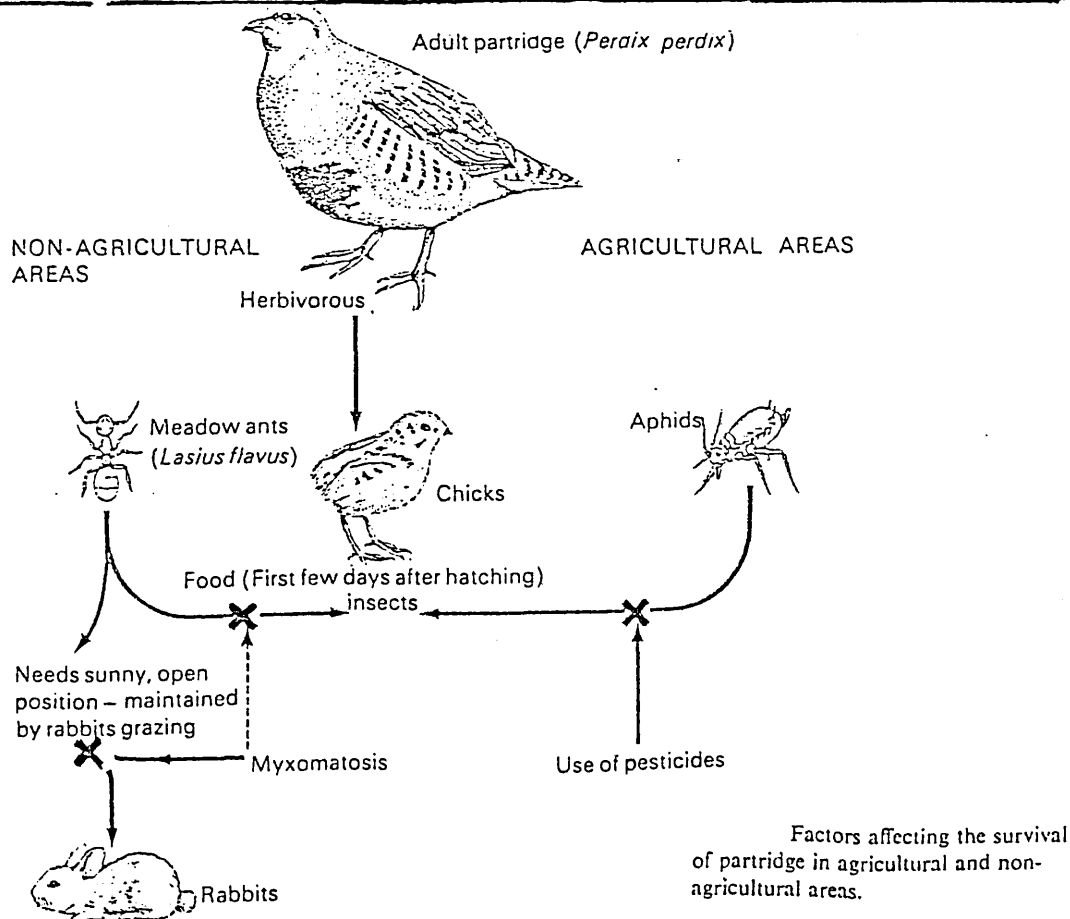


Figure 8 The partridge's niche (from Open University course S323 unit 12 p.8)



For any organism the rest of the ecosystem represents its niche.

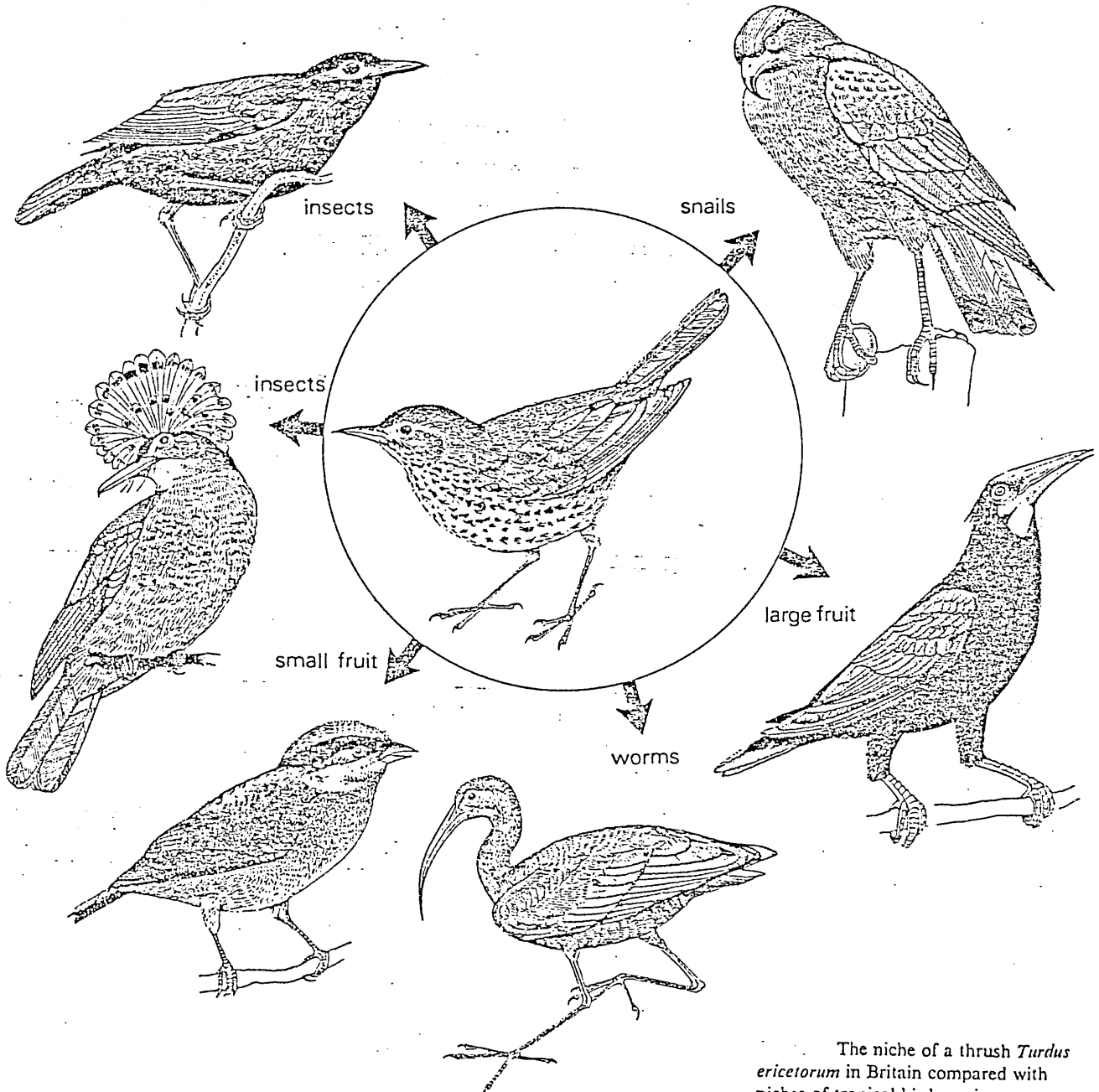
The whole system can be quite fragile, for example part of the partridge's niche includes aphids, rabbits and ants. Figure 8 is an illustration of the ecological factors which could affect the partridge's survival.

2. The niche.

The niche corresponds to the total range of conditions under which an individual, or even a population or a species, lives and replaces itself. Different species may occupy the same kind of niche, for example kangaroos in Australia and bison in North America live in the same type of environment. Other species can live in a variety of niches as for example human beings do. Large numbers of organisms making up an ecosystem can add to the stability of the system, and to the stability of each organism's niche. An organism's niche will vary according to the amount of competition the species encounters from other species within the same ecosystem. For example the white eyed bird Zosterops palpebrosa, lives at a high altitude in Burma where it has little competition. But in Malaya and Borneo where other species of Zosterops live and occupy the higher zones, Zosterops palpebrosa lives in the lowlands because the competition is so intense higher up (44). Another

example is the warbler in the North East forests of America, which lives at three different levels within the same area : the Cape May warbler (Dendroica tigrina) and Dendroica fusca live in the upper crown of the forest; Dendroica virens and Dendroica castanea live in the middle crown; Dendroica coronata in the lower crown (45). As we saw earlier competition leads to specialization and therefore speciation. If a species cannot adapt to a special niche in the face of competition, it becomes extinct. There is also a difference between regions of the globe. In the tropics, where seasonal fluctuations are minimal organisms can specialize and adapt to narrow niches. In temperate climates the seasons change dramatically, and organisms need to be adapted to a wide variety of niches to survive the seasons. The niche of the thrush Turdus ericetorum for example has to be equivalent to the niches of six tropical bird species to enable it to cope with the seasons (see Figure 9. From Open University Course S323, Unit 14 p.29).

Figure 9 The thrush's niche

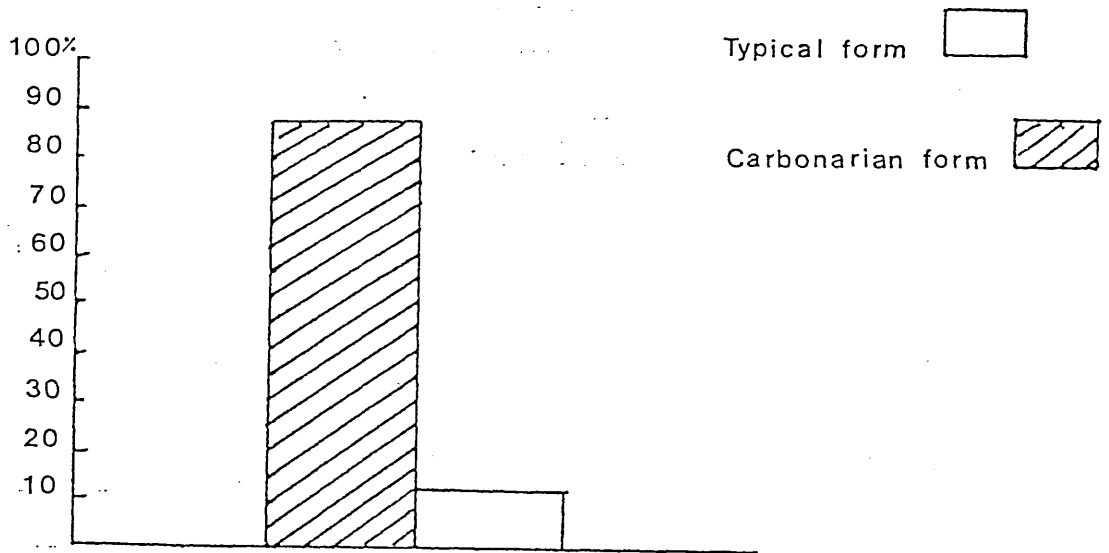


The niche of a thrush *Turdus ericetorum* in Britain compared with niches of tropical bird species.

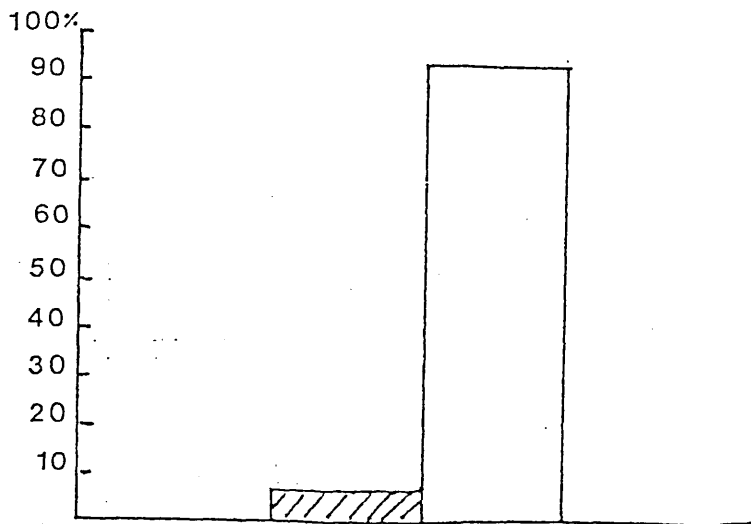
3. Adaptation

As the environment changes, species change with it—drawing upon the store of variation within their gene pools to adapt. One of the best known examples of this is the peppered moth Biston betularia (mentioned earlier). Within a normal population nearly all the moths are speckled grey (the 'typical form') and a few individuals are dark (the 'carbonarian form'). The moths live on tree trunks. These trees are usually covered in lichen, and the typical form is well camouflaged against predation by birds hunting by sight. Following the industrial revolution lichen disappeared and tree trunks were covered in soot around towns such as Manchester. Consequently, the carbonarian form proved better adapted and the common grey form became rare, since it was now conspicuous to predators hunting it. The cause of the change from grey to black in the peppered moth was selective predation following environmental change. In 1848 there were less than 1% of Carbonaria in the Manchester area, by 1898 these represented 95% of the Biston betularia moths (46) (see Figures 10 and 11).

Figure 10 Adaptation of the moth Biston betularia



Birmingham polluted



Dorset wood unpolluted

From: J.R. Berry Inheritance and Natural Selection,
p.122.

Figure 11 Biston betularia



Typical and carbonarian form of Biston betularia on soot covered bark (above) and on lichen covered bark (below).

This phenomenon is known as industrial melanism. It occurs also with ladybirds (Adelia bipunctata). In this case though, it is not due to predation but to the fact that dark ladybirds (black with red spots) can absorb more radiation. This is an advantage in areas where smoke reduces the amount of sunshine, as for example in Liverpool and Glasgow where 97% of ladybirds are black (47). Other examples of environmental change and species adaptation are found in pest resistance to poisons such as DDT (all house flies Musca domestica in Denmark are now resistant to every safe insecticide known) (48), and in bacterial resistance to antibiotics and so forth.

Organisms constantly adapt themselves to a changing environment. Resistance to DDT takes only two years to accrue in flies and mosquitoes (49). Selection pressures from the environment are constantly at work, thereby helping to maintain or select certain characteristics of a species. For example mosquitoes in the wild will need the ability to suck blood fast. If they are too slow they get killed by their host. 90% of wild mosquitoes can bite and get away with it, only 59% of mosquitoes reared in laboratories can manage this feat. Inefficient mosquitoes do not survive in the wild (50).

Other species do not change with environmental changes by adaptation and by natural selection, but instead have within themselves an adaptive genetic

mechanism which causes an existing population to change its form instead of being eliminated in favour of other better adapted forms. The desert locust Shistocerca gregaria has two forms, solitaria and gregaria. Until 1911 these different forms were named as different species. These two forms do not represent some type of polymorphism since both forms are not found together in any population of desert locust. It is rather that the desert locust as a species adopts one form or the other according to environmental conditions. Usually the species is composed of solitary grasshoppers, but occasionally these swarm. Swarming occurs as a result of changes in climate, heavy rain causing many eggs to hatch, or strong winds blowing grasshoppers together. It seems that crowding and density of population is what determines the change. The transition takes several generations. During this time the locusts change, crowding leading first to behavioural changes, which then lead to physiological changes, which lead to morphological changes (in sizes, shape, colour). The solitaria also has a high fecundity and a short life, the gregaria a low fecundity and a long life. These changes mean that the locust in the gregarian form is capable of sustained flight and of swarming (51). Other species such as aphids reproduce either sexually or parthogenically (virgin birth). They produce wingless individuals when the food supply is good and

winged individuals (by sexual reproduction) when conditions become crowded, thus enabling individuals to fly to better feeding grounds (52). Such alternation of methods of reproduction and morphological forms, following external conditions, is not uncommon in other species. Some species only metamorphose when conditions become harsh. The Axolotl (the larval form of an American species of Salamander) is an example of this. There are twenty different species of Axolotl. The Axolotl usually lives in water and remains at the larval stage throughout its life, but sometimes changes into a salamander and takes to dry land if the food in the water becomes scarce. So long as conditions are good it can reproduce itself while still in the larval stage:

The Axolotl and the Ammocoete (53)

Amblystoma's* a giant newt who rears in swampy waters, As other newts are wont to do, a lot of fishy daughters:

These Axolotls, having gills, pursue a life aquatic, But, when they should transform to newts, are naughty and erratic.

They change upon compulsion, if the water grows too foul,

For then they have to use their lungs, and go ashore to prowl:

*Amblystoma is the generic name for Axolotl.

But when a lake's attractive, nicely aired, and full of food,

They cling to youth perpetual, and rear a tadpole brood.

All these variations exist in the genetic make up of each individual organism within the species, and go towards illustrating the importance of a store of latent variety within species. Different genes can express themselves at different times, or the same genes can express themselves differently, the explanation always depending on the environment:

"there are many possibilities for the gene products which are the raw material of an individual. They are like butcher's meat: it can be stewed, roast, fried or grilled, under done or over done, seasoned or plain, sliced or served whole all our characteristics are the result of an interaction between genes and the environment and usually between different genes as well" (54). This is seen in the examples given. Even more immediate results may be observed in the case of flamingoes, which go white if they do not eat pink food (such as shrimps). Another example is Siamese cats which develop black fur on the colder parts of their bodies, usually on their toes, noses and ears but also on any part which has been shaven (55).

4. Species-specific relationships

There is a special relationship between a predator

and its prey which is species-specific and usually remains stable. If predation increased the prey would run the risk of extinction, with the result that the numbers of predators would then decline. Population sizes of predators and prey therefore regulate each other. A similar relationship exists between parasite and host (a form of predation). In this way many species evolve together. Many parasites and hosts have synchronised fertility cycles, so that when the young hosts are born, young parasites are ready to colonize them. This occurs in rabbits and rabbit fleas for example. Other species depend on each other for survival in more complex ways : there is for instance the mite, Digamasellus which hitch-hikes on the mushroom fly, Lycoriella auripila, in order to get to the mushrooms on which it feeds. This mite can also develop wings if conditions get bad and there are no mushroom flies around (56). The British large blue butterfly (now extinct?) relies on ants to feed its larvae with the ants' grubs. In return the larvae secrete a sweet substance for the ants to eat. The ants even pick up the larvae which fall off thyme bushes where the butterfly lays her eggs and then transport them back to their ant nests (57).

This sort of co-evolution is extremely common between flowers and the insects which pollinate them. In some cases flowers are pollinated by animals (insects, birds, bats and some other mammals), wind and

even water. In other cases they are self pollinating. Most commonly pollination is by insects. Insects are usually faithful to the species they pollinate. Obviously this is important if pollination is to succeed. Flowers need to be easily recognizable and need to advertize themselves with particular shapes, colours and textures. They need also to provide landing places and food to attract the insects. "The origin of flowers as we know them must ... be closely bound up with the evolution of the flower-insect relationship The evolution of flowers and insects proceeded hand-in-hand" (58).

Flowers often have rigid and specially adapted structures to ensure contact with visiting insects. Insects and bees in particular have evolved different sorts of pollen collecting devices, baskets on legs for example. Flowers open at particular times of the day to fit in with the habits of pollinating animals (and also to avoid getting wet with dew at night). Pollination involves collecting pollen (a spore containing two sperms and a third cell) from the stamen (male organ) and transporting it to the stigma (female organ). Then the process of fertilization starts and the pollen is transported to the ovary. Plants usually avoid self-pollination. Mechanisms which prevent self-pollination present an advantage because self-pollination reduces the amount of variation, such mechanisms are therefore favoured in the selection

process. Self-pollination is avoided by having the stamens mature at an earlier stage than the stigma, or by having a mechanism which prevents the pollen from reaching the stigma. Some plants can only be pollinated by different varieties of the same species. Apple trees for example need a different variety of apple tree to pollinate them. Most flowers attract insects by offering them food (nectar or pollen), and then while the insect is feeding ensure that it collects the pollen and thus transports it to the next flower. Meadow sage, Salvia pratensis is one of many such flowers. It is pollinated by bumble bees and in order to suck the nectar inside the flower the bumble bee has to touch a lever that results in the pollen being stamped onto its back. The stigma matures later and the pollen attaches itself to the stigma from the bumble bees back following the same mechanism (59) (see Figure 12).

The previous example illustrates the reliance between species on the capacity of recognition of other species.

Figure 12 Meadow sage and bees

Another example which exploits recognition is that of flowers which attract insects by exploiting their sexual drive: fly orchids (*Cypripedium*).

Sage flower Salvia

Some orchids resemble the female wasp, the male pollinates the orchid by copulating with it.

Some orchids are pollinated by being attacked by bees. Bees are attracted by being attracted by a lever.

Some orchids (*Coryanthes* and *Gongora*) intoxicate bees with their scent, or with certain fluids, so that the bees fall into a reservoir out of which they cannot escape.

Some orchids pollinate the flower by using their wings. These last relationships benefit the flowers but not the insects.

Where the relationship is mutually beneficial it is called symbiotic. Such relationships exist between many organisms apart from flowers and their pollinators.

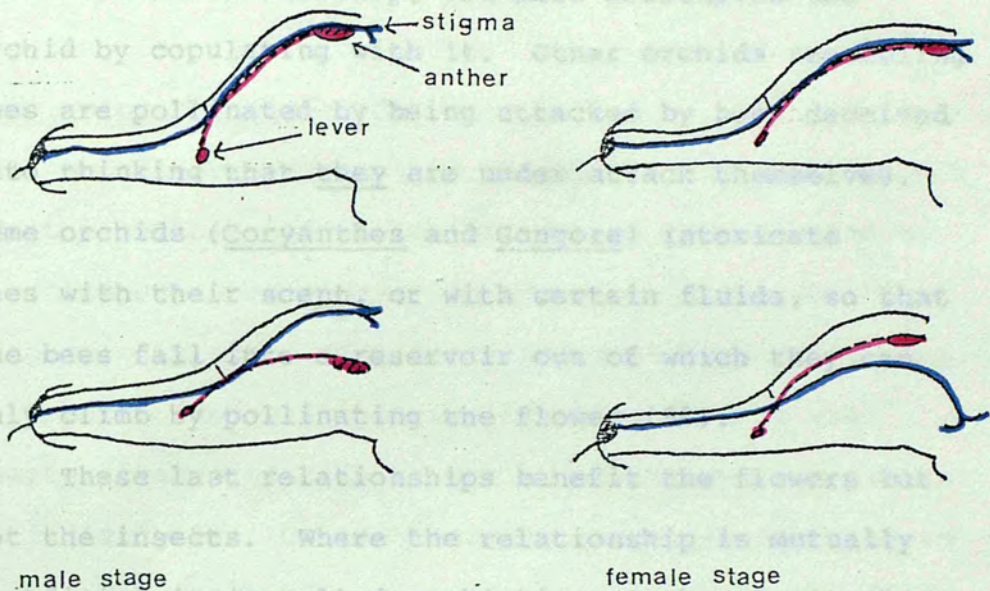
There are, for example, birds which live on the backs of water buffaloes feeding on their parasites. Other species of birds live with crocodiles.

Food between them, thereby cleaning their teeth for themselves.

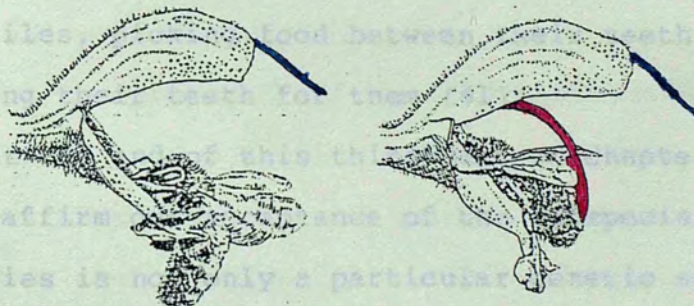
One can reaffirm the concept of a species as a particular ecological system. A species is not only a particular genetic system, it is also a particular ecological system.

This concept enables one to explain reversible change such as in the axolotl or even the peppered moth.

In these cases



Bee entering sage flower (from British Museum - Natural History - leaflet on bees)



The previous example illustrates the reliance between species on the capacity of recognition of other species. Another example which exploits recognition is that of flowers which attract insects by exploiting their sexual drive: fly orchids (Ophrys insectifera) resemble the female wasp, the male pollinates the orchid by copulating with it. Other orchids resembling bees are pollinated by being attacked by bees deceived into thinking that they are under attack themselves. Some orchids (Coryanthes and Gongora) intoxicate bees with their scent, or with certain fluids, so that the bees fall into a reservoir out of which they can only climb by pollinating the flower (60).

These last relationships benefit the flowers but not the insects. Where the relationship is mutually beneficial it is called symbiotic. Such relationships exist between many organisms apart from flowers and their pollinators. There are, for example, birds which live on the backs of water buffalos feeding on their parasites. Other species of birds live with crocodiles, picking food between their teeth, thereby cleaning their teeth for them (61).

At the end of this third Part of Chapter One, we can reaffirm our acceptance of the biospecies concept. A species is not only a particular genetic system, it is also a particular ecological system. This concept enables one to explain reversible change such as in the axolotl or even the peppered moth. In these cases

change, although permanent for the individual, is reversible as far as the species is concerned. It is only because we know that genes are maintained in the gene pool (even if they are not phenotypically expressed) that we can account for phenotypes recurring predictably with specific environmental changes.

Conclusion to chapter One

What emerges from this chapter is the necessity to adopt a certain definition of species (represented by the biospecies concept). In addition, although the chapter only aimed at a descriptive account of species, it appears from all the examples described in the chapter that a species is not an arbitrary aggregation of individuals. On the contrary, there seems to be an accepted understanding among biologists that specific relationships hold between the individuals which make up a species. This points towards the view that species are not artificial classifications of the mind, but represent real entities in nature. The point will be argued more fully in Chapter Three.

For the present, having seen that scientists describe organisms as unique but as falling into distinct kinds, we are now in a position to ask the following philosophical question : if species are real, what sort of entities are they? This question is addressed in the next chapter.

References

- (1) W.R. Thompson "The status of species" in Problems in biology, V.E. Smith (ed.).
- (2) See L.E. Mettler and T.G. Gregg Population, genetics and evolution, p.20.
- (3) R.J. Berry Inheritance and natural history, p.481.
- (4) See Science Vol. 212 (1981), p.571.
- (5) See E. Mayr Evolution and the diversity of life, p.481.
- (6) See R.C. Lewontin The genetic basis of evolutionary change, p.92.
- (7) See R.J. Berry op.cit., p.18 and V. Grant Organismic evolution, p.17.
- (8) R.C. Lewontin "Adaptation" Scientific American (1978), p.159 and also F.J. Ayala "The mechanisms of evolution" Scientific American (1978), p.53.
- (9) See R.J. Berry, op.cit., p.89.
- (10) See R.J. Berry, op.cit., p.69 and C. Patterson Evolution, p.77.
- (11) See E.B. Ford Ecological genetics, chapter 9 and R.J. Berry, op.cit., p.149 and also C. Patterson, p.85.
- (12) See R.J. Berry, op.cit., p.201ff.
- (13) Point made by Sober in "Evolution, population thinking, and essentialism" Ph. of Sc. 47 (1980), p.356.

- (14) See E. Mayr Animal species and evolution, and T.H. Dobzhansky, F.J. Ayala, G.L. Stebbins and J.W. Valentine Evolution.
- (15) See E. Mayr Evolution and the diversity of life, p.502.
- (16) L.E. Mettler and T.G. Gregg op.cit., p.30.
- (17) E. Mayr Animal species and evolution, p.137.
- (18) See R.J. Berry op. cit., chapter 2, and V. Grant op.cit., pp.23/24/25.
- (19) See L.E. Mettler and T.G.Gregg op.cit. p.27.
- (20) See E. Mayr Evolution and the diversity of life, p.518.
- (21) H. Lehman "A reply to Munson" Ph. of Sc. Vol. 37 (1970), p.27.
- (22) See V. Grant "The plant species" in The species problem, E. Mayr (ed.), p.60.
- (23) See V. Grant ibid., pp73/74.
- (24) For an account of non sexual reproduction see M.J.D. White op.cit., chapter 9.
- (25) M.J.D. White, ibid., p.2.
- (26) See E. Holm The biology of flowers, p.,124..
- (27) E. Mayr "Difficulties and importance of the biological species concept" in The species problem, E. Mayr (ed.), p.381.
- (28) See E. Mayr Evolution and the diversity of life, p.519.
- (29) See R.J. Berry op.cit., p.268.
- (30) See M.J.D. White op.cit., p.5.

- (31) See E Mayr Evolution and the diversity of life, p.420.
- (32) See L.E. Mettler and T.G. Gregg op.cit., p.19.
- (33) See G.B. White "Semispecies, sibling species and superspecies" in The evolving biosphere P.L. Forey (ed.), p.22.
- (34) See V. Grant Organismic Evolution p.169.
- (35) This view is held for example by M.J.D. White in Modes of speciation.
- (36) See M.J.D. White ibid. chapter 8.
- (37) See V. Grant op.cit., chapter 22.
- (38) See V. Grant ibid., p.179 for both these examples.
- (39) Ibid., p.180.
- (40) New Scientist (1976). p.439.
- (41) From "Noisy spiders make good lovers" The Guardian, science report Jan. 7th 1982.
- (42) See R. Van de Gohm Fascinating animal facets.
- (43) R.C. Lewontin "Adaptation" op.cit., p.159.
- (44) See V. Grant op.cit., p.187.
- (45) Ibid. p.193.
- (46) See R.J. Berry op.cit., chapter 4, and also V. Grant op.cit., pp.80/81.
- (47) See R.J. Berry op.cit., p.263.
- (48) Ibid. p.261.
- (49) See E.B. Ford op.cit., chapter 15.
- (50) See R.J. Berry op.cit., p.116.

- (51) See S.J. Gould Ontogeny and Phylogeny p.312 and Z. Waloff The upsurges and recessions of the desert locust plagues.
- (52) See R.J. Berry op.cit., pp.98/99.
- (53) Poem by W. Garstang in Larval forms and other zoological verses, p.69.
- (54) R.J. Berry op.cit., p.22.
- (55) See R.J. Berry *ibid.*, p.23.
- (56) See New Scientist Jan. 28th (1978) p.9.
- (57) See New Scientist Nov. 8th (1979).
- (58) See R.M. Proctor and P. Yeo The pollination of flowers, p.356.
- (59) See E. Holm op.cit., p.59.
- (60) *Ibid.*, pp.32-36.
- (61) See R. Pianka Evolutionary ecology, p.224.

CHAPTER TWOA PHILOSOPHICAL ACCOUNT OF SPECIES

In the first part of this chapter I shall suggest that species are natural kinds. In the second part I argue that species themselves have properties that do not necessarily belong to their individual members.

PART I. DIFFERENT POSSIBILITIES FOR SPECIES AS ENTITIES

One view I wish to eliminate from the start is that a species is a concept. Those who hold this view claim that the species lion, say, is the concept of what it is to be a lion. But a species, I would counter, cannot be a concept because things can be said of a species that cannot be said of concepts. We can say : a species grows, or it becomes extinct. So a species must be something other than a concept, which means that we are left with several further possibilities : these are that a species is a class, or it is an individual or it is a natural kind.

1. Classes

The first possibility I shall consider is that a species is the sum total of all its individual members. In other words a species is a class. The strongest

argument for this view has been advanced by Caplan, who has argued that species must be classes since we can apply biological laws to them (1). One may add that any scientific investigation will focus on the members of a species since it is only through observing specimens that scientists can discover that a species exists, and ascertain what makes it the species it is. However, one may ask: is it correct to identify a particular species with the extension of the species term? In my view it is not, because things can be true of the species without their being true of the class. For while a species may develop or become more numerous, classes cannot do so (2). Moreover a species does not have the members it has essentially. Indeed it is quite conceivable that the lion species of today might have been composed of a different set of individuals from the ones it in fact does consist of. Yet it would still be the same species, the lion species. Whereas a class, on the other hand, does essentially have the members it has.

2. Individuals

The second possibility is that a species is not a class but some sort of concrete individual. This is a view held by, among others, David Hull, who believes that a species is one large organism. He says that species have too often been seen by philosophers as spatiotemporally unrestricted classes (3). For we have

just seen, species evolve and split, whereas classes do not. Hull goes on to make a similar point when he says:

"I cannot describe intelligibly what it could mean to say that a class buds off another class. The reason for the conceptual difficulty is that such terms imply temporal and causal connections, connections which are incompatible with species as spatiotemporally unrestricted classes" (4). Hull points out that species emerge as a result of unique selection pressures (5). For this reason a species is identified by its parentage and is therefore a historical entity. Particular determinate species can exist only once (6), and species are "spatiotemporally localized cohesive and continuous entities" (7). In other words 'lion' does not refer to a universal, as for example 'table' does, but refers to an individual of which all lions are parts. In response to Caplan's view, Hull believes that generalizations about particular species are merely empirical generalizations and cannot function within explanations in the way in which laws can. Hull points out that there are no internal characteristics which make a species the species it is (as was pointed out in the preceeding chapter). Yet species form cohesive wholes which remain relatively stable through time. From this Hull draws the conclusion that a name is given to a species, and to organisms within that species, not because of any typical properties, and not because the species name is a general term (8),

but because the species name refers to a "spatiotemporally localized individual". Just as an individual person is baptized, so "a taxon has the name it has in virtue of the naming ceremony, not in virtue of any trait or traits it might have" (9). An organism is not given a name because it is typical of a species, but because it is a part of a species and is born of that species. So long as there is no spatiotemporal discontinuity a species will remain the same species according to Hull, regardless of the amount of change it may undergo, just as a caterpillar will turn into a moth while remaining the same individual (10). Absence of essential characteristics and spatiotemporal continuity being typical of the way in which we think of individuals, Hull draws the conclusion that species terms are proper names.

Hull says that seeing species as classes brings conceptual difficulties (viz. how can a class bud off another?). But one can object to Hull's own view by using precisely the same argument, for seeing species as individuals also brings conceptual difficulties. Indeed if Hull's view is taken fully seriously, strange consequences would follow : we should for instance be able to say what weight a species has! The truth is that species do not really function as concrete individuals.

Without doubt species are spatiotemporally restricted in the sense that they are determined by their ancestors and their environment. But it does not follow that there is no more than this to a species being the species it is. Species are also characterized by a gene pool. What makes a species the species it is, is something more than spatiotemporal continuity. Lions are lions as opposed to tigers not merely because of a spatiotemporal link between all lions. Hull is right in saying that morphological descriptions do not define a species—they are anyway intended primarily to be used for identification purposes. And he is right too in saying that traits (cluster properties) do not give us the nature of a species. But as we shall see later, this does not mean that species terms are not general terms. Nor does it mean that there is nothing that accounts for a variety of organisms all belonging to one kind. The fact that there is no similarity in the description of two members of the same species (caterpillar and moth for example), does not mean that the explanation for one member belonging to that species is not the same as the explanation for the other member belonging to the same species. The reason for Tom being a cat is the same as the reason for Tabby being a cat - whether they look alike or not, and whether we know the reason or not. This seems to be true independently of Tom's being born

of Tabby, or of both being born of a common ancestor.

Hull's view does not adequately explain why all the members of a species are of the same kind. All individuals within a species, according to Hull, belong to the species, simply in virtue of spatiotemporal links. But human beings and bees are not different species merely because bees are spatiotemporally related to each other and not related in the same way to human beings. Bees are spatiotemporally related because they share in whatever it is that makes bees bees (gene pool...). As I shall argue later, there are biological principles (even if we do not as yet know them), which account for bees being different from human beings. Furthermore, if we were to discover creatures on other planets which were just like bees, which looked like bees, which could interbreed with our bees, and which therefore had the same genes and habits as our bees, then, contrary to what Hull asserts, they would be bees, whatever their origins. It is indeed possible, although unlikely, that evolution on some other planet has given rise to bees, even if the evolutionary processes which resulted in bees on that planet were different from the evolutionary processes which resulted in bees on earth. However much one may wonder how this came about, one would not call them by some other name simply because they were not part of a spatiotemporal continuum.

Another reason why species cannot be seen in the

way Hull wishes to see them, is that it is not impossible (theoretically at least) for extinct species to be resurrected. Although extinct species remain extinct, there are exceptions. Zoologists have indeed been able through selective breeding from present day individuals to recreate the wild ox (aurochs) extinct for 350 years, and also the wild horse (tarpan) extinct since 1876. Their work has been based on the assumption that contemporary populations of cattle and horses must contain within their gene pools the scattered genes of the extinct forms (from which they were developed). Today we now have animals of each sex exactly like individuals from the extinct species. These animals could eventually form populations, compatible in theory (forgetting the time barrier), with those which are extinct. Another possibility for resurrecting extinct species, would be to take a fertilized egg from a present species (say an elephant), insert into it the nucleus of a mammoth (from any frozen mammoth cell), and then replace the embryo in an elephant womb. The elephant would give birth to a mammoth. This would be quite feasible since cells store well when frozen, and nuclei can be transplanted, so that fertilized eggs from one species can develop in the uterus of others. Thus we could obtain several populations of the same species which do not form spatiotemporal wholes (11).

As far as change within a species is concerned,

Hull's view accomodates a certain amount of change but it does not take into account the fact that grand scale change within a population will lead to the formation of a new species. Like the cladists Hull seems to accept only splitting as a case of speciation, and rejects evolution through time (12). Lions may have evolved from lion-type creatures and form with these a spatiotemporal whole; but they are not of the same species as their remoter ancestors. Were we to rediscover one of these ancestors it would not be a lion, and it would not be able to interbreed with present day lions : whatever it is that made those lion-like creatures lion-like is not what makes todays' lions lions. Hull's view that species are individuals must be wrong.

So far I have argued that species are neither classes nor individuals. The next possibility I shall consider is that species are natural kinds.

3. Natural kinds. The received view

I shall introduce the first version of the natural kind view by Putnam's definition of a natural kind term: "a natural kind term is simply a term that plays a certain kind of role in scientific or prescientific theory : the role, roughly of pointing to common 'essential features' or 'mechanisms', beyond and below the obvious 'distinguishing characteristics' " (13). (Although I adopt this definition, I do not agree with

other aspects of Putnam's view on natural kinds.)

Traditionally these 'essential features' have been called essences. The essence explains the 'distinguishing characteristics' of the kind. The essence of water, for instance, is H₂O. This chemical structure explains the apparent characteristics of water (liquidity, boiling at 100°C, freezing at 0°C...). Moreover, essences are seen as underlying structures, existing in each and every individual of the kind (all molecules of water are H₂O). This means that essences have an explanatory role and also enable one to determine which individuals belong to the kind (this molecule is water if it is H₂O).

Should we say then that species terms are natural kind terms and that species have essences? In order to answer this question, I shall look first at Aristotle's view, and then at more recent views such as those of Putnam and Kripke.

For Aristotle, the essence ($\phi\psi\sigma\iota\varsigma$) of an organism is that which explains its visible characteristics (its function and form), i.e. that which explains how the creature lives, moves, changes, behaves and so on. In the case of living things, this essence is in some way contained within the organism itself. But this would not be true for artifacts. Lions give birth to lions, chairs do not give birth to chairs. The essence of chairs (if they have one) lies outside themselves :

"Nature is the distinctive form or quality of such things as have within themselves a principle of motion, such form or characteristic property not being separable from the things themselves, save conceptually"... "Men propagate men, but bedsteads do not propagate bedsteads; and that is why they say that the natural factor in a bedstead is not its shape but the wood - to wit, because wood and not bedstead would come up if it germinated" (14). Although the essence comes first logically, it is not first in time :

"Matter and the process of formation must come first in time, but logically the real essence ($\phi\upsilon\sigma\iota\varsigma$) and the form of this thing come first" (15). To understand an individual we need first to know its essence. For the same reason, we understand what an individual embryo is by bearing in mind the adult it will become : "For coming-to-be is for the sake of being, not being for the sake of coming-to-be" (16) and "The seed, then, is the origin and productive agent of what comes out of it ... Yet still prior to this is that of which it is the seed; for the seed is a coming-to-be, but the end is a being. And still prior to both is that from which the seed is. For it is the seed in two ways, of that out of which it is and that of which it is" (17).

According to Aristotle, any individual organism is one of a kind represented by the type (usually the adult male). Abnormal individuals (and females) are a deviation from the type.

In the 18th and 19th centuries, after Linnaeus and before Darwin (apart from a few exceptions), species were still considered to have fixed essences. Most natural scientists believed science could find some properties which would be diagnostic of a particular species. These properties would be properties which each and every member of that species possessed. Any deviation from these properties would be the result of some outside interference with nature's programme. This view of essences resulted in the typological conception of taxonomy where the essence of the species was exemplified by type specimens.

Philosophers such as Locke and Leibniz had already made the point that the real essence of a kind is not a matter of convention. The essence is those underlying structures of the organism, which may not be known, but which cause the properties we can observe in the type specimens. These structures account, therefore, for the groupings into kinds we find in nature. These views of real essences lie close to those of Putnam (a post Darwinian!) for he has written : "If I describe something as a lemon, or as an acid, I indicate that it is likely to have certain characteristics (yellow peel....); but I also indicate that the presence of those characteristics, if they are present, is likely to be accounted for by some 'essential nature' which the thing shares with other members of

the natural kind. What the essential nature is is not a matter of language analysis but of scientific theory construction" (18). And again the same view can also be found in Kripke : "In general, science attempts, by investigating basic structural traits, to find the nature, and thus the essence (in the philosophical sense) of the kind" (19). More recently, with specific reference to biological species, Kitts and Kitts say that underlying traits such as genetic structure, serve as the explanation for species being natural kinds (20).

Now, the view I have outlined above asserts that species are natural kinds, and have essences (internal structures or underlying traits) - the essence being a set of underlying properties which is causally responsible for the properties we actually observe (teeth and claws for example). What those from Aristotle down to Kripke are claiming is that it is the underlying traits that distinguish organisms of one species from organisms of any other species; and the underlying traits also serve as an explanation of the exclusive relationship of members to their species (21).

But when we come to evaluate this claim we can see that there are good reasons in biology today why none of the above views can be held as they stand. The major blow to the traditional view of natural kinds in biology is dealt by modern knowledge of the importance

for evolutionary processes of the enormous variety found within the members of a species (see Chapter One) (22). Indeed natural selection can only operate where there is a differential. Variety means that the traditional view of essence in biology is no longer tenable. Each individual within a species is unique, and differs from all the other individuals in that species. I have tried to emphasize the point that uniqueness is a distinctive feature of biological phenomena. One piece of a given stuff will be exactly like another piece of the same stuff (for any one molecule of water is like any other molecule of water), having the same external appearance and the same internal structure. This is not so in biology. The idea that biological classification could be based on microstructure is a philosophical myth. The view does not match the facts.

Aristotle was wrong to think of variation as abnormal (a deviation from the norm) and the male as the adult type. Indeed evolutionary forces act both on embryos and also on females. In this respect and in various other respects embryos and females are just as much representatives of a species as males are. But Aristotle was not alone in this: neither Linnaeus nor Agassiz could account adequately for variation.

The main argument, then, against Aristotle and the Putnam/Kripke view, consists in species not having essences - where essences are seen as microstructures

existing in each and every individual of the kind. As a result of this, many have claimed that species are not natural kinds. Mayr (23), Sober (21) and Dupré are among those who reject essentialism in biology on account of the existence of variety. Dupré, for example, says : "given all the organisms existing at a single time, there are no privileged properties or relations by means of which these can be sorted unambiguously and exhaustively" (24).

Tiensen (25) uses an imaginary example to show how variety is an argument against this view of species as natural kinds. This imaginary example is based on the fact that variation within species permits the coexistence of two individuals which are exactly alike - both phenotypically and genetically - but which belong nevertheless to two different species. Here, each individual would be a borderline case of its own species - so much on the borderline indeed as to be exactly like another case on the borderline of another species. Tienson asks us to imagine two organisms 'Bessie' and 'Bossie' which are exactly alike in appearance and in genetic make up, yet Bessie is a cow and Bossie belongs to a different species Guelph (Martian type cow). If both have the same phenotype and genotype, there seems little reason according to Tienson not to classify Bessie either as a cow or as a guelph and Bossie either as a guelph or as a cow and it doesn't matter which. Both Bessie and Bossie can

interbreed with either species. In spite of this, cows and guelphs are not the same species. Their overall characteristics (phenotype and genotype) bear differences. It is just that variation among individuals within each species is such that Bessie is atypical of cows and rather like a guelph, and Bossie is atypical of guelphs and rather like a cow. Tienson's final point is that variety is such that there is no way of determining membership. Yet, determining membership is part of the definition given for natural kinds. We are therefore forced to conclude that species cannot be said to be natural kinds.

An additional objection one can level against the Putnam/Kripke view is that it centres on the false belief - in so far as the view appears to commit itself to this - that a reduction from characteristics to genes is possible. But genes are not sufficient to explain the distinguishing characteristics of a species. As we saw in the last chapter, other factors enter into any explanation of a species' characteristics. These other factors may include environmental, ecological or ethological factors. As we have seen, some species are differentiated by ethological factors alone (the gulls and the spiders mentioned in Chapter One). And in these cases it is learnt behaviour that is the differentiating factor.

Finally, we should note as a postscript to this section, that it is necessary to make a distinct, but

cognate, point regarding genes. Although the essence of water may be said to be H_2O , there is no proper counterpart in the case of species for the chemical composition of matter. Genes are the instructions for making individuals (see Appendix) and in this sense they are not even the right sort of thing to be microstructures of organisms, in the way in which H_2O is the microstructure of water. Similarly gene pools are not the microstructure of populations. Genes are used to instruct other molecules on how to build bodies, they are not the direct cause, nor the only cause, of what we see as bodies. There are no genes actively producing at all times what we see as fur, claws or teeth, in the way in which an atomic structure is directly and immediately responsible for the external appearance of say water. Genes are causally responsible for building bodies at a certain time of development, when the cells which make up the body are being made. But once cells are made the genes no longer play a role, they are no longer active, although they can be re-activated if necessary for repairs and for the renewal of cells.

In conclusion to this section, we can say that the Putnam/Kripke view fails. The view that a species is a natural kind at least when that is seen as something determined by a microstructure and determining an essence, is unacceptable.

4. Natural Kinds. An amended view

Are Aristotle, Leibniz and Putnam and his followers completely in error concerning species' essences? Are species' terms not then, natural kind terms at all?

If members of a species are not grouped up by reference to a collection of marks or an underlying collection of marks (i.e. an essence as described above), how are we to explain why organisms are grouped into kinds? To deny that species have at least a nature would mean that in order to be of one kind there is no particular way an animal has got to be. Yet surely this is nonsense. For groupings are not arbitrary and species are natural kinds.

Although for most philosophers natural kind terms refer to some essence seen as a microstructure, and although we now know this to be an untenable view for species, I nevertheless believe species terms are natural kind terms.

At the beginning of the last section, I defined natural kinds in terms of essences. This definition was, however, complex. First essences were given as those essential features which explain the distinguishing characteristics of a kind, and then essences were described as underlying structures enabling one to determine which individuals belong to the kind. The argument against natural kinds, set out above, does indeed show that the second part of the

definition cannot apply to species. But it does not affect the first part. For so long as we do not suppose that essences are underlying structures (existing in each and every member of a species), we may still be able to make a case for species being natural kinds. And this is what I intend to attempt in this final section of Part I. Since I no longer adopt the traditional understanding of an essence, but only one part of what figures in that understanding, I shall henceforth use the term 'nature' instead of 'essence'. I shall claim that species terms are natural kind terms in as much as each species has a particular nature that explains its overall characteristics. And although the question of membership is no longer part of our definition of a natural kind, it is still an important question in its own right, we shall therefore return to it in Chapter Four.

What a kind is is not a matter of mere description but of scientific discovery. It is by virtue of its particular nature that a kind is what it is, the nature of a species explaining its overall characteristics. Science attempts to discover the nature of things in the sense that science proceeds from observations (descriptions of what we see) to explanations. Medicine, for example, proceeds from symptomatology to etiology (26). (This shift has also occurred in taxonomy, for as we saw in Chapter One taxonomy moved from descriptive morphological classifications to

explanatory biological classifications.) The properties which enter into an explanation of characteristics of the kind need not be underlying traits in order to be scientific; they need only to be explanatory, they need to explain and predict. The explanation needs to involve causal mechanisms which work on each and every individual organism within a species. Causal mechanisms need not be microstructures, nor do we need even to make essential references to microstructures in causal explanations.

Whether something is or is not a natural kind is ascertained by scientific discovery. It may happen that what was thought to be one natural kind turns out in fact to be two. That groups of organisms are classified into the same or different species, following discoveries concerning their natures, can be shown by actual examples. One example is bacterial species causing pneumonia. Pneumonia is a disease with various causes, and is in fact the general name for a variety of symptoms (congestion of the lungs, fever....). One cause of pneumonia is bacterial infection. *Mycoplasma pneumonia* is the name of a disease caused by the Mycoplasma sp. bacteria. Until recently, what was meant by *Mycoplasma pneumonia* was the disease caused by this particular species of bacteria. Then it was found that the same symptoms were also caused by another species of bacteria. (Bacterial kinds are usually called

'strains' not species, but this does not detract from the main points of this example.) Following this discovery, it was decided to call symptoms caused by the second species of bacteria by a new name. The disease caused by the different bacteria has been called Legionnaires Disease and the species of bacteria which cause it Legionella sp. Cases of Legionnaires Disease have always existed and were thought to be cases of Mycoplasma pneumonia until it was realised that two different explanations were required for what must then be two different diseases. This has been important for the treatment of the disease, since different bacteria cause them and these different species of bacteria have different characteristics (different ecological ways for example). This means that the prevention of the diseases will follow different routes. Mycoplasma and Legionella are therefore two different natural kinds.

Many other similar examples exist. The organisms responsible for River Blindness make a similar case, this time several populations being found to be in fact different species having only slightly different ecological and genetic natures, but yet sufficiently different to make them fall into distinct groups, only some of which could cause River Blindness. (This fact led to improvement in the efficiency of the prevention of the disease (27).)

Both of these cases also illustrate the way in

which new terms such as 'Legionnaires Disease' emerge with advances in scientific knowledge. This is an actual example comparable to Putnam's example of jade and jadeite (28).

Following our definition of a natural kind in this section, a species is a natural kind if it has a nature (discoverable by science) which explains the overall characteristics of the species. The examples above show that species are indeed natural kinds.

But are there any objections to this view? One objection may stem from the vagueness that one encounters at the boundaries between species.

This is similar to the Bossie/Bessie objection mentioned above. But the difference here is that Bossie/Bessie was an objection concerning membership and this is no longer at issue. We are still left however with a question regarding such cases, namely what are we to say about borderline cases, e.g. what kind are they?

Making arbitrary decisions does not help, since an arbitrary decision does not tell us what kind of thing a creature truly is. Thus to the question: what kind of creature is a mule? We cannot reply: it could be arbitrarily either a horse or a donkey. For indeed it is not either. Mules are not in any way atypical horses or atypical donkeys, nor does the mule come from one species alone, since there is of course no 'mule' species (mules being, like most hybrids sterile). One

may be tempted to say that hybrids such as mules simply do not have a nature, do not belong to a kind. But in fact, a mule results from crossing a mare with an ass, and is therefore part horse and part donkey. So we don't need to deny completely that it has a nature, since we can say that its nature consists of bits of both species' natures. So far as the mule's distinguishing characteristics (its size, habits and so on) are concerned, we can provide an explanation: this explanation draws on the nature of horses and the nature of donkeys. A hybrid is a bit of one species and a bit of another. Although it doesn't itself belong to a kind, this does not however mean that there is no explanation for what it is. It cannot be said to belong to a kind because any mule's existence depends on there being horses and donkeys, and a mule population could not survive on its own for more than one generation because of its sterility.

A similar and related problem arises with borderline cases which result not from hybridization but from evolving populations. Such intermediary individuals belong to intermediary populations which, unlike hybrids, can survive without the parent populations (i.e. they can reproduce). On the whole these are populations in the process of speciation, and as such are considered to be of subspecies or races. Such populations could be said to be of species in formation and as such they have their own natures

which are emerging, and from which their individual members benefit. But these populations may, however, be truly borderline cases and it may be difficult to tell at which point one should start considering them as separate groups (new species) with their own natures.

This brings us back to the problem encountered in Chapter One on speciation. Science tells us when speciation has occurred. This is a difference between all the biological cases of vagueness and many traditional sorites problems - the cause of baldness has nothing to do with when one calls a man bald or with what determines whether we call a man bald or not (the number of hairs on his head is not the cause of baldness); but what accounts for a species being what it is, what causes a species to be what it is is what determines whether we are entitled to say that a population is of one species or another. When to call a man bald is not a matter for scientific discovery, naming the species a population is of is a matter for scientific discovery. Baldness has no real nature, but species do.

Vagueness does not appear to threaten seriously the claim that species are natural kinds (the amended view). There is no reason why natural kinds should not have vague boundaries. But we shall pursue this point further in Chapter Three.

PART II. SPECIES AND PROPERTIES

In this part of Chapter Two, I wish to discuss the definition of a natural kind that I have adopted here: namely that a natural kind does not include criteria for membership in the kind. Membership is not decided on the basis of either essential features or distinguishing characteristics, for neither of these necessarily belongs to every single member of a species. Moreover, both include properties which cannot be ascribed to individuals. I shall start by establishing this claim and then continue to discuss the role such properties play in descriptions of biological kinds.

1. Essential features

The essential features must be such that they explain why the kind has the distinguishing characteristics it has. They must, for instance, explain why the lion species has fur, claws, and high fertility rates, and why it is carnivorous, aggressive and so on.

Many seem to assume that one can answer these questions simply by saying that the kind has the characteristics it has because it is reproductively isolated from any other kind. This, however, is not satisfactory. Reproductive isolation may enable one to identify different kinds; but it does not explain why

this species has fur, claws and so on. It might be claimed that it does explain it, in as much as one can say that the population inherited these characteristics from the parent population. But this is not a sufficient explanation. We would still want to know why their parents had these characteristics.

Reproductive isolation and origins are both insufficient for explaining these distinguishing characteristics. Furthermore, reproductive isolation itself stands in need of explanation (e.g. why is the population reproductively isolated?). Reproductive isolation does not determine a kind; on the contrary, it is something which follows from a population being of one kind rather than another. Dupré makes this point, by saying that origins cannot be an essential feature of a kind, and he illustrates this by saying that even if a chicken did lay walnuts which grew into trees, one would not call it a grove of chickens (29). A similar point is made by Kitts and Kitts : "the fact that all horses are begot by horses is something to be explained. To suppose that an explanation is possible and to suppose further that the explanation is the same for all horses is to suppose that horses have some property in common which they do not share with members or any other species. To suppose otherwise is not to give reason to change our view of species but to give reason to abandon the concept of species altogether" (30). As mentioned earlier Kitts and Kitts

believe the common property is an underlying structure, and this as we have seen cannot be true. Nevertheless there are thoughts here that do not necessarily imply an underlying structure and these at least can be accepted as true.

What then could count as an explanation of the distinguishing characteristics of a species? In Chapter One, I adopted the biospecies definition of a species - that a species is a genetic and ecological system. Thus we can say that explanations too will draw on Genetics and Ecology, for both gene pools and ecological features determine the characteristics of a species. Moreover, these features account for reproductive isolation.

To conclude, the essential features of a species will be features of gene pools (frequency of genes, dominance of particular genes..), and of ecological relationships (role in the food web for instance). These will explain the distinguishing characteristics in as much as they are causally implicated in the production of these characteristics.

2. Distinguishing characteristics

There are no distinguishing characteristics to be found in each and every member of a species, therefore distinguishing characteristics must belong to populations rather than to individuals. Which properties do populations have that are not applicable

to individuals? First we say general things such as sexual species change more rapidly than non sexual ones. Secondly we predicate of a species specific properties that cannot be predicated of any of its members. (For example, 'smallness of populations' - if it is a species where the numbers of individuals in each populations is small, or 'low density' where the concentration of individuals per square mile is low.) Finally there are properties which are predicated of some members of a species and yet correspond to something which is true of the population or species as a whole. Take 'virulence' or 'fertility' for example, a species can be characterized as virulent or fertile in virtue of only some of its members being virulent or fertile. It may seem strange if not strained to say of a population or a species that it is virulent or fertile. In the same way, it seems strange to say that the lion species is 'carnivorous'. These may seem to be category mistakes since a species does not for example eat meat or have offspring, only its members do. Yet biologists do say such things of species. And it is actually essential that they should be able to say these things. For in cases where what we say of a species ('carnivorous', for example) is true in virtue of something attributable to all its members, then it is easy to see that we may not need to say this of the species itself (that it is for example carnivorous). Saying it of the species could

then be merely a shorthand way of talking about its members. But if a species has a property such as virulence or fertility which very few of its members actually possess, but from which all its members benefit (in virtue only of being members of that species - they benefit if for example this helps in the survival of the species), then it seems that we are obliged to say that the species itself has that property. That it is, say, a virulent or fertile species. And if we can say it for these properties, there is no reason why we should not also say it for properties which may apply to all the members of a species (the property of being carnivorous for example). These properties can all be said to be distinguishing characteristics of the species as a whole. They may differentiate it from other closely related species and they may play an important role in speciation (by conferring a selective advantage).

There are things we could not say if it were not possible to say that species have, in some sense, these properties. We could not indeed make much sense of some cases of natural selection. It is possible that a species only establishes itself successfully in a new niche because of its virulence. It is also possible to discover a new kind of creature with say canines. We could not be sure it was a carnivore, as for some reason or other it may never have eaten meat. But we should be able to say correctly that it belongs to a

carnivorous species. We could not say this if being carnivorous were not something which could, in some good sense, be attributable to species.

What then can it mean to say of a species that it is carnivorous, fertile and so on? The justification for applying these properties to species is as follows: to say these things of species is to say that certain conditions have been met. To say that a species is carnivorous, fertile, virulent, is to say not only that at least some of its members have these properties but also, that all of its members benefit (or suffer) from these properties, i.e. are in some sense affected by the presence of these properties. It is necessary to add this last point because some members can possess a property we would not wish to ascribe also to the species. Some humans have blue eyes for example, but the human species is not a blue eyed species. On the other hand you only need a few fertile fleas to have a fertile flea species.

The things we say of species in this way can be paralleled with things we say of other entities. We correctly say such things as : a battalion marches, Liverpool scored a goal or France went to war. We say these things in virtue of some individuals who do march, score goals and fight battles. It is in virtue of these individuals but it is not the same as saying simply that these individuals do these things. To say Liverpool scored a goal is different from saying that a

certain player scored a goal. The same is true for species. Some things we say of a species are true of all its members (lions are carnivorous), of some of its members (lions are fertile) or of none of its members (lions have small population sizes). Yet all these properties are in some sense true of the lion species itself. So, to say that the lion species is carnivorous, fertile and so on is to say something about the species even though this does not mean that the species itself eats meat or reproduces. The important point here is that if we did not accept that these things could be said of species, we should lose a certain measure of explanation. To repeat, it would be impossible to explain the survival of a species whose success depends on its virulence, if one could not say of that species that it was virulent. Saying these things of species cannot be seen as a category-mistake.

In summary, we have seen in Part II of this chapter that species have properties which belong to all, some or none of their members. We have also seen that individuals within a species benefit or suffer from the characteristics pertaining to the species. In order to understand what an individual organism is, one needs to have an understanding of the kind it belongs to. This understanding will depend on scientific discovery.

The conclusion to be drawn from this chapter is that species are natural kinds. Their essential

features are those which enter into a biospecies definition and their distinguishing characteristics are often properties belonging to the species themselves. This chapter has discussed species as entities, but we have yet to establish firmly that species are entities. Although much of what has been said in the last two chapters points in that direction, the next chapter will concentrate on substantiating the claim that species are real.

References

- (1) A. Caplan "Discussion : Back to class : a note on the ontology of species" Ph. of Sc. 48 (1981), p.138.
- (2) David Hull makes a similar point in "Discussion : Kitts and Kitts and Caplan on species" Ph. of Sc. 48 (1981), p.146.
- (3) E. Mayr and Ghiselin both endorse Hull's view.
- (4) D. Hull op. cit., p.146.
- (5) Ibid., p.343.
- (6) Ibid., p.354.
- (7) D. Hull "A matter of individuality" Ph. of Sc. 45 (1978), p.336.
- (8) On this point Hull says that he disagrees with Kripke. Ibid. footnote p.352.
- (9) Ibid., p.352.
- (10) Ibid., p.347.
- (11) These examples are taken from "Bring back the mammoth" The Guardian Jan. 21 (1982).
- (12) The same point is made by Caplan op. cit., p.135.
- (13) H. Putnam "Is semantics possible" (1970) in Mind, Language and reality, p.140.
- (14) Aristotle Physics II, 1, 193B
- (15) Aristotle De partibus animalium 646A, 26. I am not here putting any weight on the distinction in Aristotle between $\phi\upsilon\sigma\iota\varsigma$ and $\sigma\upsilon\sigma\iota\alpha$.
- (16) Ibid., 640A, 19.
- (17) Ibid., 641B, 30.

- (18) H. Putnam "Is semantics possible?" (1970) in Mind language and reality, p.140.
- (19) S. Kripke "Meaning and necessity" in D. Davidson and G. Harman (eds.) Semantics of natural languages, p.330.
- (20) See D.B. Kitts and D.J. Kitts "Biological species as natural kinds" Ph. of Sc. 46 (1979), pp.613-622.
- (21) See E. Sober "Evolution, population thinking and essentialism" Ph. of Sc. 47 (1980), pp.350-383 and also Kitts and Kitts op. cit.
- (22) E. Sober makes a similar point in "Evolution, population thinking and diversity" op. cit.
- (23) See E. Mayr Evolution and the diversity of life.
- (24) J. Dupré "Natural kinds and biological taxa" Ph. Review 90 (1981) p.88.
- (25) J. Tienson "Can things of different natural kinds be exactly alike?" Analysis Vol. 37 No. 4 (1977), pp.190-197.
- (26) See C. Hempel Aspects of scientific explanation (1965), pp.147/148.
- (27) See J.B. White "Semispecies, sibling species and superspecies" in The evolving biosphere P.L. Forey (ed.), pp.26/27.
- (28) See H. Putnam "The meaning of meaning" in Mind, language and reality, p.241.
- (29) See J. Dupré op. cit p.88.
- (30) Kitts and Kitts op. cit. p.618.

CHAPTER THREETHE REALITY OF SPECIES

Much of what was said in Chapter Two indicated that species were real. Important scientific discoveries, revealing the existence of new species, as in the case of Legionnaires' Disease, pointed to the fact that species are objective and not arbitrary groupings. The fact that species have properties, which are not reducible to the properties their members have, also shows that species must in some sense be real. The present chapter concentrates on justifying the claim that species are real. First, I outline the way in which variety, far from being seen as an obstacle to real groupings in nature, can on the contrary be seen as sustaining such groupings. Secondly, I argue that species are real since there are statements in biology concerning kinds of organisms, which cannot be reduced to statements dispensing with species terms. Thirdly, I look at the use biologists make of species terms, and at the scientific advantages (in terms of better explanations and predictions) which accrue from seeing species as real. Finally, I consider an objection to the reality of species.

1. A reality sustained by diversity

Variety has not weakened biologists' belief that the individuals within a species belong together :

"Penguins, bats, or even beetles are not groups arbitrarily made by the operations of our mind, like the categories in a library, but are groups produced by evolution" (1). The definition of a species adopted in Chapter One was that a species consists of individuals each of which is unique but which all share a gene pool and belong to a particular ecosystem :

"species are not merely classes of objects but are composed of natural populations which are integrated by an internal organization and this organization (based on genetic, ethological and ecological properties) gives the population a structure which goes far beyond that of a mere aggregates of individuals" (2). This sort of organization does not exist at levels of higher taxa than the species. Indeed there is no interaction between the members of a genus or a family. One would not expect for example all those species who are mammals to relate to each other in any way. The species category is the only taxon whose reality can be argued in this special way. Organisms of one species form cohesive populations, for this reason population biology has replaced studies on individual organisms. This point is made by Elliott Sober : "the population is an entity, subject to its own forces, and obeying its own laws. The details concerning the individuals

who are the parts of this whole are pretty much irrelevant... population thinking involves ignoring individuals" (3) (A species contains populations, how populations are identified as belonging to one same species will be discussed in the next chapter.)

Ignoring individuals does not mean that a new mutation in one individual may not lead that individual to have an important role to play in a population, nor does it mean that diversity itself is to be overlooked. Variety is, as we have seen, an essential part of a population but "rather than looking for a reality that underlies diversity, the populationist can postulate a reality sustained by diversity" (4). Diversity gives a species the flexibility it needs to adapt to the continual changes encountered in its environment. One mechanism for maintaining diversity is sexuality. Sober in the same article says : "The deploying of prodigious quantities of variability is not a dysfunction which sexual organisms are vulnerable to. Rather it is the principal advantage of sexuality; it is standardly construed to be what sexuality is for" (5). Diversity therefore is an essential part of a species and bell-curves are normal, "they are real they enter into explanations because the variability they represent is lawful and causally efficacious" (6). Indeed, as already mentioned in this thesis, natural selection can only operate where there is a differential.

Diversity itself is the subject matter of biological theory. There are models and theorems which are concerned solely with diversity, for instance the Hardy-Weinburg theorem referred to in Chapter One. This theorem shows how diversity, over generations, is maintained by the reshuffling of genes in sexual species. What the theorem does is to demonstrate how allelic frequency in a population will tend to remain constant from generation to generation, and how the genotype will reach an equilibrium within one generation of random mating and will remain at the frequency thereafter.

The Hardy Weinburg theorem (7) was arrived at independently by G.H. Hardy (a mathematician) and W. Weinburg (a biologist) in 1908. The basis of the theorem is as follows : it assumes that we have a population with random mating (where each individual has an equal chance of mating with any other individual of the opposite sex). On all chromosomes there are two genes (alleles) at each locus (the part of the chromosomes that carries the genes for a particular trait), one allele from each parent. Gene (allele) A and gene a for example. The three possible genotypes for these genes would be AA, Aa, aa :

Figure 13:Matrix of possible genotypes for two genes A and a:

	A	(eggs)	a
A	AA	Aa	
(sperms)			
a	Aa	aa	

If the genotypic frequencies are D for AA, H for Aa and R for aa, we have $D + H + R = 1$. And if the gene frequencies are p for A and q for a, then $p = D + \frac{1}{2} H$ (all AA individuals and $\frac{1}{2}$ Aa individuals, see matrix), and $q = R + \frac{1}{2} H$ (all aa individuals and $\frac{1}{2}$ Aa individuals). We also have $p + q = 1$, and also $p^2 + 2pq + q^2 = 1$ (see matrix, and of course $(p + q)^2 = p^2 + 2pq + q^2$, i.e. $1 \times 1 = 1$). In addition to this, the probability of mating between two individuals with AA genotypes is the product of the probabilities that each individual has the AA genotype, it therefore is D^2 . In this way we can calculate the probability of mating between all individuals, and then we can get the probabilities for all the possible genotypes of the offspring (see table 1 overleaf).

Table 1:Derivation of the Hardy-Weinberg theorem(after) D.J. Futuyma Evolutionary Biology. p. 228.

Mating	Frequency of mating	<u>Offspring genotype frequencies</u>		
		AA	Aa	aa
AA x AA	D^2	D^2	-	-
AA x Aa	$2DH$	DH	DH	-
AA x aa	$2DR$	-	$2DR$	-
Aa x Aa	H^2	$H^2/4$	$H^2/2$	$H^2/4$
Aa x aa	$2HR$	-	HR	HR
aa x aa	R^2	-	-	R^2
<u>Totals</u>	$(D+H+R)^2 = 1$	$(D+1/2H)^2 = p^2$	$2(D+1/2H)(1/2H+R)$ $= 2pq$	$(1/2H+R)^2 = q^2$

Looking at the totals at the bottom of table 1, we see that the frequency of genotypes in the offspring is $p^2 + 2pq + q^2$, that is to say exactly the same as in the parent population (see matrix : AA (p^2) + aa (q^2) + 2Aa (pq)). Gene frequencies do not change from generation to generation, and diversity is maintained (except under special circumstances, where for example environmental changes bring about new selection pressures). The Hardy Weinburg theorem can now be restated thus : under the conditions we have implicitly assumed, a single generation of random mating establishes binomial genotype frequencies, and neither these frequencies nor the frequencies p and q will change in subsequent generations (8). The theorem can be extended to three genes, with frequencies p , q and r where $(p + q + r)^2 = 1$, or more $(p_1 + p_2 + \dots + p_n)^2$.

This theorem was worked out mathematically, then tested in the laboratory and in the field. These tests showed that indeed, all other things being equal, diversity is maintained from generation to generation. The theorem can be used to check evolutionary stasis : if there is some variation in the conditions assumed and a population is undergoing evolutionary change, then the frequencies will change.

We have seen in this section how variety contributes to the stability of populations. This shows that variety is not in itself an argument for the

belief that only individuals are real. However, the Hardy Weinburgh theorem is about populations and not about species as such. I shall now outline the attitude I take to the question of the reality of species. If species terms are an essential part of some true biological theory, or indispensable to our best considered account of the nature and operation of individual organisms, then species are real. Species have without doubt been an essential part of a false theory (creationism). But of course the fact that this theory is false does not mean that species are not real, it only means that Linnaeus' or whoever's theory does not establish species' reality. If we count a theory as true, however, then the entities to which it is committed have to be counted by us as real. So far as the commitments of a theory are concerned I follow Quine's view that to be is to be the value of a variable : "entities of a given sort are assumed by a theory if and only if some of them must be counted among the values of the variables in order that the statements affirmed in the theory be true" (9). Our task now is to see whether species need to be 'reckoned among the entities' (10) in order to render biological theories true.

If we were dealing with physics and we were dubious about the credential of some notion, we could see if it were essential to any laws of physics. But there are few laws in biology, so we cannot proceed so

directly. Instead it may be sufficient to show that certain theorems or models or classes of phenomena cannot be explained or properly described without referring to species. This would mean that biological theories are ontologically committed to species, and that species terms play an essential role in important causal explanations in biology. In order to ascertain whether species terms are dispensable, I shall now look at models and theorems concerning species, and then see what other scientific interests these models and theorems subserve.

2. Models and theorems in biology

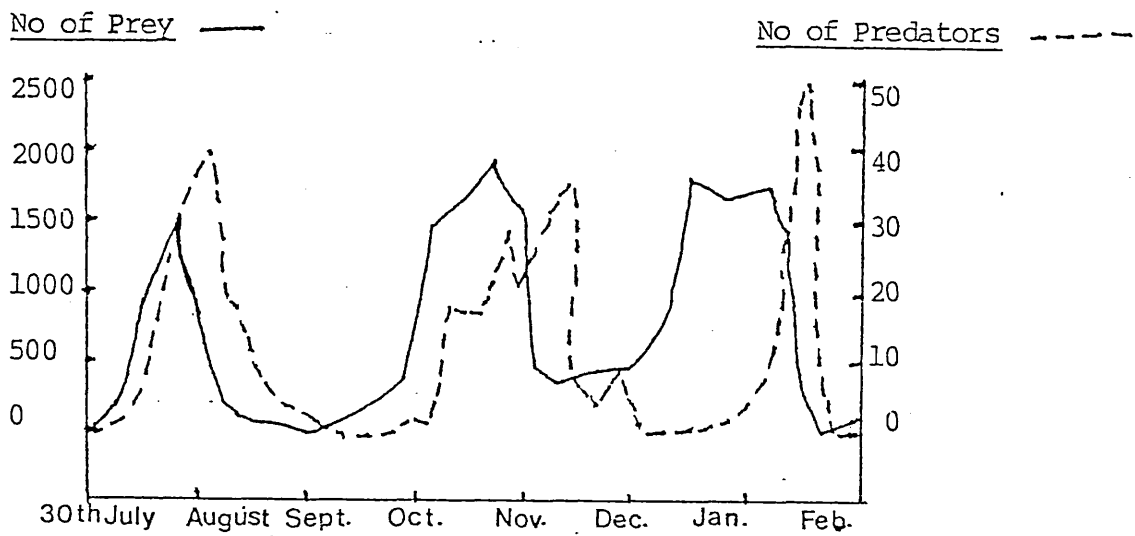
Biological theories result from studies of populations either in the field or in the laboratory. Populations vary in number, density, dispersion and so on. Populations act as systems with their own rates of loss and replacement of individuals. Regulatory processes act on the populations to keep these properties (density, dispersion...) stable. These properties are dependent on factors such as climate, temperature, moisture, food supply, competition from other species, predation, parasitism, diseases and so on. A combination of any such factors may affect the stability of the population either by keeping it stable or by stabilising it. With these models we can predict what will happen to certain organisms under certain conditions, or to certain relationships between kinds

(predator/prey for example) under certain conditions.

To see this in more detail, I shall consider some examples from Ecology. In predator/prey relationships there is a reciprocal relation in population numbers which shows cyclic oscillations (see Figure 14).

This same type of oscillation is found in almost all predator/prey population numbers. For this reason this relationship between predator and prey can be given by a series of equations called the Lotka-Volterra equations. A.J. Lotka and V. Volterra independently derived a set of equations describing the interaction between predator and prey. These equations are now used as simple mathematical models for the description and for predictions of population numbers within particular species.

Figure 14 Predator-prey relationship



From M.E. Solomon Population Dynamics 1969 p.18.

Oscillation of a predator mite Typhlodromus and its prey a plant mite Eotetranychus in a complex laboratory habitat (3 trays of oranges with some paraffin barriers).

The equation for the predator population is : (11)

(dependent on the prey density)

$$\frac{dN_1}{dt} = (\text{individual birth rate} - \text{individual death rate}) \times N_1$$

$$= (B_1 N_2 - D_1) N_1$$

$$= B_1 N_1 N_2 - D_1 N_1$$

N_1 : the number of predators

B_1 : a constant measuring the prey birth rate

N_2 : the number of prey

D_1 : a constant measuring the prey death rate, which is dependent on predator numbers.

The equation for the prey population is:

(dependent on the density of predators)

$$\frac{dN_2}{dt} = (\text{individual birth rate} - \text{individual death rate}) \times N_2$$

$$= (B_2 - D_2 N_1) N_2$$

$$= B_2 N_2 - D_2 N_1 N_2$$

B_2 : a constant measuring predator birth rate, which is dependent on prey numbers

D_2 : a constant measuring the predator death rate.

The predator prey interactions as predicted by the equations are : (12)

Joint abundance of two interacting populations:

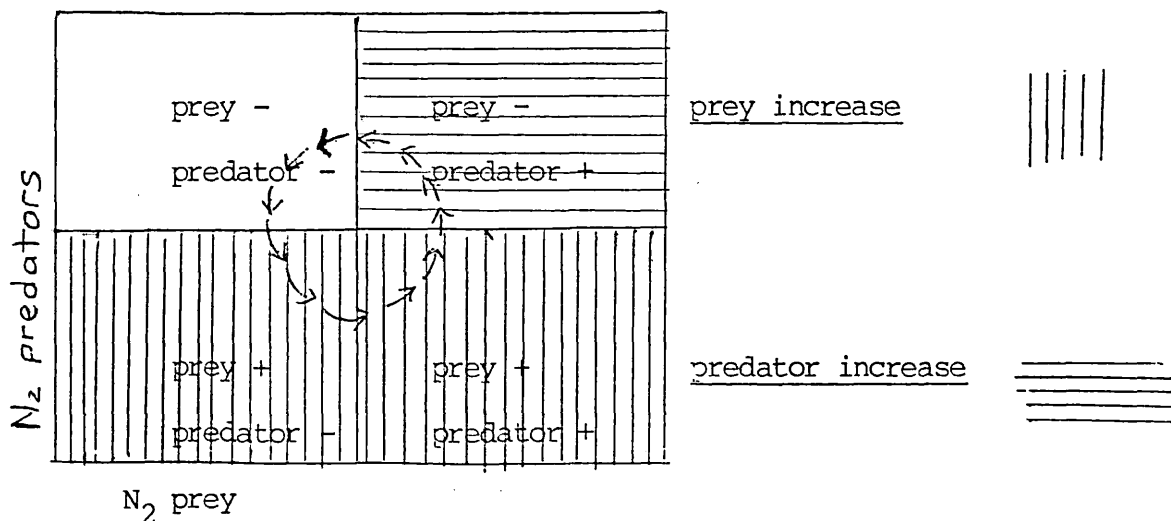
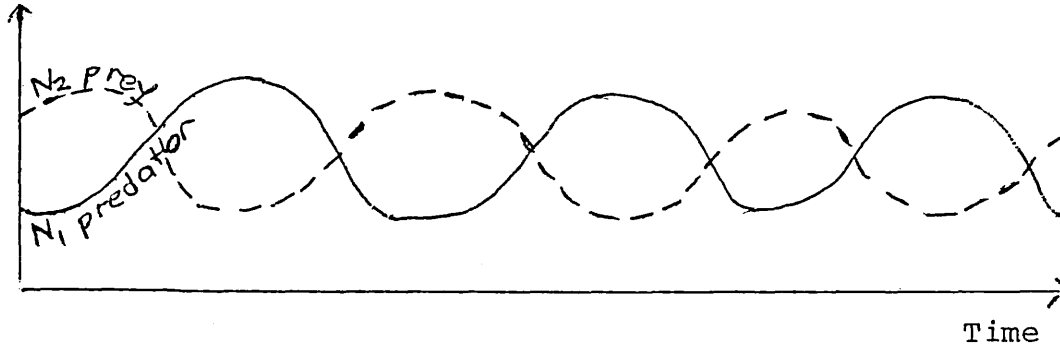


Figure 15

When this graph is plotted as a function of time we get:

Figure 16



This graph shows that the equations are characterised by a periodic solution : the populations oscillate in a systematic way. The amplitude of the oscillations depends on the starting densities (different predator species consume different numbers of prey). Any population will continue indefinitely to follow the cyclical path on which it starts. These equations are satisfied in the example given above (Typhlodromus and Eotetranychus).

To say that there is a particular relationship (expressed by these equations) between any two kinds of populations, where one kind preys on the other, is to say that there exists interspecific relationships which cannot be understood without reference to different kinds of organism in general.

But as they stand, in their generality, one may think that these equations quantify over 'predator' and 'prey' and not over species. This is true if all we

wish to say is that 'the population numbers of any populations of predator and prey will oscillate in a systematic fashion, all other things being equal'. However, the equations say more than this, they describe and predict definite population numbers over time. And these numbers vary from one kind of organism to another, but are constant for different populations of similar organisms, where the appropriate criterion for similarity has to be explained in terms of belonging to the same species. The graphs for different kinds of predators and prey oscillate at different rates (N_1 and N_2 have different values), whereas the graphs for the same kinds of predators and prey oscillate at the same rates. These kinds can only be understood as particular predator species and particular prey species, as for example Typhlodromus and Eotetranychus. So that, once we know the values of N_1 and N_2 for two populations of Typhlodromus and Eotetranychus, then we know that for any population of Typhlodromus and any population of Eotetranychus, population numbers will always vary in exactly the manner described by the equations - all other things being equal.

These equations could not be understood by reference to individual organisms alone, or by reference to prey and predators classes alone. A commitment to the Lotka Volterra equations is a commitment to the existence of individual species.

As well as models to describe and predict the relationship between certain kinds of populations, biology also uses models to predict what may happen to a particular species under predictable environmental changes. These models too make essential references to species terms. For example, the population model for the winter moth (Operophtera brumata) shows the different mortality factors of any population of Operophtera brumata. It can therefore be used to see whether any particular population of the winter moth is stable or not. If it is not stable, the model can also be used to see which factors are causing the change in population density. The model is valid for any population of Operophtera brumata. The model will have been originally drawn up from a life table such as the one shown in table 2. From the life table biologists can construct a model of the interaction between the winter moth and its parasites, (see table 3, from Varley, p.130). As with the predator/prey models, these life models use specific species terms, for example the parasites in the winter moth's life table.

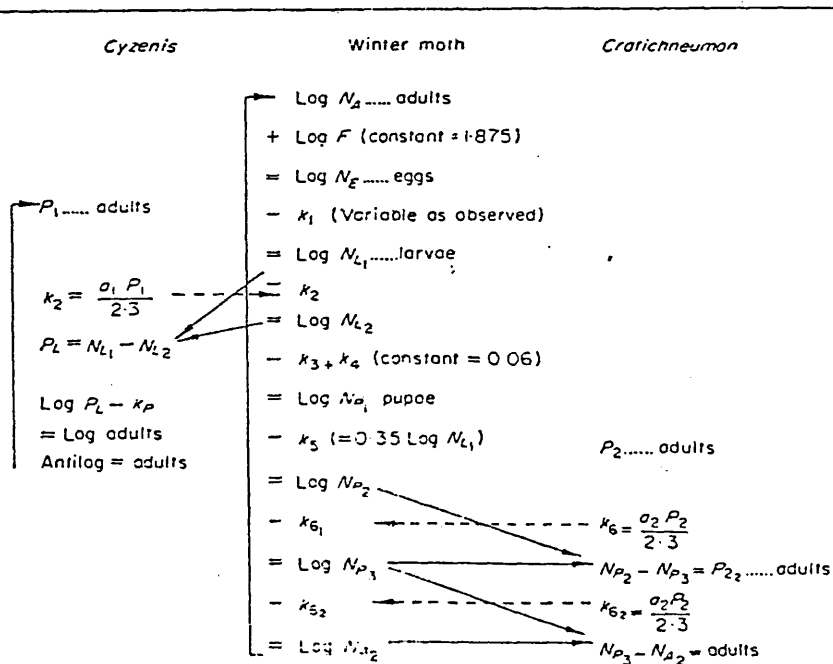
If the species terms used in the models are only abbreviations for something else, then of course the models and equations are committed to that something else and not to species. Could these ecological principles be reformulated without loss in a way that dispensed with species terms? Reference to a species

Table 2 Population components used in key-factor analysis of winter moth life tables. Winter moth adults N_A ; eggs N_E ; full grown larvae N_{L_1} ; larvae surviving *Cyzenis* N_{L_2} ; surviving other insect parasites N_{L_3} ; surviving attack by Microsporidian N_{P_1} ; *Cratichneumon culex* adults C .

Name	Formula	Density relationship	Qualitative effect on population
Winter disappearance	$k_1 = \log N_E - \log N_{L_1}$	Big independent variable	Key factor causing change
Parasitism by <i>Cyzenis</i>	$k_2 = \log N_{L_1} - \log N_{L_2}$	Weak delayed density dependent factor	Cycles?
Parasitism by other insects	$k_3 = \log N_{L_1} - \log N_{L_3}$ $\approx 0.1 - 0.031 \log N_{L_1}$	Weak inverse density dependent factor	Instability
Parasitism by Microsporidian	$k_4 = \log N_{L_1} - \log N_{P_1}$	Effect small.	Negligible
Pupal predation	$k_5 = \log N_{P_1} - \log (C + N_A)$ $\approx 0.35 \log N_{L_1}$	Density dependent factor	Stability = regulation
Parasitism by <i>Cratichneumon</i>	$k_6 = \log (C + N_A) - \log N_A$	Delayed density dependent factor	Cycles

From: Insect population ecology, Varley et al, p.128.

Table 3 A model of the interaction between winter moth and its parasites



term is essential even if just one sort of scientific statement is irreducible. And such irreducibility suffices for the reality of species to be established, since this would show that reference to species is essential for that statement at least to be true. A sceptic might react by saying 'so much the worse for that statement'. But the statements we are concerned with answer questions it would be irrational for us to give up. Neither the predator/prey models nor the population models described above could have been formulated in terms of individuals or populations alone. They quantify over types of populations. Species might as well be just this - not populations but kinds of populations. Anything that is true of an individual or of a population is no more than a spatiotemporal generalization. On the other hand, anything, that is true of a kind of population (a species) goes beyond actual cases. It applies to any other similar kind, under similar conditions. Theories about species are of a different calibre.

But to make the point concerning the reality of species more forcefully, let us look at another specific example : the relation between a host and its parasite, the rabbit and rabbit fleas (this is again a predator/prey relationship). And let us see if this can be rephrased without the use of species terms. Rabbits and their fleas (Spilopsyllus cuniculi) have a very complex species-specific relationship : their

life cycles are synchronized. When female does become pregnant, the does' hormones induce maturation of female flea ovaries, and also some changes in male fleas (the rabbit hormones passing through the blood upon which the fleas feed). When the baby rabbits are born, the fleas move onto them and copulate (this is probably triggered off as a result of another hormone released by baby rabbits). The fleas then lay their eggs in the rabbit nest. These hatch and mature and take as their hosts the young growing rabbits. The cycle then starts all over again (13). All this was discovered as a result of attempts to control myxomatosis, which is spread by rabbit fleas. Experiments in the laboratory with fleas and rabbits were unsuccessful for a time, as the fleas would not reproduce. This was because the rabbits were kept in separate cages and did not breed. It was then discovered that fleas will only reproduce on reproducing rabbits. The discovery of this relationship enabled biologists not only to increase their understanding of rabbits and their fleas, but also to advance research on myxomatosis.

The rabbit/flea relationship is a very specific one, particular to those two species. The relationship is between one species and another. It won't do to say simply that to each rabbit there is a flea colony. Bucks, for example, do not stand in the same relationship as the does or as the young to fleas. If

the relationship were expressed in terms of individual rabbits it would miss the point of an interspecific relationship. The statements describing this relationship quantify indispensably over species terms. These statements go beyond actual populations. Such statements do not merely describe a population, but they explain why the relationship is as it is. For this reason, these statements predict what would happen in any such populations. The statements quantify over kinds of populations (over species). To repeat, populations are spatiotemporally restricted, species are not. There is no way for anyone who accepts the statements, and the questions it answers, to deny that species are something real. I shall now consider in more detail the questions statements about species answer.

3. The use biologists make of species terms

Species terms are used in statements answering many different scientific questions. By looking at some of these statements and the questions they answer, we will get some idea of what would be lost if we dispensed with species' terms.

Many questions in medicine are answered using species terms. I have already referred to some of these in the thesis. In Chapter One I mentioned the mosquito species responsible for malaria. Until the problem was formulated in terms of species, there

seemed to be no answer to the following question : why had preventive measures by the WHO failed? Once the mosquito populations were seen to be of different species, rather than being seen merely as a series of varying populations, it was possible to explain the failure. Seeing the mosquito populations as of different species, meant recognizing that the different populations had different breeding habits and different ecological habits. And this in turn meant that different measures were needed to eradicate each different kind of population. Up until that point, any measure tried had been applied to all the populations, instead of different measures to different populations. In Chapter Two, we saw that questions concerning Legionnaires' Disease and river blindness were also answered using species terms. Some medical statements require reference to several different species. To answer questions about the bubonic plague, for instance, one would need to refer to three different species : Mus rattus (the black rat), rat fleas, and the bacteria Bacillus pestis transmitted by the fleas. As I have said before, predictions could not be made if these statements quantified over individuals or populations, as these are spatiotemporally restricted. Without the ability to predict, preventive medicine and medical treatment would be a hit or miss affair.

In agriculture and farming too, many questions could not be answered without reference to species. We

saw in this chapter that one cannot explain the spread of myxomatosis without formulating our statements in terms of species (Lepus cuniculus, Spilopsyllus cuniculi, Myxoma virus). The life models discussed earlier can be used in pest control. A farmer, knowing how a species of pest lives, can see which parameters need to be varied to reduce the pest population. (For an example of this, concerning the use of the life table for the winter moth, see Varley et al. op.cit., pp.131 to 134). Seeing organisms as of different species, rather than as belonging merely to different populations, means that certain consequences follow. Genes, for example, can spread across populations of one species, but not across populations of different species. This knowledge is used in pest control, where one can rear in a laboratory organisms which carry deleterious genes, and then release these organisms in the wild to debilitate the natural population (14). The important point to emerge from all these examples is that, by referring to species, scientific statements can explain things which would otherwise remain unexplained. When one knows something is true of a species, one knows it is true of any population of that species. And this contrasts with generalizations concerning populations. From this knowledge other consequences follow : knowing this is a Bacillus pestis population, for example, definite precautions need to be taken. If we were not to look upon this

population as being of a certain kind we would lose this explanatory power. It is explanatory power that is lost if we dispense with species' terms.

Several additional points can be made to support my claim that species are real : the fact that important biological relations exist between different kinds of population (such as predator/prey, parasite/host and all those relationships mentioned in Chapter One), is an indication of the reality of species. This point is made by Lehman (15). A separate point made by Elliott Sober in "Evolution, population thinking and essentialism" (16) is that something should be considered real if it has causal efficacy, and unreal if it is an artifact of a causal process. Without doubt species do have causal efficacy;

Typhlodromus for example causes the population numbers of Eotetranychus to be regulated (to oscillate in a systematic fashion). Rabbit fleas cause myxomatosis and so on... Finally, it is interesting to note that the study of folk taxonomies reveals that different cultures classify organisms into the same species categories as Linnaean taxonomy (17). If other categories were real groupings in nature, these too might have been expected to register in various languages, but they do not.

4. Vagueness. An objection to the reality of species

Vagueness has often been invoked in arguments against species being real. The examples used in such arguments are the same as those mentioned in the section on vagueness in Chapter Two. Borderline individuals whether hybrids or new organisms in the process of speciation show that boundaries between species are vague.

It seems that if species are real, they must have definite boundaries and form discrete units. C.E. Bessey claims that since individuals vary, the boundaries between species are unclear, and this means that taxonomists can choose the limits of a species. This in turn means that species are not real : "so species have no actual existence in nature. They are mental concepts, and nothing more. They are conceived in order to save ourselves the labour of thinking in terms of individuals" (18). Bessey continues by saying that "since we make use of species for the purpose of saving labour ... it follows that those species whose limitations are so faint or vague that we apprehend them with difficulty have no reason for existence" (19), (i.e. we should not even conceive of them as species).

The first thing that can be said against views such as Bessey's is that on the whole species have clear boundaries, and species remain stable through

millions of years. An average species of invertebrates lives between 5 and 10 million years. When new species occur, they appear quickly, since any changes which represent an advantage spread rapidly through the population, and any changes which represent no great advantage (and do not lead to speciation) usually disappear from the population. Evolutionary change on the relatively rare occasions when it occurs occurs fast, usually in small isolated colonies (see Chapter One) where gene frequencies can change dramatically. This is the founder principle. A small isolated colony in a new environment can develop rapidly into a new species. The formation and extinction of species only takes 100 or 1000 years, this represents 1% of the life-span of a species. A very short period in geological time. This accounts for saltation (discontinuity), i.e. for the fact that transitions between species appear to be missing in fossil records. Most changes and even most new species fail to make any impact on the world. They usually become extinct following pressure from more successful organisms : "evolution, at higher levels is fundamentally a story of the differential success of species, not the slow transformation of lineages" (20). One change in millions may lead to the formation of a new species and one new species in a thousand may make it, if it has some remarkable new advantage over existing species, if it "opens the door to a new world" (21). A single

species gave rise to birds and a single one to mammals. Species are stable entities "with very brief periods of fuzziness at their origin, although not at their demise because most species disappear clearly without changing into anything else" (22). In a stable environment common species remain common and rare species remain rare.

However, there are cases where boundaries are vague. The idea that reality of species requires boundaries to be fixed and definite in space and in time may seem intuitively right, but it is wrong. So long as there are clear central cases where we can definitely recognize populations of a specific kind, even if some populations or individuals fall between two kinds, we can still claim that species are real. The vagueness is about boundaries and not about the central cases.

Exceptions undoubtably show that boundaries between species can in reality be vague and just that. There is no implication from this concerning the reality of species. Vagueness should be tolerated if it makes possible the solution to problems which could otherwise not be understood. Indeed evolutionary processes cannot be explained without taking into account the role of borderline cases. Mutants can give rise to new species. Furthermore, many of the examples mentioned above - which make use of species terms - rely for their explanatory value, on the fact that

species have gene pools. By their very nature gene pools have fuzzy edges. If abandoning vagueness makes scientific answers too complex or too artificial (too far removed from reality), then vagueness should be tolerated.

Even if it is not a serious threat to reality, vagueness does however call for a closer look at the way in which organisms and populations are identified as belonging to one species or another. This is what I intend to examine in the next chapter.

References

- (1) E. Mayr Evolution and the diversity of life, p.427.
- (2) E. Mayr "Species concepts and definitions" in The species problem E. Mayr (ed.).
- (3) E. Sober "Evolution, population thinking and essentialism" Ph. of Sc. 47 (1980), p.370.
- (4) Ibid., p.370.
- (5) Ibid., p.377.
- (6) Ibid. p.369.
- (7) also refered to as the Hardy Weinburg 'law' or 'formula'.
- (8) as given by D.J. Futuyma in Evolutionary biology, p.228.
- (9) W.V., Quine From a logical point of view, p.103 (and elsewhere).
- (10) Ibid., p.13.
- (11) E.O. Wilson and W.H. Bossert A primer of population biology, p.130.
- (12) Ibid., p.132.
- (13) See Miriam Rothschild "The rabbit flea and hormones" Endeavour 24 (1965), pp162-8.
and M. Rothschild and B. Ford "Hormones of the vertebrate host controlling ovarian regression and copulation of the rabbit flea" Nature 211 (1966) pp261-5.
- (14) R.J. Berry Inheritance and natural history, p.261.

- (15) H. Lehman "Are biological species real?" Phil. Sc. 34, (1967) p.166.
- (16) E. Sober op. cit., p.371.
- (17) H, Lehman op. cit., p.159; and E Mayr Evolution and the diversity of life, p.517 where he discusses his study of bird names in New Guinea; and S.J. Gould in "Species are not specious" New Scientist, August 2nd 1979.
- (18) C.E. Bessey "The taxonomic aspect of the species question" Am. Naturalist No. 42, p.218
- (19) Ibid., p.223.
- (20) S.J. Gould op. cit.
- (21) E. Mayr op. cit., p.523.
- (22) S.J. Gould op. cit.

CHAPTER 4INDIVIDUATION AND IDENTITY OF SPECIES

In the previous chapter I argued that species were real. In accordance with Quine's dictum "no entity without identity", they are entities for which identity questions make sense. It follows that if we are to vindicate their reality, then we need an account of species identity. We need to say what is at issue when we seek to tell species apart, or try to settle the question whether or not one species has persisted through change, or has become extinct as a new species emerges.

If species are real, then there must be some means of identifying populations as belonging to different species (i.e. some sufficient criteria for recognising populations as of different, or as of the same species). This is to be distinguished from whatever it is that explains why populations are of a species (as this may or may not be the same as the identifying criteria), that is to say whatever explains why all the populations within a species have the same overall characteristics. This question was discussed in Chapter Two. However, Chapter Two left untouched the question of membership. The account we need to find of the identity and difference of species will not resemble any account that would suit universals as

traditionally conceived - if only because of the essential heterogeneity of species, and the potentiality that species have for change. Properties or universals as traditionally conceived could scarcely admit either feature. Faced with the fact of variety and change, the account we need cannot elucidate species identity simply in terms of characteristics belonging to all and only the individuals making up the species.

We first need to be clear about the way in which we are using the terms 'species' and 'population'. Biologists are neither clear nor consistent in their use of the term 'population'. Here we shall attempt to keep to one use of that term. We shall say that a population is a group of organisms sharing the same geographical area and related to each other by descent. A population may last for thousands of years, in the sense in which one particular colony of ants has occupied, say, one particular mound of earth for thousands of years. Here, individuals die, but the population lives on. Descent is important in this connection because, had the mound been abandoned by the ants, and then at a later stage colonized by individuals from elsewhere who were not related to the original colony, then one would not say that these individuals made up the same population as the first ones. They would be a second population of ants. A population is in this sense a spatiotemporal unity. A

population is also an interbreeding group of individuals. The individuals within a population belong not only to a population but also to a species. The population itself is not a species. I shall say that a population is of a species. Let it be clear that this leaves room for the possibility that a population will evolve and become of a new species while remaining one and the same population. The population of ants mentioned earlier could evolve over the years to such an extent that it is first of one species and then of another. That would not make it any less the same spatiotemporal whole or any less the same population. What is more the two populations of ants colonizing one and the same mound at different times, could turn out to be of the same species. My interest here is of course in species identity and not population identity. I am only concerned with populations in so far as they bear on the problem of species identity. How then are species individuated?

1. Phenotypes and genotypes

One may think, as indeed biologists used to, that species are individuated by phenotypic or genotypic characteristics. In that case in order to distinguish one species from another, we should need only to look at phenotypic or genotypic differences. We have already excluded any account of species sameness based on characteristics belonging to all and only the

members of a species. Diversity at the genetic level is just as great as diversity at the phenotypic level. There are no phenotypic or genetic characteristics to be found existing in each and every individual within a species and not in any member of any other species. So neither phenotypes nor genotypes can give us any straightforward criterion for species identity. There seems no alternative therefore but to look at populations as the key to our problem. This will concur with our recognition of species as composed from the populations that are of these species.

2. Reproductive isolation

One criterion for species difference mentioned in Chapter One was reproductive isolation. Two populations are said to be of different species, if they are reproductively isolated from each other. As we saw in Chapter One different mechanisms result in reproductive isolation. These mechanisms can be genetic, ethological or ecological. Since a species can change yet persist as the very same species, this suggests that it is not change in itself that matters here, but whether the change leads to reproductive isolation or not. Large amounts of change in one population would probably isolate it reproductively from its parent population, but even a single chromosomal change can result in reproductive isolation (as in polyploidy).

It might seem then that two populations are of the same species if the only barrier to reproduction is either spatial or temporal : in other words they could reproduce if they were brought together in space, or could be brought together in time. The proposal here is that the species that one population is of, is the same as the species that another population is of, if and only if the two populations can interbreed in the wild (putting aside problems concerning space and time).

As a first attempt, one might try to elaborate this criterion as follows:

Axiom one:

$(X R Y) \text{ iff } (X S Y),$

where X and Y are variables for populations,
R is 'reproduces with' and S is 'is species similar to'.

Axiom two:

Reflexivity of R : $(\forall X) (X R X)$

(Any member of a population can reproduce with any member of the opposite sex in that population)

Axiom three:

Symmetry of R : if $(X R Y)$ then $(Y R X)$

Axiom four:

Transitivity of R :

if $((X R Y) \text{ and } (X R Z))$ then $(Y R Z)$

Definition :

A species is a maximal set of entities that are R-related to one another.

This would count as a criterion for species identity, since R is postulated to be an equivalence relation.

Are the principles invoked here, true in nature? No, they are not. Transitivity is not guaranteed in reproducing populations. The following imaginary example illustrates this problem: let us imagine three populations A, B and C. It could happen that the members of each population can reproduce with the members of the other two populations. However, a problem arises when this is not the case. There are cases where the members of A can reproduce with those of B, those of B with those of C, and yet the members of A cannot reproduce with those of C. Here transitivity breaks down. This would occur where A, B and C are not completely isolated reproductively. And so, there is a certain amount of hybridization between A and B and between B and C. In other words a few individuals from A can reproduce with a few from B and a few from B, with a few from C. In these cases we would normally say that A, B and C are not of the same species.

Our criterion is therefore inadequate for identifying species sameness. We need to distinguish between interbreeding and hybridization. The above

attempted definition employs R to cover both.

Hybridization means either reproduction between small numbers of each population, or the failure to produce fertile offspring. Interbreeding means reproduction between large numbers from each population, producing fertile offspring. We could try to restrict our criterion for species sameness to interbreeding (calling the relation I-relatedness). We could redraft the axioms in terms of I-relatedness and the definition would now become:

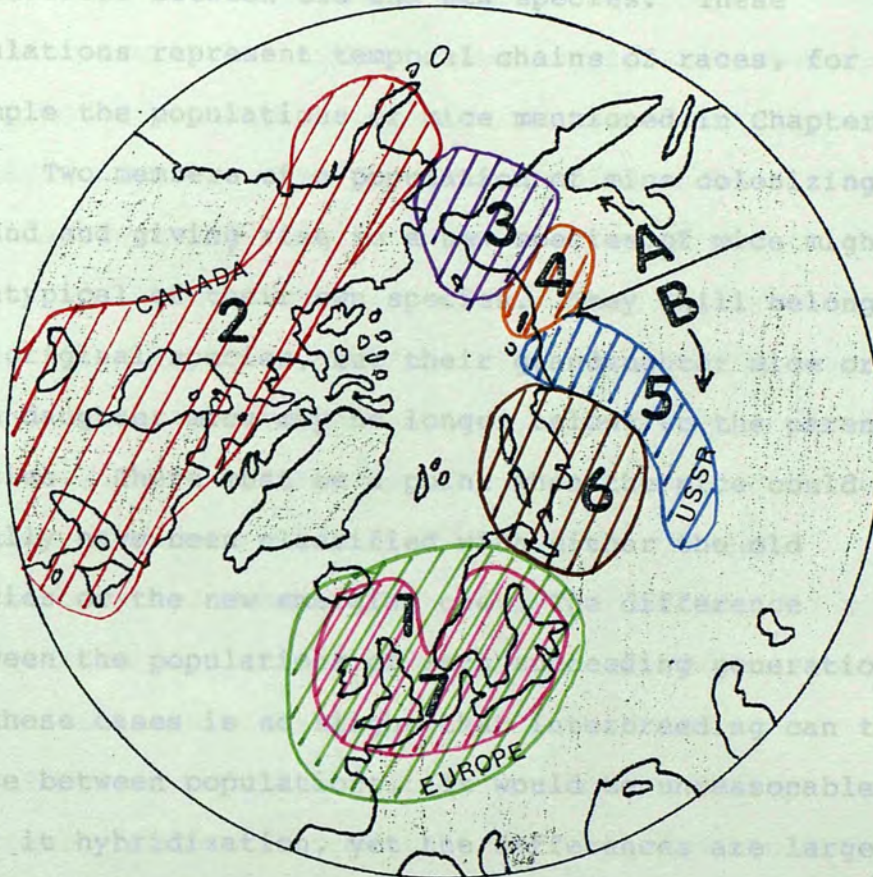
A species is a maximal set of entities that are I-related to one another.

Are the principles invoked this time, true in nature? Although for the majority of cases transitivity would be preserved, in some cases, it would still break down. This would not be because of the problems of hybridization, but it would be because of a problem of vagueness. This is the vagueness that occurs between the boundaries of slightly varying populations.

These are cases where one would not call the relationship between two populations one of hybridization because each population fully interbreeds with the next. And yet one nevertheless could have two or more different species. For example, populations sometimes form rings or chains of populations, where each population merges slightly with the next. Viewed from one angle all the populations are of one species,

since they can all interbreed with their neighbouring populations. But viewed from another angle, they must be split into two species somewhere, since the two end populations cannot interbreed with each other. One example of this is the gulls which form a circumpolar ring around the North Pole. The two ends overlap in Britain. Here herring gulls breed with other populations of gulls to the West, and the lesser black-backed gulls with other populations to the East. These two populations however do not interbreed and do not even look alike. But the further West one goes, the more the herring gull begins to look like the lesser black-backed gull; and the further East one goes the more the lesser black-backed gull looks like the British herring gull. The decision has been to call, arbitrarily, all gulls west of Northern Russia Larus fuscus, and all those to the East of that line Larus argentatus. This divides the ring into two species of gulls (1) (See Figure 17).

Figure 17 Circumpolar ring-species of gulls



- Species A:
1. Herring gull L. argentatus argentatus // // //
 2. American herring gull L. argentatus smithsonianus // // //
 3. Vega herring gull L. argentatus vegae // // //
 4. Birula's gull L. argentatus birulae // // //
- Species B:
5. Henglin's gull L. fuscus henglini // // //
 6. Siberian lesser black-backed gull L. fuscus anteriorius // // //
 7. Lesser black-backed gull L. fuscus graellsii // // //

The same vagueness occurs in diachronic cases. When populations evolve there are borderline populations between old and new species. These populations represent temporal chains of races, for example the populations of mice mentioned in Chapter One. Two members of a population of mice colonizing an island and giving rise to a new species of mice might be atypical of their own species. They still belong to the original species, but their granddaughter mice or even daughter mice may no longer belong to the parent species. There must be a point when the mice could equally have been classified with either the old species or the new emerging one. The difference between the populations of each succeeding generation in these cases is so slight that interbreeding can take place between populations. It would be unreasonable to call it hybridization, yet the differences are large enough to bring about the fact that the end populations in the chain cannot interbreed.

These cases show that transitivity breaks down when we have a long chain of populations with slight variations. Why do biologists not say that all the populations belong to one species? Why divide the chain into two species at all? Because dividing it into two species enables us to say that within each division transitivity is preserved. This however is cool comfort since it is no longer true in this case (a chain divided into two species), that the populations

of two different species are reproductively isolated (since the borderline populations are not). This, therefore, still represents a difficulty for a reproductive isolation criterion for species sameness.

There is another situation where transitivity breaks down, this time not because of vagueness. An imaginary example (but no doubt such cases exist) can illustrate this new problem : We could have three populations A, B and C. Population A comes into season twice a year (spring and autumn), population B comes into season only in spring, and population C only in autumn. A interbreeds fully with B and C, but evidently B and C do not interbreed since they do not come into season at the same time of the year. One can imagine other similar examples.

There is a further related problem. We may have difficulty in deciding whether the relationship between two populations is one of interbreeding or hybridization. This would truly be a Sorites problem. How many individuals in any population need to be able to reproduce with those of another population for one to say that the two populations can indeed interbreed and not merely hybridize? There will be cases where it is an arbitrary decision, and where A and B may equally be said to be the same species or not. The problem occurs not only with populations which have split, but also with populations which are coming together, as in introgression (mentioned in Chapter One). This problem

of vagueness is inherent to species identity, it is indeed because species are composed of populations which vary and change that the problem exists. The problem is both a diachronic and a synchronic one.

Gene pools explain how reproductive isolation works. Maybe an elucidation of the gene pool concept will solve some of the problems faced by the reproductive criterion for species identity; and it may provide us with an alternative means of identifying species.

3. Gene pools

The individuals within a population form a genetic unit, a gene pool. A gene pool is a group of compatible genotypes (compatible for reproduction), such genotypes are similar in certain respects such as chromosome number and chromosome structure. A gene pool is also a well integrated gene complex in as much as a gene pool is a collection of genotypes related or relating to each other. This relatedness is formally similar to the one used in talk concerning human beings, where one may say that a human being is related to another either by descent or by marriage. So for two organisms x and y we could say that they share the same gene pool if they are related either by recent descent or by bonds of mating.

More formally we could list a set of principles sufficient to define the bounds of descent or mating

which will provide the alternative criterion for identifying species. These need to be tight enough to exclude variations such as hybrids which do not belong to the gene pool, and yet be loose enough to include variations such as monsters which do. We shall say that two individuals x and y are part of the same gene pool if they are G-related (G = belong to the same gene pool):

1. if (x could mate with y producing fertile offspring) then (x is G-related to y).
 2. if ($\exists z$) (x could mate with z producing fertile offspring and y could mate with z producing fertile offspring) then (x is G-related to y).
1. would apply to individuals of different sex, and 2. to individuals of the same sex.

The assumption here is that x , y and z are G-related if they can mate when brought together. Space and time barriers are ignored.

Principles 1 and 2, omit some hybrids from the set of G-related individuals (those which are sterile), but they do not omit those which can reproduce. On the other hand, the principles exclude some abnormal individuals (since some grossly deformed individuals are sterile). Yet, these individuals do belong to the species. Moreover 1 and 2, cannot be used as criteria for individuals from asexual species. So we need to add something to include all these individuals.

3. if (x is descended from y and x is phenotypically and genetically similar to y) then (x is G-related to y).

We need to add 'phenotypically and genetically similar' because, it could be that x and y are related by descent yet of different species if a great amount of change has occurred between the two generations concerned. And indeed we would not want to include all x's ancestor's since ultimately they would have been of a different species. Furthermore, with polyploidy in plants we can have a situation where x is descended from y and yet of a different species from y. Such cases would be excluded, since y would be genetically quite dissimilar from x. And perhaps in this sense some monsters do not belong to the same species as their parents; cases such as these could be treated ad hoc.

We could express G-relatedness as an ancestral form of the relation of mating or of being related through a mate. In other words for an individual x to be G-related to y it would be sufficient to belong to every population which contains y and all mates of members of that population. This is another way in which we can express 1. and 2. We can express 3. by saying that x belongs to any population which contain y, the phenotypically and genotypically descendents of the descendents of y, and so on.

We now see that a gene pool is not merely a set of genotypes (a set is not indeed a relational concept). A gene pool is not a kind of genotype either since two populations could have the same kind of genotype yet not share the same gene pool or be of the same species. Indeed, they may not reproduce when brought together, as happens for example in two species isolated by ethological barriers. This is why biologists say that the members of a species share a gene pool. By this term they mean to refer to the relational bonds between individuals in a gene pool.

Do we now have a means of identifying populations? Can we say that two populations are of the same species if their gene pools could be shared, satisfying one or other of the principles above? Would it work for the synchronic and the diachronic cases?

G-relatedness would not be a valid means of identifying populations because there is, a severe restriction to be placed on it. All individuals related in the manner described under 1. 2. and 3. (or the ancestral relations) belong to the same gene pool only if the chain of relatedness is not too long! If the chain is long it could be that the first and the last individuals in the chain are not G-related in spite of satisfying one of the above principles. This could happen where there have been slight changes all along the chain in any one characteristic, the changes finally accumulating and operating a barrier to mating.

This is presumably what has happened with the individual gulls in the chain of races mentioned above. And for 3., the changes being such that over a long period of time the first and the last in the chain no longer resemble each other. Transitivity of G-relatedness cannot be guaranteed. We cannot therefore make G-relatedness an equivalence relation. An account of population sameness in terms of gene pools has not solved our problems and we are left once again with no satisfactory account of species identity.

Conclusion to Chapter Four

In this chapter we have seen that reproductive isolation, which is the standard criterion used by many biologists for species sameness, carries with it many serious problems. And we have seen that gene pool sameness suffers from the same faults. We started the chapter by saying that if species were real, we should be able to give criteria for their individuation and identity. We seem to have failed to find any satisfactory criterion. Should we therefore conclude that after all we have said in previous chapters, species are not real? In the next chapter we shall look at two modern biological views which indeed deny reality to species.

Reference

- (1) From Colin Patterson, Evolution pp. 7, 8, 9.

CHAPTER FIVETWO REDUCTIVE THEORIES

In the last chapter we failed to provide satisfactory criteria for the individuation and identity of species. It seems therefore appropriate at this point in the thesis to look at the views of those who deny reality to species. The argument for the reality of species, given in Chapter Three, was that if some important biological statement is committed essentially to species, then species are real. So, a view which denies reality to species will, in our terms, be one which claims that in scientific statements species terms are dispensable. Such a view will be arguing that species terms can be reduced, without loss, to other terms. It should of course be noted that no biological theory has ever claimed to have reduced species in any serious sense of 'reduce'. To achieve reduction we would need to axiomatize theories, and there are certain obstacles to this in the present state of biology. However, any view claiming that species terms are dispensable is reductive. I shall consider two reductive views in this chapter : numerical taxonomy and neo-Darwinism. Numerical taxonomists claim that species can be reduced to sets of characteristics belonging only to individuals; and so scientific statements referring to

species are not committed to species but to these characteristics. Neo-Darwinism claims that, in statements concerning evolutionary processes, species terms can be replaced by terms relating only to genes. This chapter is divided into two parts, each part concentrates on one of these reductive claims.

PART I. NUMERICAL TAXONOMY

Numerical taxonomy is a nominalistic view. Such views are not new, Bessey whom I have already referred to in Chapter Three, claimed in 1904 that only individuals are real, and that species terms are tolerated in biology simply because they represent a shorthand way of referring to a series of individuals. He says : "nature produces individuals, and nothing more. She produces them in such countless numbers that we are compelled to sort them into kinds in order that we may be able to carry them in our minds" (1). Numerical taxonomists make a similar claim, saying that species terms are merely a convenient way of referring to sets of characteristics belonging to a series of individuals. Is this claim true? I shall first give a straightforward account of numerical taxonomy, including as far as possible the reasons for their claim. I shall then assess the claim.

1. A nominalistic approach

Numerical taxonomists hold that there are no typical individuals and no typical characteristics. Any individual and any character displayed by an individual is as important as any other. Numerical taxonomists have, on the basis of this belief, devised a method which they claim is strictly empirical and numerical. They start by gathering as much information as possible, collecting as many organisms as possible, and recording as many characters as possible (morphological, physiological, behavioural, genetic, ecological), "every character is of equal weight in creating natural taxa" (2).

In this sense numerical taxonomists claim to be objective: there is to be no preselection of organisms as typical or characters as important. Once characters are recorded, classification begins: organisms are grouped following the number of shared character states. For numerical taxonomists there cannot be a limited set of characters defined for a species, since one can never be sure of having observed all possible individuals : "every systematist knows of instances where a character previously considered to be diagnostic of a taxon is lacking in a newly discovered organism that clearly belongs to the taxon" (3). In addition to this, quite new character states may emerge. For this reason Sokel and Sneath choose to speak of polythetic taxa: "for practical purposes we must consider the possibility of a taxon being fully

polythetic, since we cannot be sure that we have observed any characters that are common to all members" (4). Sokal and Sneath compare polythetic to polytypic (Simpson's concept), and on p.21 of Principles of numerical taxonomy they say : "in a polythetic group, organisms are placed together that have the greatest number of shared character states". This is opposed to monothetic where "the possession of a unique set of features is both sufficient and necessary for membership".

The formal expression of polytypic taxa is given by Beckner (whom Sokal and Sneath quote) : "A class is ordinarily defined by reference to a set of properties which are both necessary and sufficient (by stipulation) for membership in the class. It is possible, however, to define a group K in terms of a set G of properties f_1, f_2, \dots, f_n in a different manner. Suppose we have an aggregation of individuals (we shall not as yet call them a class) such that:

1. Each one possesses a large (but unspecified) number of the properties in G.
2. Each f in G is possessed by large numbers of these individuals and
3. No f in G is possessed by every individual in the aggregate.

By the terms of 3, no f is necessary for membership in this aggregate : and nothing has been said to either

warrant or rule out the possibility that some f in G is sufficient for membership in the aggregate" (5).

The phylogenetic history and the genetic aspects of organisms are not necessarily relevant for numerical taxonomists, although they may enter into the overall calculation as character-state themselves. Numerical taxonomists concern themselves only with overall resemblances. Such a view is familiar in other fields. As Sokal and Sneath themselves say : "polythetic concepts are by no means restricted to taxonomy or even to biology, for Wittgenstein emphasized their importance in ordinary language and especially in philosophy. Polythetic ideas are implied by the concepts of 'meaning', 'referring', 'description' and so on. There is a close parallel between Wittgenstein's 'family resemblance' and taxonomic resemblance" (6).

Once data are collected numerical methods are used. It is from these methods that groupings of organisms emerge. A matrix is drawn up showing the differences and similarities between the characters of a sample of organisms. From the matrix taxonomic resemblances between OTU's (7) are worked out. (OTU stands for operational taxonomic unit, it is any group of organisms being used in a study where overall resemblances are being calculated.) OTUs may differ from study to study depending on the group chosen each time; in other words an OTU is merely the basic group

in a given study. The relationship between them is expressed as a fraction calculated using various coefficients of association. This method, according to Sokal and Sneath, is unlike that of other taxonomies in as much as it is repeatable and objective. They believe it is objective because it takes all characters into consideration without selection. And it is repeatable for two reasons. First because there is no choice involved on the observer's part (everyone will simply observe what there is). And secondly because given the same data, calculations will yield similar results for different scientists. One claim made by numerical taxonomists is that throughout this taxonomic work, there is no need to refer to species. What other biologists call species can be seen to be sets of characteristics. The taxonomic units (OTU's) are all that other biologists, using taxonomic classifications, need. Species terms are therefore dispensable.

Sokal and Sneath claim that species terms have no particular use. They say : "we do not object to nonoperational concepts categorically, although we would prefer more operational concepts to less operational ones, but when the nonoperational concepts are vague and ill-defined and have no heuristic value, we are opposed to them, concepts such as the biological species (*sensu* Mayr et al.).... are more of a hindrance than a stepping stone to new discoveries and it is for this reason as much as their low operational value that

we wish to redefine them or possibly even dispense with them" (8).

2. Critique of numerical taxonomy

Sokal and Sneath claim that their methods show that taxonomy is not committed to the existence of species. In this section I shall assess whether their methods justify such a claim.

One reason Sokal and Sneath give for dispensing with species is that 'species' carries too much theoretical weight. Indeed, if we accept the existence of species, then we accept that organisms relate to each other in certain ways; and that their characteristics are determined to some extent by this relationship. Such an attitude towards organisms would, for Sokal and Sneath, threaten objectivity.

In their claim to be objective Sokal and Sneath maintain that all characters of an organism must be recorded. But counting characters can only be done against a background of the sort of theory numerical taxonomists wish to dispense with. At the very least the number of characters an organism is said to have must be dependent on some amount of theory, since the number of characteristics will depend on the way in which an organism is being viewed. Vernon Pratt makes this point (9). In order to count characters one needs to specify a description, and the number of descriptions is itself indefinitely large. Vernon

Pratt draws an analogy between counting characters, and counting the numbers of heaps in a bag of flour :

"Both are unanswerable questions. However, just as you can count characters once they have been specified, so you can count heaps once they have been poured out.

And just as you can describe a plant in an indefinite number of ways and so alter the number of characters indefinitely, so the number of possible heaps that the bag of flour may be poured into is indefinitely large"

(10). Furthermore, although Sokal and Sneath claim that no character is to be selected as important, they do in fact give advice on selecting characters. They recommend choosing those characters for which "problems of estimation are less serious and hence more likely to be overcome" (11), and also those which may be of

"greater interest and usefulness to systematists and biologists in general" (12). Data must be useful if they are to explain anything, and Sokal and Sneath do in fact select data which make sense. Why else do they choose to consider the shape of leaves on a tree as important, but not the number of leaves? Why do they choose to consider as one character only, having pink eyes and white fur (albino characteristics)? Sokal and Sneath indeed appeal to genetics to explain this choice of a principle of counting (13). The question of choosing which characters to consider as relevant when classifying organisms is called 'weighting'. Without doubt, different characters have different information

content, and some are just noise (14). Refusal to accept this is not what most people would call being objective. Sokal and Sneath's claim to be objective in their sense of 'objective' is nonsense. But they themselves do not practice what they preach, their choice is guided by theory just as much, and in the same way, as it is in any other taxonomy.

Do the theories which guide the choice of characteristics, include theories which are essentially about species? If the character traits that are chosen as operational are those which explain most other characters, then characters relating to genes and gene pools become likely candidates. Once we are thinking in terms of gene pools, we are thinking in terms of species (since a gene pool is by definition the set of genes belonging to a sexual species). And this is true even if we cannot as yet identify gene pools. Numerical taxonomists see organisms belonging to a species (or a gene pool) because they resemble each other. It is more correct to say that they resemble each other because they belong together. As seen many times in this thesis, species terms are relational terms : "the word species corresponds very closely to other relational terms such as, for instance, the word brother. A given person is not a brother on the basis of certain intrinsic properties of his, but only in relation to someone else. A population is a species only with respect to other populations. To be a

different species is not a matter of degree of difference but of relational distinctness" (Mayr) (15).

Numerical taxonomists seem to misunderstand the causal link between similarity and relationship. Mayr also says : "it is the same as with identical twins. Two brothers are identical twins not because they are so extraordinarily similar, but they are so similar because they are both derived from a single zygote, that is, because they are identical twins" (16). So, if genetic traits are chosen as having a greater explanatory role to play in taxonomy, this means that theories about species are invoked in taxonomy. It is contradictory to accept genes as important in as much as they explain characteristics, and yet refuse to accept their role in the gene pool. Genes are grouped into gene pools because of the links existing between different sets of genes.

A further point to be made, against the numerical taxonomists claim, is that if one accepts (as numerical taxonomists do) that a character is important if it is relatively constant within a particular group, then one is presupposing that groups are already chosen, and that some classification has already been made (17). The OTUs mentioned earlier could well have been groups of females, or males, or different age groups, but in fact they are the usual groupings of organisms (races and species). And this is precisely what numerical taxonomists claim not to do.

In conclusion to Part I we can say that the claims numerical taxonomists make about species are not a consequence of the actual methods of numerical taxonomy. The methods themselves are not in question here. Numerical methods in taxonomy are in many ways sound and have produced good results for example in arthropods (insects, arachnids), where there are large numbers of character states (all seemingly important), and here computation is a help. It is important to note that the methods yield, on the whole, the same groupings as those found in traditional taxonomy. What is in questions, is the claim that these methods are independent of any theory about species. From all we have said above, it seems that there is no justification (on the basis of the methods alone) for the claim that species are dispensable. Moreover, the arguments given in Chapter Two, concerning the properties of species, still stand. These properties are characteristics and as we saw, they are not reducible to properties of individuals. Nothing in the methods of numerical taxonomy undermines those arguments.

Numerical taxonomy does not succeed in its claim that species are dispensable. Are the arguments of the second reductive claim any more convincing ?

PART II. NEO-DARWINISM

Neo-Darwinism is an evolutionary theory. The aim of this part of Chapter Five is to see whether theories which deny that species play a role in evolution can hope to achieve a reduction in evolutionary theory from species to genes. Much of Part II is based on Richard Dawkins book The selfish gene. Like most sociobiologists Dawkins argues from a neo-Darwinian point of view. I shall not be concerned with the moral implications of sociobiology. In the first section of Part II, I shall outline the claim made by neo-Darwinians, and I shall assess it in the second section.

1. The selfish gene

For Dawkins, our genetic make-up explains the way we are. Genes interact with each other inside bodies which are the survival machines for the genes. Individuals and species are secondary in as much as they are merely a "gene's way of preserving the genes unaltered" (18). He says that bodies started off as fairly simple protective constructions (cells), but they then evolved to become more and more complex. Genes now "swarm in huge colonies, safe inside gigantic lumbering robots, sealed off from the outside world, communicating with it by tortuous indirect routes, manipulating it by remote control. They are in you and

in me; they created us, body and mind, and their preservation is the ultimate rationale for our existence" (19). And he adds : "A monkey is a machine which preserves genes up a tree, a fish is a machine which preserves genes in the water, there is even a small worm which preserves genes in German beer mats. DNA works in mysterious ways" (20). Since genes are the only effective elements in living organisms, one of the major obstacles to sociobiology has been to account for altruistic behaviour. Dawkins shows that in fact altruistic behaviour is advantageous to individual genes. Altruism exists chiefly between close relatives (offspring, siblings). Therefore, by insuring the survival of a relative, a gene insures that copies of itself, which are more likely to exist in relatives, survive. "What is a single selfish gene trying to do? It is trying to get more numerous in the gene pool. Basically it does this by helping to program the bodies in which it finds itself, to survive and reproduce... the key point... is that a gene might be able to assist replicas of itself which are sitting in other bodies" (21). That is to say, acts which seem to be for the good of the species turn out to be for the good of the gene. For Dawkins, in evolution it is not groups nor individuals which are selected but genes. A gene which gains survival advantages in the gene pool increases in frequency (altruistic behaviour has this effect too), good genes are blindly selected as those which survive

in the gene pool (22). Adaptation for the good of the species does not exist, since if there were only one gene which benefitted itself (survived) but was detrimental to other genes within the species, that gene would spread rapidly throughout the population (23). And as mutations are chance occurrences, such genes have no doubt occurred time and time again, and wiped out any 'good for the species' genes.

What kind of entities function as units of natural selection? For Dawkins the unit of natural selection is that which survives. Tautologically whatever survives is what is selected. Since natural selection is the differential survival of entities, some degree of permanence and reproductive success is required for such entities. They need "longevity, fecundity and copying-fidelity" (24). Actual (token) groups, organisms and genes die, what survives is their type. This means that whether it is groups, individuals or genes which are the units of natural selection depends on whether they are capable of reproducing themselves accurately, of being what Dawkins calls 'replicators'. For Dawkins a replicator is "an entity in the universe which interacts with its world, including other replicators, in such a way that copies of itself are made" (25). A good replicator would be an entity capable of reproducing exact copies of itself, thus insuring that the type survives. The unit of natural selection therefore must be that which survives in

copies of itself. It is also that which benefits from selection pressures in as much as it will increase in frequency in ensuing generations.

For Richard Dawkins, the replicator unit is the gene : "The best way to look at evolution is in terms of selection occurring at the lowest level of all... the fundamental unit of selection is not the species, nor the group, not even strictly the individual, it is the gene" (26). In other words it is genes which compete in the struggle for existence, not individuals, not species. Strictly speaking individuals do not reproduce, genes do. Only genes survive in exact copies of themselves, retain their individuality, and faithfully reproduce any changes that occur within their structure. Only genes have the simplicity and invariance needed for replication. Individuals and groups, Dawkins says, are not replicators since they vary from generation to generation. They are "like clouds in the sky or dust storms in the desert. They are temporary aggregations or federations. They are not stable through evolutionary time. Populations may last a long while but they are constantly blending with other populations and so losing their identity" (27). Romantically, he adds "genes, like diamonds, are forever". For the neo-Darwinians, not only are genes the units selected, but genes also play a causal role in evolutionary change. They exert 'power' as Dawkins puts it (28), in as much as they direct the synthesis

of proteins and thereby direct the making of bodies ("machines created by genes for their own survival" (29)). Ultimately then, according to the neo-Darwinians, evolutionary processes must be understood in terms of genes, and genes alone. This claim does not mean that genes cause evolution, only that evolution results from changes in genes, and (now a causal claim) that genes are solely responsible for the making of bodies. Genes are the only effective elements in terms of which the characteristics of individuals, groups and species may be properly understood.

2. The unit of natural selection

Before assessing the neo-Darwinian claim that the gene is the unit of natural selection, one important comment needs to be made regarding natural selection itself. For neo-Darwinians natural selection is the only mechanism which explains evolutionary change. Evolution for them occurs following changes in genes (due for example to mutations). These changes provide a source of variety upon which the forces of selection can operate. Different genes give rise to different features, some features are better suited to their environment than others, so the genes which produce the more successful features survive. It is questionable whether natural selection is the only mechanism for evolutionary change. The assumption that it is rests

on the idea that every aspect of a living organism is perfectly adapted for a particular purpose, an idea strangely reminiscent of the claims made by the supporters of the argument from design in another context. This implies that organisms are divided into parts, which can only be understood in terms of their separate fitness values, since only the genes for those parts which are fit survive. Yet there are characteristics which have evolved for non-adaptive reasons. The chin, for example, is not the outcome of a separate gene, but of architectural constraints (30) (in this case the alveolar and mandibular growth fields which are both regressing but at different rates, thereby producing a chin). In addition to this, there are many imperfections not accounted for by adaptationists. This means that this facet of neo-Darwinism is in doubt irrespective of whether the gene is or is not the unit of natural selection.

Natural selection is not the only mechanism for evolutionary change, but without doubt it is one of the most important mechanisms. However, is the gene the unit of natural selection? To answer this the terms needed to explain evolutionary processes must be identified. If sentences using terms such as 'individual', 'group', 'species', can be replaced without loss wherever they occur in evolutionary explanations, by sentences using only the term 'gene'; then indeed genes are the units of natural selection.

They are those entities which in the long run survive. They survive in scientific theories in as much as references to them are an essential element of these theories. They also survive in the real (actual) world in the sense of being the entities which actually do benefit from natural selection. Is this unequivocally true of genes?

Neo-Darwinians claim that natural selection operates on genes. An objection often levelled at such a view is that selection pressures act not on genes themselves, but on the way they are expressed in the phenotype. As R.J. Berry says : "it is only phenotypes which are subject to selection, strictly speaking it is impossible for selection to act on an allele because it is phenotypes not genotypes which have children. The reproductive success of a phenotype is its fitness" (31). A gene survives because it has advantages over other genes in a particular environment. But it interacts with the environment only through the phenotype. The force of natural selection therefore acts only indirectly on the genotype. Neo-Darwinians recognise this, but claim that although natural selection acts on phenotypes, it is more properly understood at a more fundamental level of reality.

The proper question, according to neo-Darwinians, is what survives as a result of the selection (what is replicated)? It is what survives that is the unit of

natural selection. So, is it phenotypic characteristics, or is it genes that survives? For neo-Darwinians only genes survive, since only they reproduce exact copies of themselves, unlike their phenotypic expressions which are blurred and blend with each other in subsequent generations. The phenotype "is the all important instrument of replicator preservation : it is not that which is preserved" (32). I shall now outline several points against the claim that the gene - in as much as it is more fundamental than other aspects of living organisms - is the unit of natural selection.

(i) Firstly, for a reduction from phenotypes (a higher level), to genotypes (a lower level), there must be a one to one correspondence between phenotypic traits and genes. But there is no such correspondence. Some phenotypic traits do result from only one gene, or one set of genes, but many result from any number of genes (i.e. different genes can give rise to the same traits). Therefore individuals with the same phenotype could have equal fitness regardless of their genotype. In addition to this many genes are replicated without being selected, or without their phenotypic expression being selected. Elliott Sober discusses this point in "Significant Units and the Group Selection Controversy" (33). He points out that since it is the phenotype which is selected, any other genes which happen to belong to the individual with that phenotype will also

be selected. The role played by individual genes may be relatively insignificant. This point concerning the reduction of phenotypes to genes is worth explaining in more detail. This is what I intend to do in the next few paragraphs.

Undoubtedly genes initiate the process which produces a phenotypic trait. But the direct expression of a gene is merely a protein, and many other components enter into the making of a trait. The fact that a genotypic change will probably have an effect on the phenotype does not mean that a particular trait is reducible to a particular gene. One cannot give a complete analysis of selection without reference to phenotypic traits themselves. It is the phenotypic characteristic that is relevant to selection, it is the properties themselves of fur (warmth, water repellent qualities) that cause the gene responsible for fur to be selected and replicated. This is equally evident in explanations of mimicry, where an edible species of butterfly imitates the wing patterns and colours of a distasteful species, thus avoiding being eaten by predators. It is those wing patterns and colours the predators single out. Natural selection favours a certain wing pattern and colour, whatever genes produced it. What survives is that wing pattern and colour. Dawkins answers this objection by saying that so long as the gene for mimicry survives, selection is acting for the good of that gene, and that gene is

therefore a unit of natural selection (34). But any explanation of the evolution of mimicry by natural selection which did not take phenotypes into account would be incomplete.

A further difficulty with the idea that a reduction from phenotype to genotype is possible, is that the genetic difference between two species does not necessarily correlate with the phenotypic difference between them. The DNA length for Vicia sativa (common vetch) is the same as for men and mice, whereas Vicia faba (broad bean) has a DNA five times as long, although the two plants species are more similar to each other than men are to mice (35). The difference between two species may be due to a difference in karyotype, that is to say a difference not in the DNA itself, but in the way in which the total DNA is broken up into chromosomes (36). For example there is a greater genetic difference between two very closely related species of *Drosophila* (40% of their genes differ), than between man and chimp (37). And yet the two fly species look alike, and the two ape species do not. One reason for this is that genes have different effects in different contexts. In such cases it is not the gene which is selected, but the gene within a context. The context may include other genes and also other characteristics at higher levels possessed by the individual or even the species. In many ways it seems that natural selection acts upon

human beings as human beings, and on chimps as chimps and not on their genes. A one to one reduction from phenotypic characteristics to genes is not possible.

(ii) A second point against the claim that the gene is the unit of natural selection concerns fitness. Quite often what is fit and what survives is not a gene but is either a combination of genes, or a combination of phenotypic traits. Either of these may characterize a species.

It might be useful to look at some examples of genes being selected in a context which necessarily includes other genes or other properties, over and above the gene level. For example in a cold environment mammals with thick fur will tend to survive better than those with thin fur or no fur. Where there is snow mammals with dark fur will fall prey to predators, being more conspicuous than those with white fur. In countries where the snow falls only in winter, animals with white fur will be killed by predators during the summer (this time being more conspicuous than those with dark fur). So, in some regions mammals which have the following combination of genes :
'fur-white in winter-dark in summer' will survive. The ermine (a weasel) is one such animal, so is the stoat in some regions on the British Isles. In this case it isn't the gene for 'fur' that is selected, since the ordinary furry weasel may die in such an area (eaten by predators in winter). It isn't the gene for 'white',

since a white ermine with no fur would die of cold. And it isn't even 'white fur', since a white weasel would also die eaten by predators in summer. So it is the combination of these genes which is selected, i.e. fur which turns white in winter and brown in summer. The same would apply also to any organism which goes through metamorphosis. It is the combination of genes (the life cycle as a whole in this last case) which is the unit of natural selection.

Where natural selection seems to favour a combination of genes one might wish to say that it is a conjunction or a disjunction of genes which is being selected. So genes (this and that gene, this or that gene) would still be the units of natural selection. This would be the last resort for a selfish gene theory. Some combinations such as pink eyes and white fur in albinos might be well explained by this sort of theory. But in most cases this would be inadequate. In the first place, one needs to refer to the phenotype to explain why a trait is selected and in the second place, sets of characteristics behave as units in a way which is not reducible to sets of genes. That it is a combination of genes which is selected is clear if one considers the possibility of there being two or more species, one with the combination and one without. If both compete for the same niche, one species may die out, the other survive. The one that survives, survived because the combination was selected. (It is

true that species need not compete for selection to take place. Selection simply occurs where there are several varying units, what matters is that the possibility of selection is there.)

A well documented case of a combination of genes acting as a unit, is that of sickle cell anaemia given in Chapter One. Here heterozygotes are selected as advantageous over homozygotes. Homozygotes for normal red blood cells die of malaria, homozygotes for sickle-cells die of anaemia, heterozygotes are protected from both illnesses. It isn't the sickle cell gene which is selected, it isn't the normal gene either (since individuals with two of either of these genes die); but it is the combination of both which is selected. This illustrates how one same gene can be lethal in one context, and yet have a high fitness value in another. Richard Dawkins feels that ESS (the concept of an evolutionary stable set of genes), adequately accounts for such cases (38). Each gene in a combination being selected in turn, against the background of other genes which are parts of its environment : "gene-pools come to consist of genes, that do well in each others company"... "If we find harmonious and integrated units at one level, these do not have to be produced by selection among units at that level. ESS theory shows us how harmony and integration at a high level can be produced by selection among component parts at a lower level" (39).

ESS have evolved as a result of the selection at the genic level. With such a mechanism Dawkins might presumably claim in the case mentioned earlier of the ermine (this isn't one of Dawkin's examples), that the gene for fur survives as advantageous over the no-fur gene, white-fur is an advantage in an environment which already includes the fur gene, white-in-winter-only is an advantage in an environment which already includes fur and white. This for Dawkins is how a combination of genes is built up and then can seem to act as a unit (40). It may be that, as Dawkins says, genes manage to survive by getting into good company. But this does not mean that it is that gene which is selected, it survives because the combination is selected. As mentioned above, this is clear from examples involving competition. What survives and is replicated is the combination.

(iii) A third point against the neo-Darwinian claim is the possibility of group selection. Group selection explains sexuality. Sexuality is the mechanism which maintains variety within a group. Without variety groups cannot adapt to environmental changes and therefore tend to become extinct. Variation is in itself advantageous. The polymorphism found in populations of the land snail Cepeae nemoralis given in Chapter One is a good example of selection for variation as such. Without variation the species would die out. Here it is the group of genes as a whole that

is selected. (As mentioned in Chapter One, selection acts against species which do not display variation, those plant species for example which do not reproduce sexually cannot maintain variety, and cannot therefore adapt to environmental changes (41).) A gene for sexual reproduction is therefore for the good of the species since it insures variation. In sexual reproduction the parents can each draw upon either of two alleles for any trait. So for the offspring, who will inherit one allele from each parent, there may be four possibilities for any trait. Of the two the offspring inherits, only one will express itself. The other however may be passed on to the next generation (an additional hidden variation). In mating an individual throws away half of his genes. A gene that allies itself to sexuality has only a 50/50 chance of survival. For the gene it is a risky business, for the species on the other hand sex is wholly advantageous. To repeat, variation and sexuality are selected, and are more beneficial to the species, than to any individual genes. Dawkins counters this by saying that sexuality is maintained simply because it benefits the gene for sexuality, even if it is disadvantageous to all other genes in any one organism (since it means that half of them may not be passed on to the next generation) (42). However, even if sexuality arose as a result of gene selection, the fact that sexual species predominate and that asexual ones die out,

suggests that selection is operating at the level of the group.

Elliott Sober has reviewed examples of group selection. These are cases where selection is of an objective characteristic of the group, which is not individually shared by all the members of the group. In his article "Significant Units and the Group Selection Controversy" (43), he argues for group selection quoting some experiments conducted by Wade (44) on the flour beetle Tribolium castaneum. In these experiments 40 populations of the beetles were used for breeding. Each of the 40 populations founded new populations (new colonies, communities), until each of the 40 had itself created 40 new populations (amounting in all to 40 x 40). Each time they were selected and bred from again. The experimenter selected each time the smallest populations on the one hand, breeding from them several times, each time re-selecting the smallest populations. On the other hand the experimenter also selected the largest populations, and bred from them separately, each time re-selecting the larger populations to breed from. In addition to these two groups of populations (small and large), there was a control group consisting of populations which were bred several times with no selection for population size. In these experiments it is the property of smallness, or largeness of population size which is being selected, regardless of the characteristics of any

individuals within the group. Some populations achieved smallness in numbers by lengthening their developmental time, others by cannibalism, others by a rise in infertility. But for all it was the same property 'smallness' which was being selected. Sober also gives two other examples of group selection occurring in the wild. One concerns Myxoma and rabbits in Australia (45), where there is group selection among the myxoma viruses for low virulence. Since virulent viruses kill their hosts and with them the viruses' own livelihood, the rabbits have survived by becoming immune to the virus, and the viruses have survived by enjoying an overall lower virulence within each virus population. The virulence varies from individual to individual within a population, but each individual virus benefits from the overall low virulence of the group, and therefore has identical fitness. The fitness is determined by a property of the group. The other example quoted by Sober is that of the male segregator distorter t gene in Mus musculus, which determines selection for the group regardless of whether all individuals in the group have the gene or not. Females benefit from the same selective force, although they never carry the gene.

The point made by Sober here can be made concerning almost any group of organisms showing variation. In any group where it is advantageous to have some members with a certain characteristic, there

will be selection of that group in preference to other groups with no members having that characteristic. All the members of the group, where some individuals have the characteristic, benefit from the selection simply by being members of the group. They have the same fitness as those with the advantageous characteristic. Examples of these abound. Any bee benefits from there being good worker bees in the colony, any ant benefits from good guard ants in its population... In each example a characteristic of some individuals make the whole population fitter. And therefore each organism within the population is as fit as any other in virtue of the group's fitness. These points concerning fitness, echo the point made in Chapter Two on the properties of species. Sober points out that accounts of fitness involve quantification over properties (46). If the properties are properties of species, then it is species that are selected in the process of natural selection (i.e. it is species that survive).

Neo-Darwinians maintain, however, that even in such cases it is still genes which are faithfully reproduced and which survive. So it is still genes which are the units of natural selection. This seems to be an over-simplification. First, it isn't genes themselves which survive, but as we said earlier gene types (47). But group types survive too. Individual groups are (as Dawkins has said) unstable, but group types survive just as well as gene types. If a group

with a certain set of characteristics survives, then in future generations it is that phenotype which is being replicated, which survives and therefore which is the unit of natural selection by the terms defined by neo-Darwinians themselves. One could perhaps hold a weak form of neo-Darwinism, maintaining that it is genotypes and a certain environment (or within a certain environment) which are selected and survive. But what makes this theory preferable to the obvious alternative? Natural selection acts on tigers as tigers and not on their genes. It is the same kind of organism which is being reproduced. Species, as kinds of organisms with certain characteristics, do have an important role to play in evolutionary theory.

(iv) So far, in all the criticisms levelled at neo Darwinism, we have accepted that the important question is : which entities survive? But this is not the best way of putting the question since it has become obvious that all sorts of things survive. More precisely we may ask as some neo-Darwinians in fact do: who benefits from natural selection? It may be a question concerning which entities are the most important, genes, individuals or species? Mary Midgley makes this point saying that genes only represent potential individuals, and that potential entities are important only in terms of what they will become : "could we think of the blueprints as more important than the builders, the mix than the pudding,

the match than the fire?" (48). But the question needs to be refined even more. It isn't so much a question about which entities benefit or which are important. The question is : what things survival is invoked in the explanation of evolving processes? All the above points (i to iii) show that it isn't only genes.

Elliott Sober and Richard Lewontin make a related point, and argue that neo-Darwinism in choosing genic fitness as the entity in terms of which we should think of natural selection, are misrepresenting the true causes at work in evolution (49). Without doubt natural selection has an effect on gene frequencies, but this does not mean that it is selecting genes. To say that some entity is selected for is, for Sober and Lewontin, to say that that entity has a causal role in evolutionary processes. Genic fitness is not a cause but an effect. Genic fitness (the fitness of a particular gene) is mathematically derived from genotype frequencies and genotype fitness (the individual's or population's gene complex). Genic fitness is not a cause, it is an artifact. Sober and Lewontin make this point saying that : "selfish genes and grue emeralds bear a remarkable similarity" (50). They add "grue is not a property for the same reason that genic selection coefficients are pseudoparameters in models... non-properties cannot be causally efficacious" (51).

In summary our argument against neo-Darwinism has been, first that there is no one to one correspondence between genes and phenotypic characteristics; secondly that genes cannot be taken singly, their role in selection depends on their context; thirdly that cases of natural selection of groups and of properties attributable to species are not accounted for by neo-Darwinians; fourthly that neo-Darwinians misconstrue the role played by genes in the course of natural selection.

Richard Dawkins believes that his theory is at least as plausible as any other evolutionary theory because it is as compatible with the facts as any other theory (52). But there are too many cases where it doesn't truly fit the facts and in those cases where it does fit well, is mere consistency enough? (53). Other theories might indeed be simpler. It seems that the neo-Darwinian hope of reducing species (or even individuals) to genes cannot be fulfilled.

Conclusion to Chapter Five

Numerical taxonomy and neo-Darwinism are the two main biological theories which make any claim concerning the dispensability of species. Neither theory has been successful in its claim. This is a good indication that species should still be considered as real. In view of this fact we need once again to look at possible criteria for species sameness and

difference. This will be attempted in the next and final chapter of this thesis.

References

- (1) C.E. Bessey "The taxonomic aspect of the species question" American Naturalist, 42, p.218.
- (2) R.R. Sokal and P.H.A. Sneath Principles of numerical taxonomy, p.5.
- (3) Ibid., p.70.
- (4) Ibid., p.22.
- (5) M. Beckner The Biological Way of Thought, p.22.
There is also a similar but updated version of the formal statement of a polytypic concept by Beckner in "Metaphysical Presuppositions and the Description of Biological Systems" in Form and Strategy in Science p.26 Edited by J.R. Gregg and F.T.C. Harris, here Beckner gives as an example Wittgenstein's games. Sokal and Sneath do not refer though to this version.
- (6) See Sokal and Sneath op. cit., p.2. and N. Jardine "A logical basis for biological classifications" Systematic Zoology 18 (1969).
- (7) Sokal and Sneath op. cit., p.65.
- (8) Ibid., p.18.
- (9) V. Pratt "Numerical taxonomy: a critique" J. Theor. bio., 36 (1972).
- (10) Ibid., p. 587.
- (11) Sokal and Sneath op. cit., p.53.
- (12) Ibid.

- (13) In this connection see M. Ruse Philosophy of Biology, chapter 8 "The phenetic challenge".
- (14) E. Mayr The growth of biological thought, p.223.
- (15) E. Mayr Evolution and the diversity of life, p.518.
- (16) Ibid., p.517.
- (17) Similar point in V. Pratt, op. cit., p.590.
- (18) Richard Dawkins The selfish gene, p.25.
- (19) Ibid., p.21.
- (20) Ibid., p.22.
- (21) Ibid., p.95.
- (22) Ibid., p.92.
- (23) Ibid., p.8.
- (24) Ibid., p.37.
- (25) Richard Dawkins "Selection and the extended phenotype" Z. Tierpsychol., 47 (1978).
- (26) Richard Dawkins The selfish gene, p.12.
- (27) Ibid., p.36/37.
- (28) R. Dawkins "Selection and the extended phenotype", op. cit., p.67.
- (29) See R.C. Lewontin "Sociobiology - a caricature of Darwinism" PSA 2, (1976) pp 22/23, and S.J. Gould and R.C. Lewontin "The spandrels of San Marco and the panglossium paradigm: a critique of the adpatationists programme", Proc. R. Soc. Lond., B.205 (1979).
- (30) R. Dawkins The Selfish gene, p.2.

- (31) See R.J. Berry Inheritance and natural selection, p.61 and p.306. See also R.C. Lewontin Genetic basis of evolutionary change, p. 20ff.
- (32) Richard Dawkins "Replicator selection and the extended phenotype", op. cit., p.69.
- (33) See Elliott Sober "Significant units and the group selection controversy" PSA, Vol. 2 (1980), P. Asquith and R. Giere (eds.).
- (34) Richard Dawkins The selfish gene, p.112.
- (35) R.J. Berry op. cit., p.73.
- (36) Ibid.
- (37) In this context see M.J.D. White Modes of speciation, p.43, and all of chapter 3. See also C. Patterson Evolution, chapters 1 and 9 and V. Grant Organismic evolution, p. 286.
- (38) See R. Dawkins The selfish gene, pp. 90/91/92/.
- (39) R. Dawkins "Good strategy and evolutionary stable strategy" in Sociobiology: beyond nature/nuture? (1980), G.W. Barlow and J. Silverberg (eds).
- (40) R. Dawkins, The selfish gene, p.90.
- (41) In this context see M.J.D. White Modes of speciation. chapter 9.
- (42) R. Dawkins, op. cit., p.47.
- (43) Elliott Sober op. cit.
- (44) M. Wade "Group selection among laboratory populations of Tribolium" Proc. Natl. Acad. Sc. USA. (1976).

- (45) These examples quoted by E. Sober are from R.C. Lewontin "The units of selection" Annual Review of Ecology and Systematics, 1 (1970).
- (46) Elliott Sober "Evolutionary theory and the ontological status of properties" Phil. Studies. 40, 147-176 (1981).
- (47) J.L. Mackie "The law of the jungle" Philosophy, 53 (1978). See also E. Sober and R.C. Lewontin "Artefacts, cause and genic selection" Ph. of Sc. 49 (1982).
- (48) M. Midgley Beast and Man, p.91.
- (49) E. Sober and R.C. Lewontin, op. cit.
- (50) Ibid., p.158.
- (51) Ibid., p.176.
- (52) R. Dawkins op. cit. p.131.
- (53) See S.J. Gould "The art of storytelling", New Scientist, Nov. 1978, p.530.

CHAPTER SIXA CRITERION FOR SPECIES SAMENESS

The first chapter described species as genetic and ecological systems. The second chapter suggested that species were natural kinds. The third chapter argued that species were real. Following this it seemed natural in the fourth chapter to look for criteria of species identity. The standard criteria used by taxonomists do not square with our philosophical intuitions. Vagueness is a problem for identity in philosophy. If something is real it should be possible to find definite identity criteria. This is not a problem for biologists, biological sciences are probabilistic and vagueness is not of concern to them. Acknowledging that the failure to find satisfactory criteria for species sameness might seem to cast doubt on the reality of species, we went on in the fifth chapter to examine theories that seek to dispense with species. We found that both the reductive attempts considered failed in their claim. In the light of this failure it seems appropriate to return now to the view that species are indeed real, and look again for criteria of species identity. This is the aim of Chapter Six.

The chapter is divided into three sections. The first section looks at a non-reductive criterion for

classification. The second section attempts a new approach at the individuation and identity of species, and reviews examples which bear out the new approach. The third section draws conclusions, on the basis of the two previous sections, concerning the nature and reality of species.

1. A non-reductive approach

In Chapter Four we saw that all criteria for the individuation and identity of species failed in as much as there were exceptions to each criterion. One cannot exhaustively classify all organisms by their individual characteristics, or by criteria based on reproductive isolation, or by gene pools. Perhaps the difficulty that we encountered in Chapter Four was that we were insufficiently realistic about species and their identity. The problem may have been that we stayed too closely within a reductive pattern of explanation. Indeed all our criteria in Chapter Four were reductive in nature. They all depended on some internal characteristic of populations. They sought to exploit the idea that the individuals or populations of the same species are related to each other in a way in which the individuals or populations of different species are not. This was the basis of all criteria. It was a bottom to top approach, which rested on at least one questionable assumption. This is the assumption that relations between individuals or

populations can be characterized independently of the species they are of. Dropping this assumption, we can now look for a non-reductive criterion of identity or elucidation of species identity, a criterion which is not founded solely in the internal or constituent properties of populations.

Identifying the population to which an individual belongs calls for a different answer from identifying which populations are of which species. The principles of G-relatedness, expounded in Chapter Four, did indeed cast some light on ways of assigning individuals to populations. But, if we make the experiment of seeing species more realistically, then we can contemplate the possibility of assigning populations to species by looking down on populations (and maybe on individuals too) from the level of the species, instead of trying to reach upwards to the species entirely from the level of populations or the level of individual organisms. In this new framework, my main interest is not in individuals, but in populations - both the individuation of populations and the relation of populations to species. For species, as we have said before, are made up of populations. We do not need an antecedent theory about the way in which individuals are identified in order to define species identity - so long as we have the prospect of finding some alternative access to species themselves.

Our failure in Chapter Four will remind anyone who knows, of the long history of failures to find a satisfactory general criterion for the correct demarcation of semantic categories. There, a new perspective on the whole problem has been achieved by Gareth Evans in "Semantic structure and logical form" (1). Rising above the difficulties that have been encountered by all those who have tried to define semantic categories in 'immanent' fashion, from within the recourse of their own particular theory of syntax and semantics, what Evans suggests is a 'transcendent' approach to the problem. The semantic category of a word is the class it will be assigned to by any theory that measures up to the explanation of relating sound to meaning. Categories must be set up in such a way that expressions, that are counted by the best explanatory theory as functioning similarly, end up in the same semantic category. What has to be explained can be stated in a fashion that is not internal to any particular semantic theory. And this is what makes it possible to lay down a general criterion of correct demarcation for all particular theories. Thus words must be assigned to the same category if they behave (function) in the same way. If two words are assigned to two different categories yet behave in the same way, this represents a 'lost generalisation'. But two words should be seen to belong to two distinct categories if this makes possible new and better explanations than

those which are possible if they are seen as belonging to one category only. Bad categorization stands in the way of good explanation. Good explanation will provide "the most determinate and yet economical statement of the kind of semantic contribution made by any expression of a given type". (2).

2. A new criterion for species identity

Taking inspiration from Evans's approach in linguistics, we can now attempt a similar transcendent approach to categorizing populations in biology. The complex nature of biological theory as compared with linguistic theory is bound to make this task difficult. Although linguistic theory is not altogether clear, it is one theory and it can say in advance what its aims and objects are. Biology is clear neither about its objects nor about its aims. Many biological sciences are still young (ecology for example) and ill-defined. The subject matter of biology - the living world - is so complex and diverse that each different way of approaching it constitutes an independent inquiry (evolution, genetics, ecology, physiology and so on). Each of these disciplines concentrates on different aspects of the living world and has its own aims and its own objects (populations, individuals, cells, genes). It is populations we are interested in here. We need a means of identifying when a population is of one species or when it is of another species.

In order to know which sort of theories might be called in to help individuate species, we need to know something about the explanatory role of species. Semantic categories relate sound to meaning, what would be the equivalent of this for species? Very schematically, one could say that species provide an explanation for the characteristics organisms and populations have, by invoking genetic systems and ecological structures. Once we have an idea of the work species do in scientific explanations, then we can proceed along the same lines as Evans does for semantic categories. We can say that any biological theory which enables us to group populations in such a way that their characteristics are explained by a genetic system and ecological structures, can be used in the individuation and identity of species.

Philip Kitcher (3) seems to be doing something along these lines (although he does not refer to Evans), when he suggests that we should stop looking for a criterion for species sameness. He believes that since all criteria have exceptions, we could - as a solution - accept them all. Kitcher claims that each method of identifying species is based on a particular theory about the way in which organisms should be grouped. In this Kitcher is echoing views held by Mayr and others. Mayr, for example, says : "the most important meaning of a classification is that it is a scientific theory, with all the qualities of a

scientific theory. First of all, it has an explanatory value... it is sometimes argued that the descriptive and the explanatory aspects of classifications should be neatly separated. This is impossible. A good classification of organisms is automatically explanatory" (4). Biological theories which underlie taxonomy are theories explaining the overall characteristics of organisms. For Kitcher there are "two main types of inquiry which generate different schemes for classifying organisms" (5). The first relies on historical explanations, invoking the evolutionary forces behind any characteristics organisms or populations may have. This leads to one type of taxonomy. The other concentrates on explanations invoking immediate causes (how one characteristic is affected by something in its proximity). This leads to another type of taxonomy. It isn't clear in Kitcher's article which taxonomies he is thinking of; but certainly cladism goes well with genealogical theories, and morphological classifications (including numerical taxonomy) with the second type of theory.

Kitcher's view does not, however, achieve our aim. It doesn't cover all the theories which do the job 'species' do. There seems to be no good reason why we should limit ourselves to theories in taxonomy. So, following Evans, we can state that our criterion includes any theory which groups populations into

species if by grouping populations into species we make sense of phenomena which otherwise would remain unexplained. We need to bear in mind that the explanation is any explanation of characteristics which is given in terms of genetic systems and ecological relations.

We wish, to make the most determinate yet economical classification of populations into species. We can compare the behaviour, and function (in ecosystems and so on) of different populations. We can say that if by assigning two populations to one species we lose a certain measure of explanation, then this is an indication that the categorization is mistaken. If on the other hand by assigning two populations to one species we gain a certain measure of explanation, then we can take it that the assignment is correct. Another way of putting the same point (and adding strength to it) would be to say that when two populations are seen as of two different species (where they were previously seen as of one species), and when this new categorization opens up new scientific vistas (new areas of research), then this is a strong indication that the new categorization is correct. If, on the other hand, it means that our understanding of natural phenomena is reduced, then the categorization is mistaken. If scientists are successful in their predictions, once the populations are seen as of different species, this is a good indication that

allocating these populations to different species is a correct assignment. In such cases, seeing the different populations as of one species represented a lost generalization. This would show how bad categorization does indeed stand in the way of good scientific explanation.

Following this criterion, suppose we have two populations which differ in some respects only, which for example do not look alike yet share ecological systems. We will say that these two populations will be seen as two races within one species, if seeing them thus enables us to understand natural phenomena which could otherwise not be explained. The two populations will then be seen to be playing 'upon a theme', the populations being variations and the species the common theme. Compare the point Evans makes concerning 'and' and 'or' : he says that [P and Q] and [P or Q] have the same semantic structure "the word 'and' plays upon a theme it has in common with 'or'" (6). Linguistics imposes a typology of semantic categories which are like themes. The members are like variations in these themes. Conversely, if studies on two populations, which had appeared to be two races of one same species, yielded greater scientific advances (in understanding and prediction) when the two populations are seen as of two species, then we would say that these are not different races within one species but indeed populations of different species.

It may appear that we have two different tasks which should be distinguished here. One is the assignment of populations to taxonomic categories (race, subspecies, species), where we ask whether the differences existing between two populations make them of different species or simply of different races within one species. This task would involve comparisons with other populations, and the question asked would be : are the differences species specific or racial? The other task is to decide whether two populations are of the same species or of two different species. This is not taxonomic ranking, we would not be looking here for the taxonomic categories (races, subspecies, species) of these populations (i.e. we would not be asking whether these two populations should be classified as of different races, sub-species or species). But we would be looking for their taxa within the species category alone (i.e. are these two populations both of the A species or of the B species, or is one of the A species and the other of the B species?). These indeed appear two different tasks (taxonomic ranking and assignments within the species category), but in both cases the question is in fact the same. We find two populations, similar in many respects but different in some, and we ask ourselves : are they of the same species or of two different species? And indeed another way of putting this same question is : are these two populations of one species

with racial variations (in which case their differences would be merely racial and not species specific), or are they of two species (each with its own specific characteristics)? This is now the same question as the one in the first task outlined above, e.g. one of ranking taxa (are they of different races, subspecies or species?).

To summarize, species can be seen as themes and races and sub-species as variations upon these themes; two races will be said to be of the same species or of different species depending on the explanatory advantages of such categorizations. Such explanations, if they involve species, are given in terms of genetic systems, ecological relationships (and whatever else we know characterizes the species). The decision whether to attribute the differences between populations to differences in race, subspecies, or species will depend on the heuristic value of any one of those decisions.

Unlike all the criteria given in Chapter Four, this criterion applies equally well to sexual and to asexual species. Indeed, the decision to assign two populations to two separate species does not necessarily depend on their reproductive habits. Would we still, as in Chapter Four be left with a problem concerning vagueness? Yes, but to a much lesser degree. There will be times when a population could equally be said to be of one species or of another, in as much as nothing is to be gained by classifying it as

of one species or of another. We can learn from Science when decisions have to be arbitrary, as for example in cases of rings of races (gulls' example in Chapter Four). Here the ring is divided into two species, because seeing it as one large diverse species simply does not explain enough (there are too many differences between the end populations, in terms of ecology and so on). Populations central to each species will be clearly different, and yet there will be intermediary populations placed arbitrarily in one of these two species.

If we accept that species are real, and that nature clearly separates populations into species, then we can use biological sciences to see whether the criterion outlined above matches biological practice. To this end, I shall now review some examples. We have already described in the PhD many suitable examples. The decision to assign the populations responsible for Malaria and the populations responsible for River Blindness to different species, enabled scientists to answer a host of questions, and to plan a programme of eradication. Seeing the populations as of different species meant recognizing different reproductive patterns (e.g. different gene pools) and different ecological patterns. These explained in turn, the populations characteristics. This means taking different measures to control the disease. Legionnaires Disease was another example where

identifying populations as of different species led to improved prevention and cure, following a recognition of different breeding habits and different ecological habits. These are all examples of populations first seen as of different races within one species, and then reclassified as of different species. In each case, research was aided by the reclassification. Scientific spin offs resulted from seeing the populations as of different species, rather than classifying them as anything else. There are also examples of populations being seen as of one species when previously one had thought they were of two species, for instance the realization that the smoothed-stemmed foxglove is of the same species as the hairy-stemmed one (both are Digitalis purpurea). This is important for the production of Digioxin (used in heart failure), which is extracted from Digitalis. The realization that the two kinds of populations of locust (gregaria and solitaria) are not of two different species, but two alternative forms of the same species is another example. This has enabled farmers to control locust swarms by controlling the solitary form alone.

We are now in a position to be more precise about the species category, and attempt to specify what is special about the species classification (as opposed to any other classification). Some classifications in biology are at taxonomic levels other than the species, and some cut across species. Examples of the former

would include classifications into races, genera, families. These could be for the purpose of making generalizations which apply to only one feature found in all organisms at that level. For example generalizations about gestation periods or lactation would apply to all mammals. Generalizations about certain diseases may apply only to some racial groups (sickle-cell anaemia and blacks for instance). An example of a classification which cuts across species would be all the plant species which produce anti-histamine, this sort of classification is used in the drug industry. In contrast to these classifications, does the species category have any privileged status in biology?

What does looking at organisms as being of different species (as opposed to anything else) entail? In all cases, seeing the populations as of different species, or as of one species, means looking at the situation from a different angle. It means adopting a different scientific attitude towards understanding the situation and towards predicting future paths of development. In particular, it means seeing the populations as different genetic units and different ecological units. If populations are of the same species certain consequences follow. As we have seen in this chapter, sharing a gene pool and an ecology means that characteristics will be the same for the populations of one same species. These consequences do

not follow when the populations are of different species.

3. Conclusion

The different consequences which follow from assigning populations to species imply that certain relationships hold between the members of a species. Correct classification leads to good results in biology. The examples also vindicate the assumption we started with, concerning species. Seeing species as genetic and ecological enables one to explain the characteristics of populations.

Species represent well integrated complex systems. As we saw earlier in the thesis these systems have their own rate of loss and replacement, and thus maintain their stability. This degree of integration does not exist in any other taxonomic category, whether it be at the level of races or genera. Races are not determinate systems and the members making up a genus are in no way related to each other. Species act as homeostatic yet dynamic systems, when changes occur they are usually controlled and regulated within the species (as in the case of the Axolotl or the locust). Species regulate themselves in response to changes in the environment. As well integrated systems, species are not so much different groups of organisms as distinct groups of organisms. They may have very few differences between them, yet quite definite gaps

between them.

In conclusion to this thesis we can say that there is much to be gained from seeing species as real. Furthermore, given that contemporary statements in biology are committed to species, it would be absurd to accept the truth of these statement, and yet deny the reality of species. Different philosophical attitudes towards species can accommodate the fact that species are real. However, the view I have taken in this thesis has been that species are natural kinds, and that what makes a species the species it is is not a description but having a particular nature.

We may still wonder why there should be species in nature at all? Why did evolution not produce merely a series of varying organisms? Mayr (7) answers this question by saying that forming species makes evolutionary sense. Indeed we have already seen that competition and survival lead to speciation, in forming say a new genotype which produces organisms which can exploit new niches in the environment. This advantage can only be maintained if genotypes are preserved and form discrete groups in nature.

REFERENCES

- (1) Gareth Evans "Semantic structure and logical form" in Truth and meaning : essays in semantics, G. Evans and J. McDowell (eds.).
- (2) Ibid., p.211.
- (3) Philip Kitcher "Species", Ph. of Sc. 51 (1984), pp.308-333.
- (4) Ernest Mayr Principles of systematic zoology, p.79.
- (5) Kitcher op. cit., p.321.
- (6) Evans op. cit., p.214.
- (7) Ernest Mayr Evolution and the diversity of life, p.520.

APPENDIXDIFFERENT LEVELS OF REALITY IN BIOLOGY

The aim of this section is to give an outline of the biology of different aspects of the living world, and the relation between these different aspects.

1.	The living world	P.218
2.	Classification of organisms (taxonomy)	P.219
3.	Cells	P.221
4.	Microstructure of cells	P.221
5.	Nucleus of the cell	P.222
6.	Chromosomes	P.222
7.	Reproduction	P.224
8.	Genes	P.228
9.	DNA	P.229
10.	Translating the genetic code	P.233
11.	Building a body	P.233
12.	Sources of variation (mutations etc.)	P.237

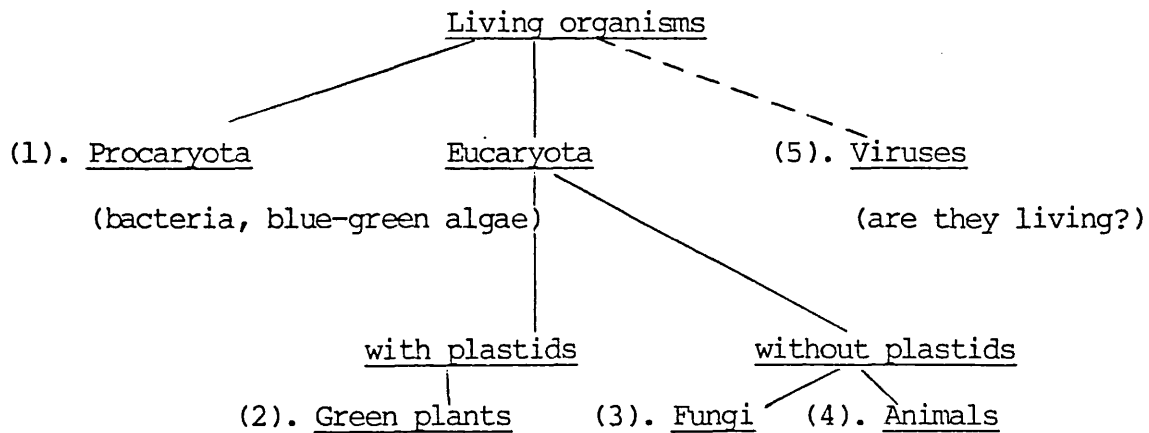
Orders of magnitude:

<u>Entities</u>	<u>true size</u> (logarithmic)	<u>Equivalence.</u>	
<u>a flea</u>	10^{-3} m (1mm)	10000m (10km)	
<u>an average cell</u>	10^{-6} m (10 μ m)	100m	
<u>a macromolecule</u> (proteins are macromolecules)	10^{-8} m (10nm)	10cm	limit of <u>microscope</u>
			limit of <u>electron microscope</u>
<u>a molecule</u>	10^{-9} m (1nm)	1cm	
<u>an atom</u>	10^{-10} m (10 ⁻¹ nm)	1mm	

m = metre, cm = centimetre, mm = millimetre

μ n = micrometre, nm (nanometre)

1. The living world is divided into five kingdoms:



Procaryota : cells without membranes (to separate the organelles within the cell).

Eucaryota : cells with membranes.

Plastids : these enable plants to use light (energy) to drive synthetic reactions (photosynthesis is the process by which plants convert sunlight into energy). Fungi and animals get their energy by consuming other living organisms.

2. Classification of organisms :

Taxonomy is the classification of organisms. Organisms are grouped into species, species are grouped into genera, genera into families, families into orders, orders into classes, classes into phyla (for animals) or divisions (for plants). Each of these categories comprises different taxa. Species are the lowest ranking taxa.

Examples :

An animal (Homo sapiens):

A plant (Rosa canine):

Sapiens	←—————	Species	—————→	Canine
Homo	←—————	Genus	—————→	Rosa
Hominidae	←—————	Family	—————→	Rosaceae
Primate	←—————	Class	—————→	Pteropsida
Mammalia	←—————	Order, Subdivision	—————→	Embryophytina
Chordata	←—————	Phylum, Division	—————→	Chlorophyta
Animal	←—————	Kingdom	—————→	Plants

Chordata : animals which have segmented bodies, axial notochords, dorsal tubular hollow nervous systems, paired gill slits, bilateral symmetry.

For plants one often adds between family and class: series (here dicotyledonae) and subclass (here angiospermidae).

Pteropsida : ferns and seed plants.

Embryophytina : embryo forming plants.

Chlorophyta : green plant.

3. Cells: All living organisms are made of cells, unicellular organisms of one cell. Cells come in different shapes and sizes.

4. The ultrastructure of the cell:

In human beings, all cells have a nucleus except red blood cells. The size and shape of the nuclei varies from species to species, and within a species from organism to organism. Cells have a membrane surrounding them, inside the membrane is the cytoplasm. Several structures exist within the cytoplasm, these are subcellular organelles. They include mitochondria, centrioles, endoplasmic reticulum, Golgi apparatus, ribosomes and the nucleus.

Each organelle is highly specialized :

The membrane is organized so as to let only certain substances into the cell and others out.

The mitochondria make the energy for the cell.

The centrioles are involved in cell division.

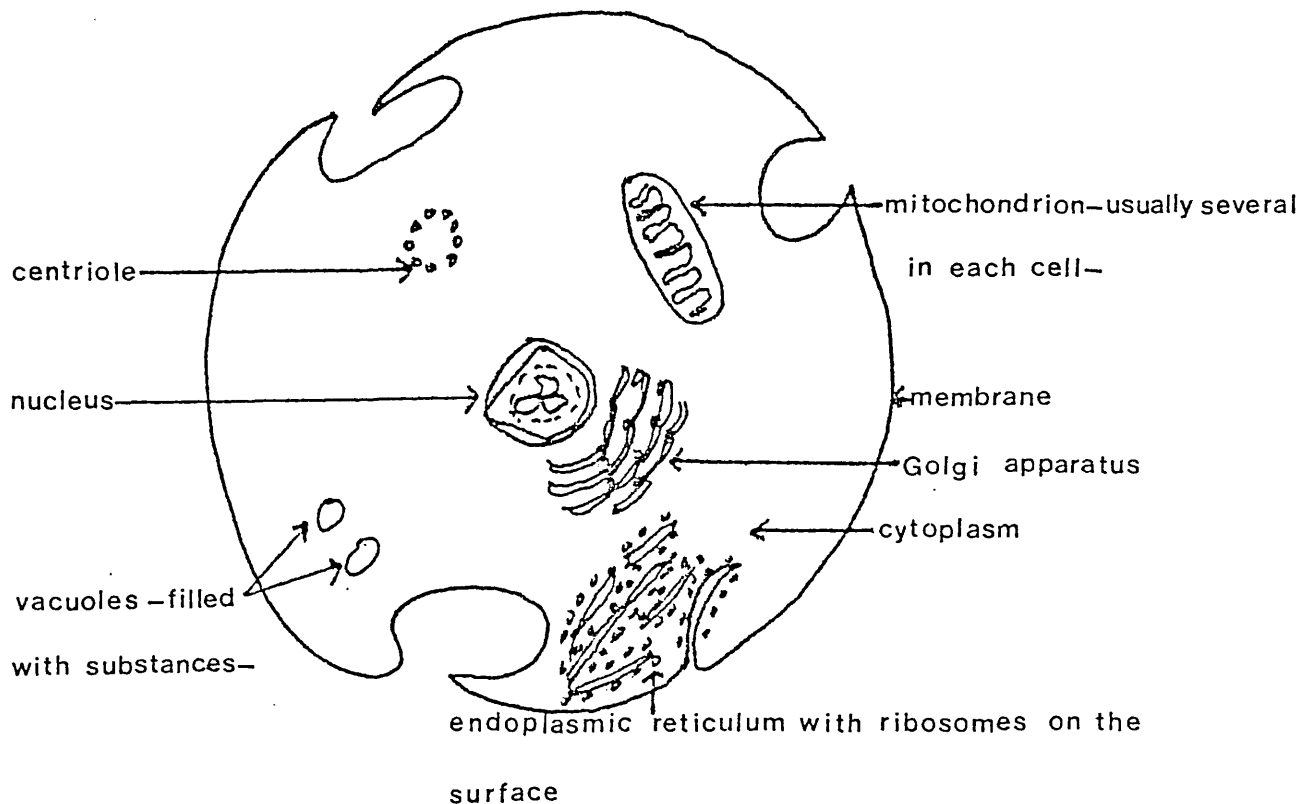
The endoplasmic reticulum is involved in protein synthesis (packaging chemicals).

The Golgi apparatus adds carbohydrates to proteins.

The ribosomes assemble proteins.

The nucleus carries the genetic information.

Figure 18 Schematic view of a generalized cell :



5. The nucleus:

The nucleus is partially separated from the cytoplasm, which surrounds it, by the nuclear envelope. The nuclear envelope has pores to enable molecules to go in and out of the nucleus. The nucleus is made up of a nucleolus, and a general substance called the chromatin network. During cell division, the chromatin organizes itself into chromosomes. Only at this time do the chromosomes become visible. The chromosomes carry the genetic information. All cells have a nucleus (with a few exceptions) which contains chromatin. Every cell in the body carries the whole genetic information for that individual, within its nucleus.

6. The chromosomes:

Chromosomes are made of protein (70%). This protein does not function in the transfer of genetic information. It is the role of nucleic acid (DNA, 30%) to pass on the genetic information. The quantity of deoxyribonucleic acid (DNA) contained within the nucleus is constant within the cells of the organisms of any one species. It does, however, vary from species to species.

Each species has a fixed number of chromosomes in each and every cell of its members. Human beings have 46 chromosomes, drosophila 6 to 12 depending on the species.

Chromosomes form pairs within the nucleus. Half the chromosomes are inherited from the mother, and half from the father. In human beings there are 22 matching pairs of chromosomes (same size, shape, each half coding for the same traits). The last pair do not match, they are the X and Y chromosomes, XX codes for female, XY for male.

Photomicrograph of stained human chromosomes:



1 Chromosomes of normal Human Male (displayed in sequence below)

2 Same but for Female

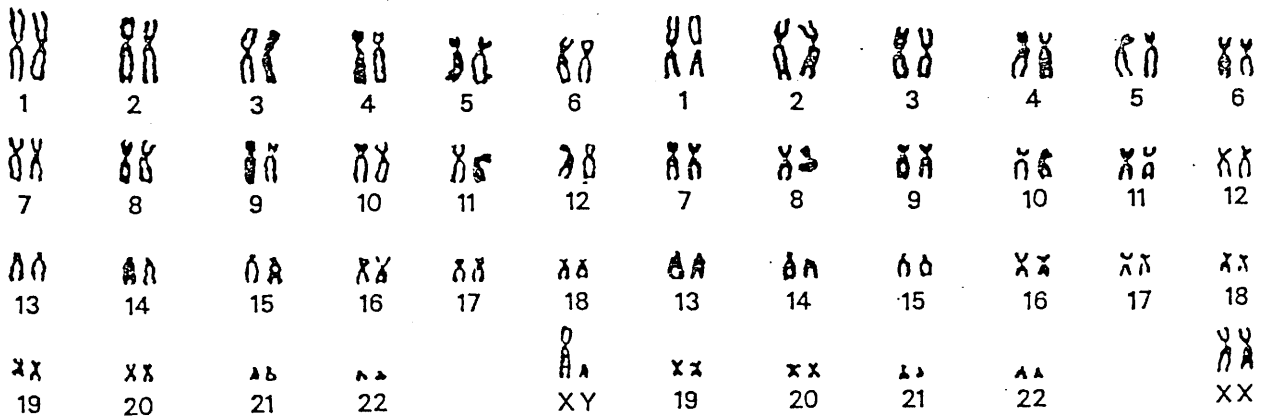


Figure 19

7. Reproduction:

Cell division occurs constantly throughout the body, new cells being needed for growth, repair and replacement. When division occurs, each chromosome within the nucleus of the cell separates into two strands (chromatids). These strands then separate into two identical sets of chromatids. The cell then divides. The two new cells have identical chromosomes to the original cell.

This process is called mitosis :

Mitosis:

(imaginary organism)

cell divides :

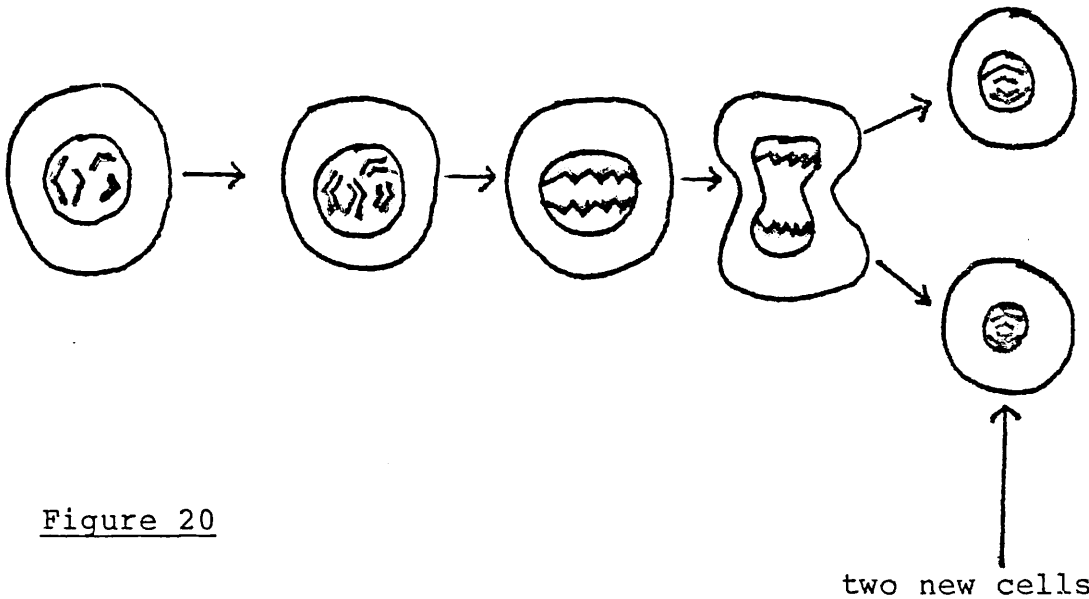


Figure 20

In reproduction, cells undergo a different kind of division. This occurs in specialized reproductive organs (ovary, testis). Here the cells undergo meiosis. As with mitosis the chromosomes separate

into two strands (chromatids), but also pair up. So for example, human being's 46 chromosomes form 23 pairs. When the cell divides half the chromosomes go into one new cell and the other half into the other. But unlike mitosis, the two daughter cells now have different chromosomes (pairs of chromosomes code for the same traits, but often different aspects of those traits, for example blue or brown eyes). One individual having received chromosomes from both parents may carry a gene for blue eyes (from her mother), and one for brown eyes (from her father). At meiosis, the chromosome with the blue eyed gene goes into one daughter cell, the chromosome with the brown eyed gene into the other (whereas in mitosis it was an identical pair blue/brown into each new cell). The daughter cells then divide again, this time following the same mechanism as mitosis, each daughter cell dividing into two identical new cells with half the chromatids each. The new cells then have 23 chromatids each. The final outcome of meiosis is 4 new cells, each pair of cells having different chromosomes from the other pair, but each cell within a pair having identical chromosomes.

Meiosis (same imaginary organism as above, with only 4 chromosomes):

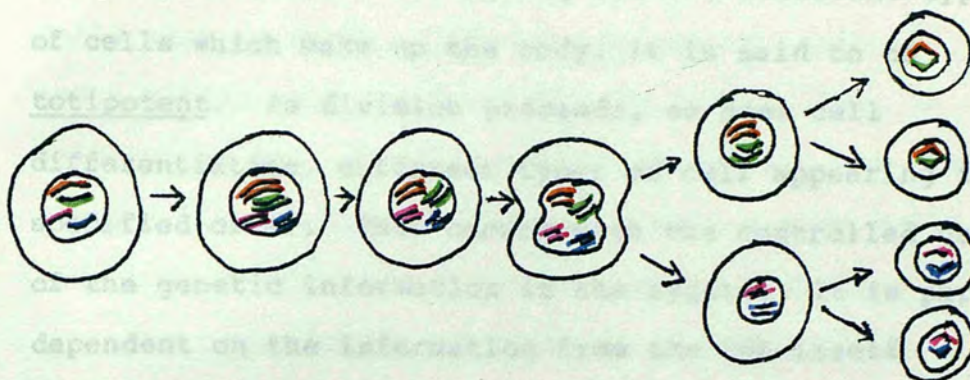


Figure 21

4 new cells

Only germ cells (egg and sperm) are used in reproduction. These cells are called gametes. Unlike the other cells in the body which for human beings have 46 chromosomes, germ cells have 23. At reproduction, when two gametes fuse to form a zygote (which will grow into an embryo), the new cell (the zygote) has 46 chromosomes. Germ cells are haploid (they contain only half the number of chromosomes), all other cells are diploid.

It is these germ cells, produced by meiosis, that are used in reproduction. Fertilization is the fusion of 2 germ cells, one from a female, the other from a male (egg and sperm). These two cells form a zygote. This single celled zygote, immediately undergoes mitosis and forms two cells which divide into four cells, then 8, 16, 32 etc... as the embryo grows. There is no direct route of growth between a zygote and an adult. In the human species for example, neither the zygote nor the adult have a tail, but the embryo does.

A zygote contains all the information (and has the capacity to use it) for making all the different types of cells which make up the body, it is said to be totipotent. As division proceeds, so does cell differentiation, different types of cell appearing in a specified order. This occurs with the controlled use of the genetic information in the zygote. It is partly dependent on the information from the DNA itself (predetermined timing of the use of genetic information is particularly evident in metamorphosis), and partly on the interaction with the environment (signals from the environment which switch genes on and off).

The development from zygote into differentiated cells of an embryo is called morphogenesis. The influence on development from surrounding cells is crucial to differentiation, this is called embryonic induction. A cell will develop in a certain way depending on where it finds itself (for example becoming nerve cell if it finds itself near other nerve cells...). In a developing embryo a cell, which because of its location would have become one type of cell, can be transplanted to another part of the embryo and become another type of cell. But once a cell becomes set on a path (its position having influenced which genes are switched on) it is determined, and will thereafter develop into a particular type, it can no longer change its path. In some organisms cells remain totipotent, for example one can take a cell from a

full grown carrot and it will eventually grow into a new carrot (differentiating into skin, leaves etc..). Cells such as these, although totipotent, maintain their differentiation according to their place, in association with their neighbouring cells. All cells contain all the genetic information, but most cells cannot be reactivated to produce a new organism.

The organization of cells is also important, a hand is different from a foot, yet each contains the same type of cells (skin, bone, muscle, blood, etc...).

8. Genes:

Genes are carried on the chromosomes. Genes code for traits. The DNA of the chromosomes are the genes. The total number and kinds of genes encoded in the DNA of a nucleus is the genotype. The total number of traits an individual has is the phenotype. The genes carry the information needed for the body to make a trait (such as 'blue eyes'). Chromosomes are like threads with the genes carried along them. The genes are lengths of DNA (DNA is a giant molecule), the genes are sequences of chemical subunits along the DNA molecule. The part of the chromosome which is not DNA is protein. Each gene or sequence of subunits is a template for the synthesis of one protein molecule (proteins eventually build up into the visible characteristics we see e.g. blue eyes, this is a long and complicated process; strictly speaking the outcome

of a gene is only a protein). The DNA molecule on one human chromosome contains in the region of 100 million subunits. These subunits are sufficient to code for 5 million proteins, in fact only 100,000 different types of protein are known in our bodies. What the surplus DNA is doing, no one knows for sure.

9. Deoriboneucleic acid (DNA);

DNA is a long molecule with a chain-like backbone. DNA probably looks like a double helix. Each strand of DNA is a long molecule itself, the two backbones of both these strands crossing over :

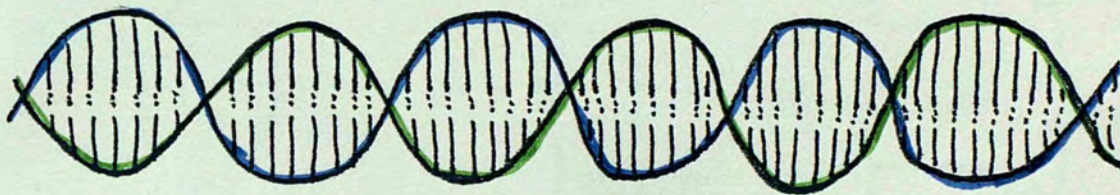


Figure 22

(schematic)

The two strands twisting round each other carry bases, these bases form bonds between the two strands, holding them together. There are only 4 bases in DNA: adenine (A), thymine (T), guanine (G) and cytosine (C).

Adenine always bonds with thymine (A-T), and guanine with cytosine (G-C). The two strands of DNA can unzip, and then synthesize two new strands, each joining on to the old ones, the two original strands act as templates, guanine joining cytosine, cytosine joining

guanine, adenine joining thymine and thymine joining adenine. The backbone of the strands is made up of sugars and phosphates (see Figure 23). Each DNA strand can be represented chemically (see Figure 24).

Figure 23 DNA replication

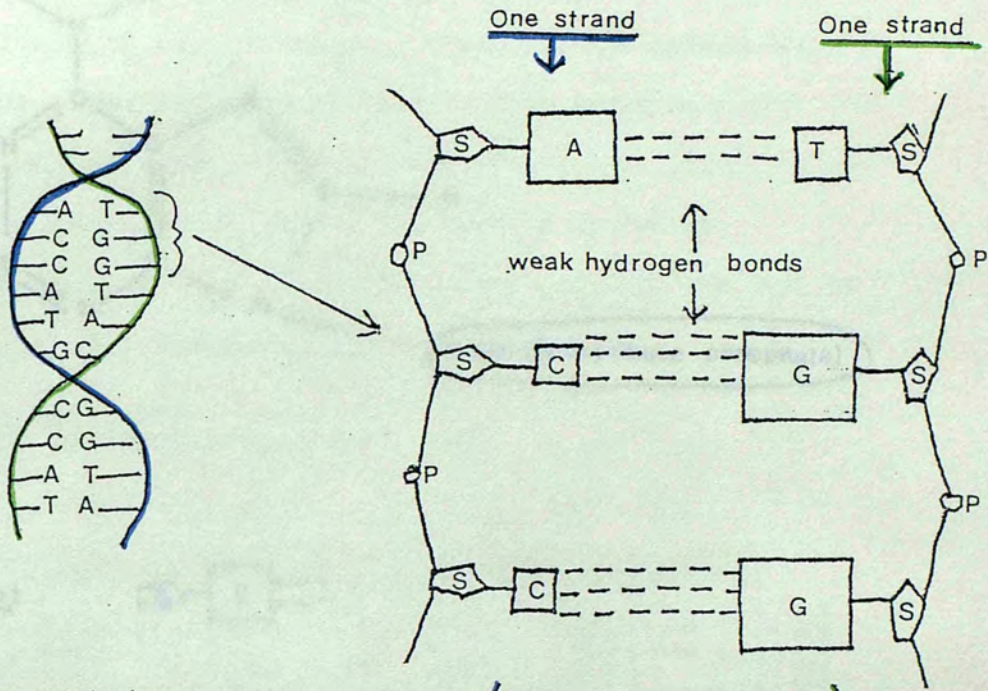
H = hydrogen, N = nitrogen, C = carbon, O = oxygen, the lines between show hydrogen bonds

Figure 23 DNA replication

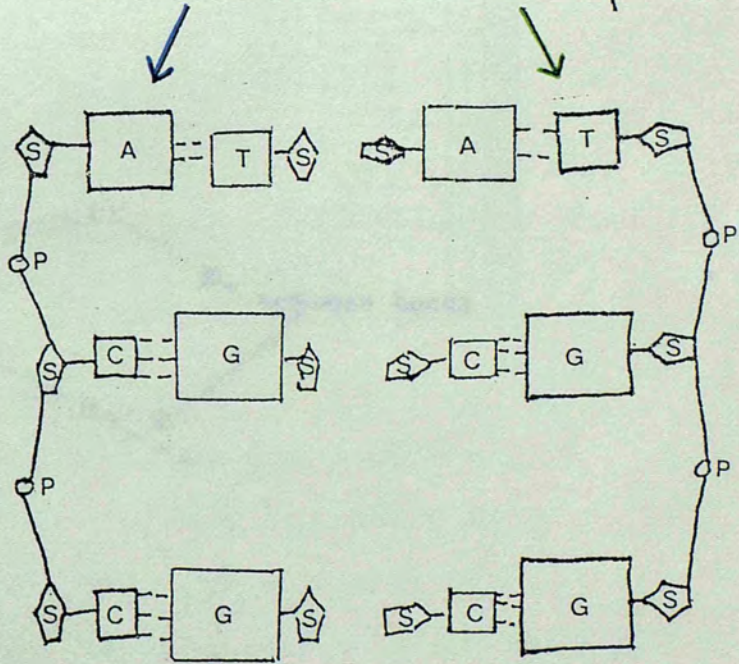
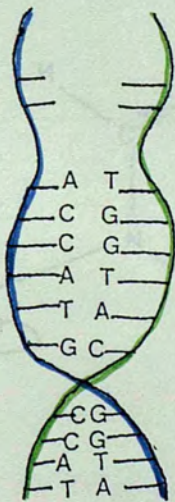
Adenine:

S = sugar P = phosphate

Graphic representation:



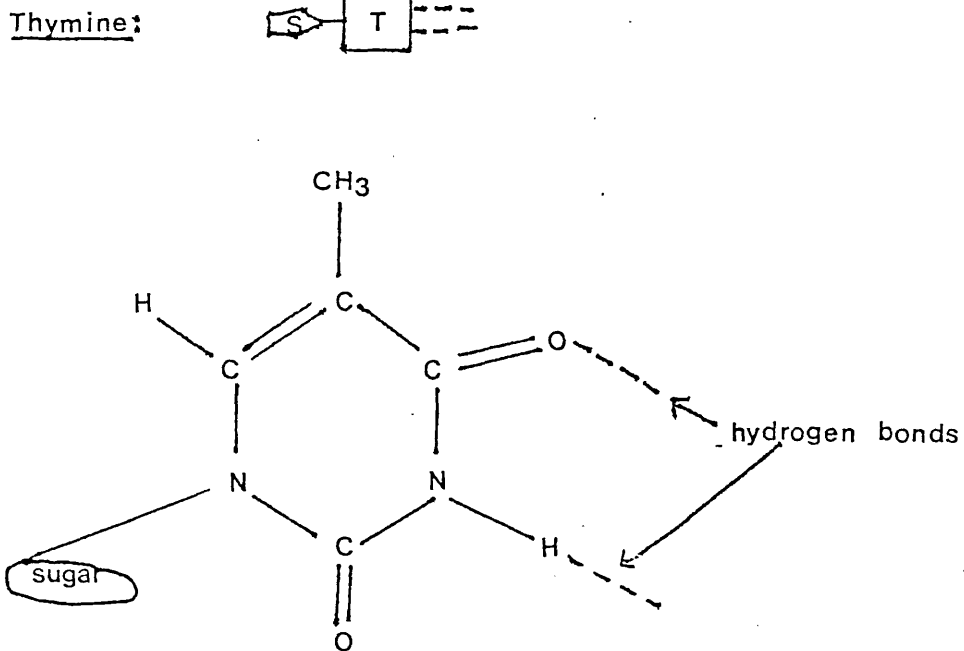
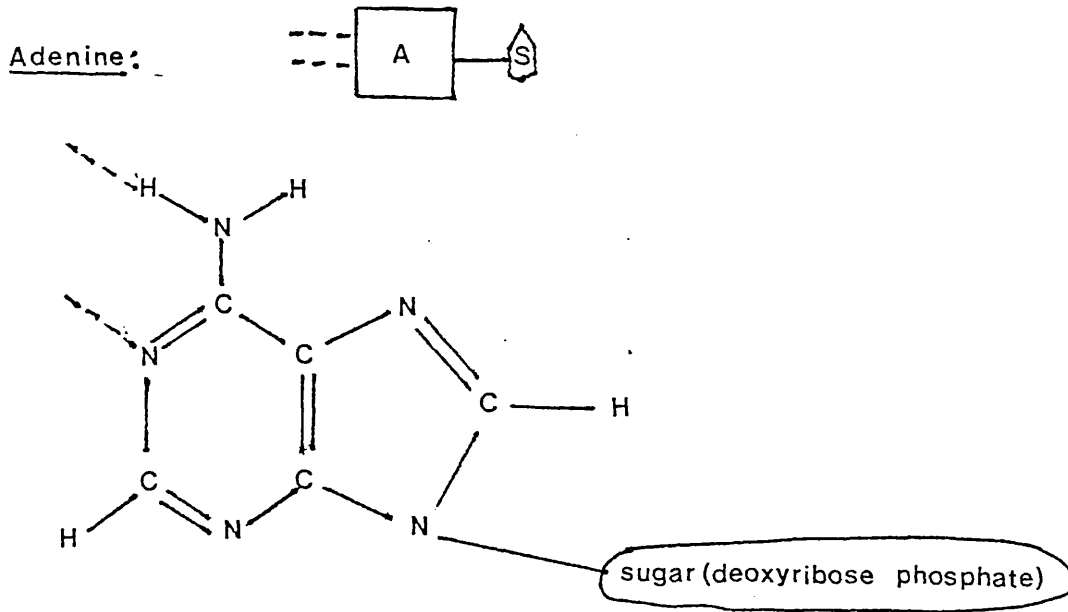
During the unzipping:



two new molecules forming along the old ones

Figure 24 DNA, chemical structure:

H : hydrogen, N : nitrogen, C : carbon, O : oxygen, the lines between them are chemical bonds.



10. Translating the genetic code:

The four bases on the DNA molecule (A,T,G,C) form a code. This is the genetic code. This code is universal, it is the same from yeast to human beings. Three bases taken together form a codon, each codon codes for one amino acid. Amino acids are the building blocks for proteins. Proteins as we saw make up bodies. There are 64 codons in the genetic code, several may be needed to code for one amino acid. There are 20 amino acids. Some codons serve as punctuation, for example a 'stop' to signify the end of some piece of information.

Figure 25 The genetic code:

		SECOND LETTER					
		A	G	T	C		
FIRST LETTER	A	AAA Phenylalanine	AGA Serine	ATA Tyrosine	ACA Cysteine	A	THIRD LETTER
		AAG Phenylalanine	AGG Serine	ATG Tyrosine	ACG Cysteine	G	
		AAT Leucine	AGT Serine	ATT Stop	ACT Stop	T	
	G	AAC Leucine	AGC Serine	ATC Stop	ACC Tryptophan	C	
		GAA Leucine	GGA Proline	GTA Histidine	GCA Arginine	A	
		GAG Leucine	GGG Proline	GTG Histidine	GCG Arginine	G	
		GAT Leucine	GGT Proline	GTT Glutamine	GCT Arginine	T	
	T	GAC Leucine	GGC Proline	GTC Glutamine	GCC Arginine	C	
		TAA Isoleucine	TGA Threonine	TTA Asparagine	TCA Serine	A	
		TAG Isoleucine	TGG Threonine	TTG Asparagine	TCG Serine	G	
		TAT Isoleucine	TGT Threonine	TTT Lysine	TCT Arginine	T	
	C	TAC Methionine	TGC Threonine	TTC Lysine	TCC Arginine	C	
CAA Valine		CGA Alanine	CTA Aspartic Acid	CCA Glycine	A		
CAG Valine		CGG Alanine	CTG Aspartic Acid	CCG Glycine	G		
CAT Valine		CGT Alanine	CTT Glutamic Acid	CCT Glycine	T		
CAC Valine	CGC Alanine	CTC Glutamic Acid	CCC Glycine	C			

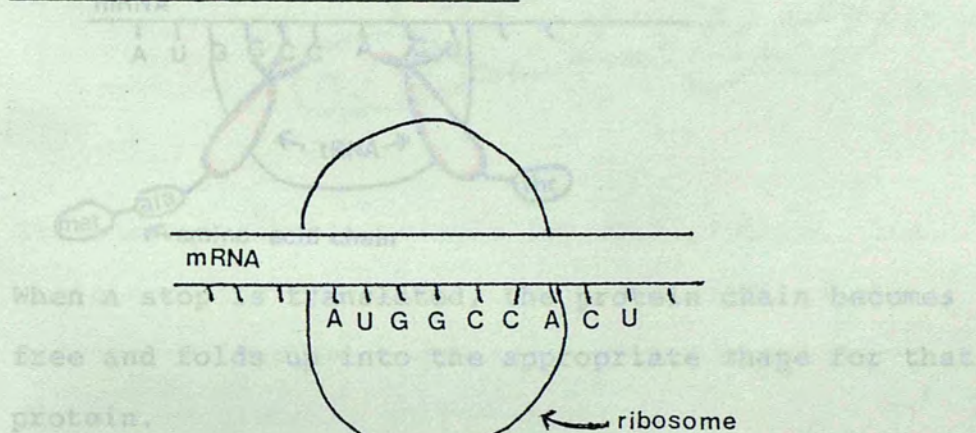
11. Building and maintaining a body:

DNA carries the genetic code, mRNA is a single strand molecule which carries the code from the nucleus to the cytoplasm (messenger RNA). DNA acts as a template for mRNA; mRNA has also 4 bases complementary

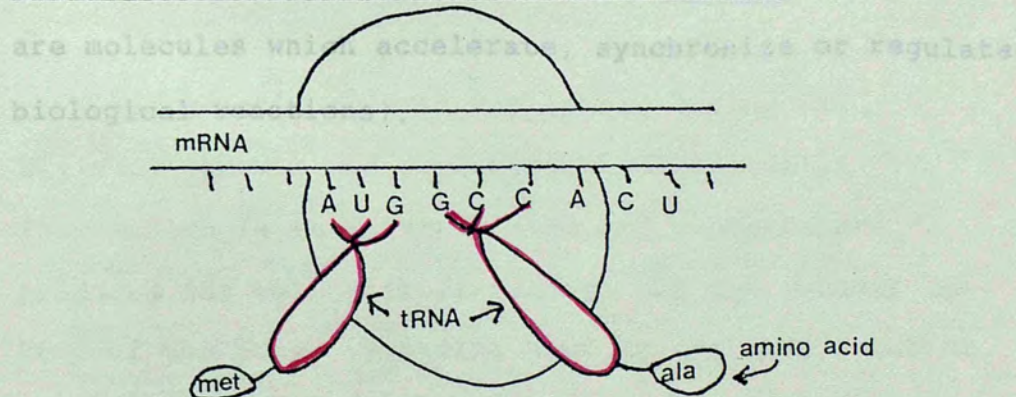
to those of DNA except that instead of thymine it has uracil (U), which bonds to adenine. In the cytoplasm, the code is translated on the ribosomes into amino acids. Here another RNA binds mRNA to the anticodons carrying the amino acids corresponding to mRNA's codons. This new RNA is called transfer RNA (tRNA). So the sequence of decoding is DNA----> mRNA----> tRNA----> amino acids----> proteins. The sequence is also: nucleus----> ribosomes-----> protein free in the cytoplasm----> out of the cell.

Figure 26

mRNA bonding to the ribosome :



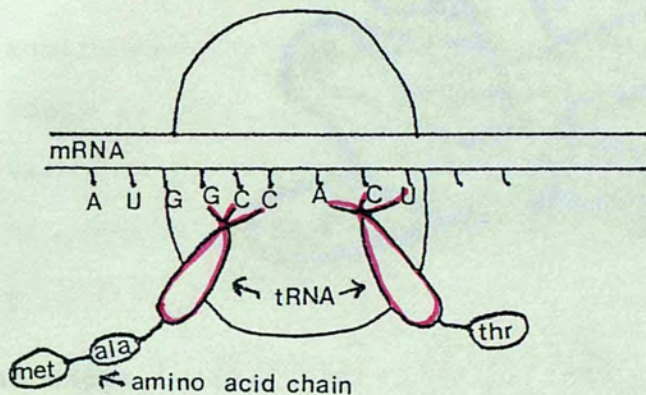
tRNA and its anticodon carrying amino acids :



For example : AUG-GCC-ACU etc... form the message which corresponds to : n-formyl methione (met), alanine (ala) and threonine...

A reaction takes place between the amino acids, bonding them together as they leave each tRNA anticodon. The amino acids then form a chain, while tRNA moves along the ribosome as the next bit of the code is being translated :

Figure 27 . Building a chain of amino acids :





When a stop is translated, the protein chain becomes free and folds up into the appropriate shape for that protein.

Each length of DNA determines the structure of a particular protein chain (including enzymes, enzymes are molecules which accelerate, synchronize or regulate biological reactions).

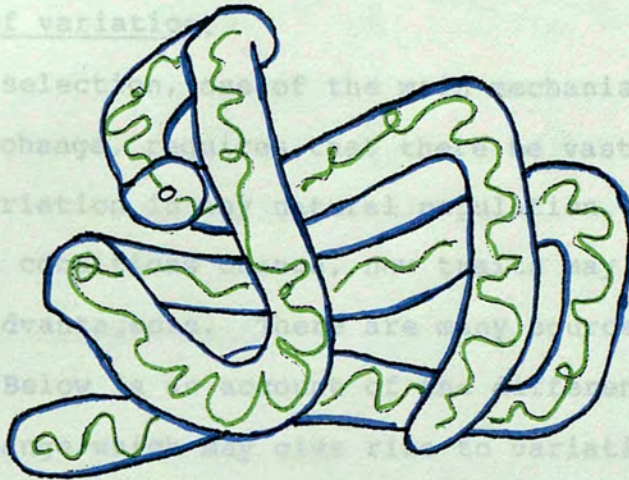
Figure 28

An example of a folded chain of amino acids -the protein myoglobin :

overall shape : 

amino acid chain : 

(both very schematic)



The shape is characteristic for that protein. The chain contains 153 amino acids. The first 15 are :
 glycine----leucine----serine----aspartic acid----
 glycine----glutamic acid----tryptophan----
 glutamine----leucine----valine----leucine----
 asparagine----valine----tryptophan----glycine---- etc.

The genetic code is replicated during cell division (growth and replacement). The genetic information is read, translated and proteins are produced for cell differentiation and the general upkeep of the body. Proteins used by the body (such as haemoglobin in the blood cells) are constantly being

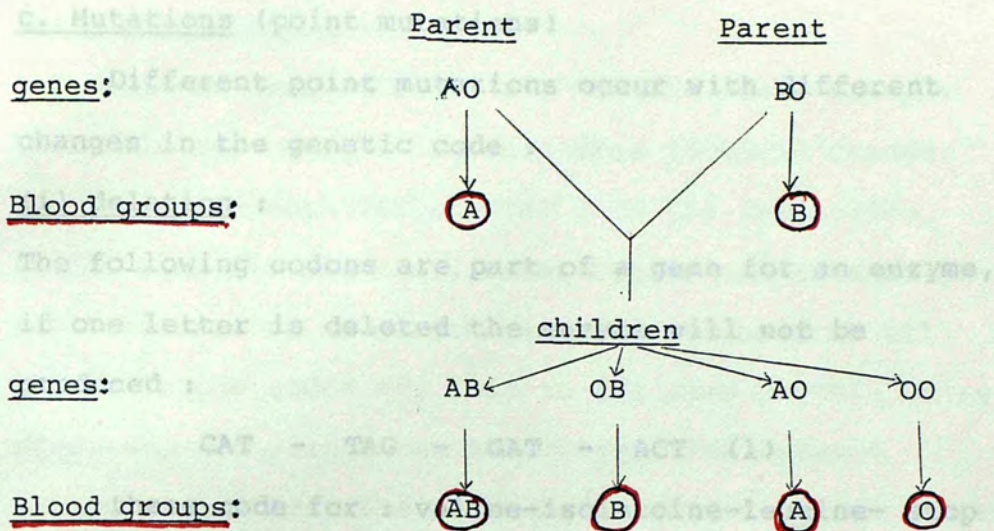
made (translated from the genetic code). Other substances that circulate through the body (enzymes, hormones etc...) once produced in the cell, pass through the cell membrane into the blood stream, and into a cavity such as the gut.

12. Sources of variation:

Natural selection, one of the main mechanisms for evolutionary change, requires that there be vast amounts of variation in any natural population. As environmental conditions change, new traits may be found to be advantageous. There are many sources of variation. Below is an account of the different types of genetic change which may give rise to variations.

a. Multiple alleles

This leads to a reshuffling of genes. For example, there are 4 different human blood groups : A, B, AB and O. A and B are dominant to O. That is to say that an individual who inherits an A or a B from one parent, and an O from the other will have an A or B blood group. A genes are neither dominant nor recessive to B genes, therefore an individual who inherits an A from one parent and a B from the other, will have an AB blood group. An individual will only have an O blood group if he receives O from both parents. In this way the following reshuffling of genes can occur, producing new phenotypes (these here are AB and O):



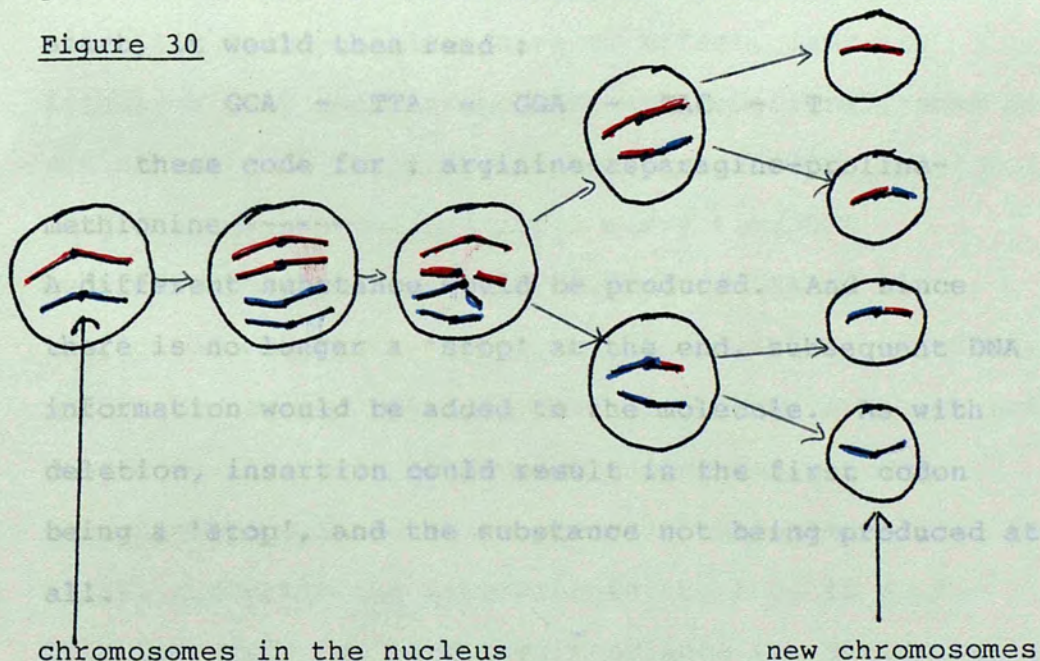
from Patterson, Evolution, p.41.

Figure 29 Multiple alleles

b. Crossing over of chromosomes

During meiosis chromosomes may be crossed and produce a new chromosome with a new combination of genes. Two or more cross-overs can occur at a time.

Figure 30



from Patterson, Evolution, p.43.

c. Mutations (point mutations)

Different point mutations occur with different changes in the genetic code :

(i) deletion :

The following codons are part of a gene for an enzyme, if one letter is deleted the enzyme will not be produced :

CAT - TAG - GAT - ACT (1)

these code for : valine-isoleucine-leucine- stop
if the first C is dropped the message becomes:

ATT - AGG - ATA - CT ; ATT= stop

Since the code starts with 'stop', nothing would be produced.

Deletion could also result in a change of message, and a different substance being produced.

(ii) insertion :

If in the above code a G could be inserted at the start, it would then read :

GCA - TTA - GGA - TAC - T

these code for : arginine-asparagine-proline-methionine-----

A different substance would be produced. And since there is no longer a 'stop' at the end, subsequent DNA information would be added to the molecule. As with deletion, insertion could result in the first codon being a 'stop', and the substance not being produced at all.

(iii) substitution :

A G could be changed for a T : in the above example TAG could become TAT. In this case it would change nothing since both TAG and TAT code for isoleucine. But as with (i) and (ii), substitution can lead to a new substance or no substance being produced at all. A change in one codon may lead to the same protein being produced, but with a new structure. For example haemoglobin (the protein which transports oxygen in red blood cells) has different segments of amino-acids in different species.

The basic source of mutation is error in replicating the DNA. That is to say the message is wrongly copied. Certain chemicals and physical events (such as Xrays) can cause a rise in mutation rates. On the whole the mutation rate per gene is one in 100,000 per generation (2), that is for mutations with visible effects. Many mutations have no effect, many are lethal, a very small proportion are beneficial, some are neutral but still have a visible effect.

Since mutations can occur every time DNA replicates, and since cells divide and DNA is replicated constantly throughout an organisms lifetime, mutations accrue. The only mutations however which are passed on (the only ones which matter for natural selection) are those which occur in the germ cells. So of all the mutations happening in the body in a lifetime, very few have any importance for evolution.

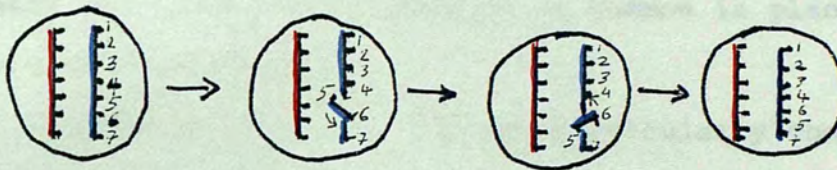
d. Chromosome mutations

Chromosomes may become rearranged as a result of radiation or the effects of certain chemicals. Again there are different types of chromosome mutations : deletion, duplication, unequal division, fusion. Two of the most common are :

(i) inversion :

Figure 31

Imaginary example of an organism with two chromosomes which break and mend in a new arrangement of genes :



chromosome segments numbered 1 to 7

(ii) translocation :

Figure 32

Same organism with two chromosomes which break and mend in a different way, also resulting in a new arrangement of genes :



e. Polyploidy

This type of genetic change is extremely common in plants. It occurs when chromosome numbers are doubled.

This happens when the chromosome division into chromatids is not followed by a division of the nucleus, so that instead of two sets of chromosomes (i.e. as in the normal diploid), the new organism will have 4 sets of chromosomes. Polyploids are rare in animals, but half the number of flowering species of plants are polyploids. Self-fertilization is essential for polyploidy to lead to a new species since an individual with a new number of chromosomes could not reproduce with other individuals with different chromosome numbers (the chromosome pairs could not match up). Self-fertilization is common in plants, rare in animals.

Examples of polyploids are particularly common in agricultural plants. The history of bread wheat is one such example (3). Originally bread wheat was from Triticum monococcum which has 14 chromosomes. A hybrid was then formed between this and a grass Aegilops speltoides which also has 14 chromosomes. A doubling of chromosomes in this hybrid produced Triticum durum, the wheat now used for pasta. This wheat produced another hybrid with Aegilops squarrosa, a grass, the hybrid's chromosomes doubled again. The wheat we now have is Triticum aestivum, a hexaploid (six sets of chromosomes) species with 42 chromosomes, derived from the original diploid (2 sets) Triticum monococcum.

f. External sources of variation

Variation may also arise from hybridization between species producing genetic changes due to gene flow or gene migration (introduction and spreading of new genes into a population).

References

- (1) C. Patterson Evolution pp.44/45.
- (2) Ibid. p.45.
- (3) Ibid. p.58.

In addition the following sources have been used in preparing this appendix:

D.J. Futuyama Evolutionary biology, 1979.

Open University Course Units from the following courses:

S100 : Science foundation course

S225 : Comparative physiology

Genes and development

S249 : Genetics

S321 : Physiology of cells and organisms.

BIBLIOGRAPHY

- ACHINSTEIN, P. "The object of explanation" in
Explanation, Körner, S. (ed) (New Haven : Yale
 University Press, 1975).
- ARISTOTLE De partibus animalum
Physics
- AYALA, F.J. "The mechanisms of evolution" Scientific
 American Vol. 239 (1978) pp. 48-61.
- BARLOW, G.W. and SILVERBERG, J. (eds.) Sociobiology :
 beyond nature/nuture (Boulder Colorado :
 Westview, 1980).
- BARNETT, S.A. (ed.) A century of Darwin (London,
 Heinemann, 1958).
- BATESON, P. "Neo-Darwinism : a discussion" Theoria to
 Theory 13, N^o4 (1980).
- BECKNER, M. The biological way of thought (New York :
 Columbia University Press, 1955).
- BECKNER, M. "Metaphysical presuppositions and the
 description of biological systems" in Form and
 strategy in science, Gregg, D.R. and Harris,
 F.T.C. (eds.) (Dordrecht : Reidl, 1964).
- BERRY, R.J. Inheritance and natural history (London :
 Collins, 1978).
- BESSEY, C.E. "The taxonomic aspect of the species
 question" Americal Naturalist 42 (1904)
 pp. 218-224.

- BLACKMAN, R.L. "Species, sex and parthogenesis in aphids" in The evolving biosphere, Forey, P.L. (ed.) (British Museum Natural History : Cambridge University Press, 1981) pp. 75-86.
- BLACKMAN, R.L. and DAY, M.C. "Species and speciation" in The evolving biosphere, Forey, P.L. (Cambridge and British Museum Natural History : Cambridge University Press, 1981) pp. 3- 7.
- BLACKWELDER, R.E. "A critique of numerical taxonomy" Systematic Zoology 16 (1967) pp. 64-72.
- BRAITHWAITE, R.B. "Neo-Darwinism : a discussion" Theoria to Theory 13, N^o2 (1979).
- CAIN, A.J. Animal species and their evolution (London : Hutchinson, 1954).
- CAPLAN, A.L. "Back to class : a note on the ontology of species" (Discussion) Ph. of Sc. 48 (1981) pp.130-140.
- COLLIER, R. "The unit of natural selection" Theoria to Theory 14, N^o4 (1981) pp. 339-345.
- DARWIN, C. On the origin of species by means of natural selection (1st edition, London : John Murray 1859).
- DAVIDSON, D. and HARMAN, G. (eds.) Semantics of natural languages (Dordrecht: Reidl, 1972).
- DAWKINS, R. The selfish gene (Oxford : Oxford University Press, 1976).

- DAWKINS, R. "Replicator selection and the extended phenotype" Z. Tierpsychol. 47 (1978) pp. 61-76.
- DAWKINS, R. "Good strategy and evolutionary stable strategy" in Sociobiology, beyond nature/nuture Barlow, G.W. and Silverberg, J. (eds.) (Boulder Colorado : Westview, 1980) pp. 331-364.
- DOBZHANSKY, T. Genetics and the origin of species (New York : Columbia University Press, 3rd edition, 1951).
- DOBZHANSKY, T. "Species after Darwin" in A century of Darwin, Barnett, S.A. (ed.) (London : Heinemann, 1958).
- DOBZHANSKY, T., AYALA, F.J., STEBBINS, G.G. and VALENTINE, J.W. Evolution (San Francisco : Freeman, 1977).
- DUPRÉ, J. "Natural kinds and biological taxa" Philosophical Review 90 (1981) pp. 60-90.
- ENÇ, B. "Necessary properties and Linnaean essentialism" Canadian Journal of philosophy 5 (1975) pp. 83-102.
- EVANS, G. "Semantic structure and logical form" in Truth and meaning : essays in semantics Evans, G. and McDowell, J. (eds.) (Oxford : Clarendon Press, 1976) pp. 199-223.
- EVANS, G. and McDOWELL, J. Truth and meaning : essays in semantics (Oxford : Clarendon Press, 1976).
- FALES, E. "Natural kinds and freaks of nature" Ph. of Sc. 49 (1982) pp. 67-90.

- FODOR, J.A. "Special sciences (or : the disunity of science as a working hypothesis)" Synthese 28 (1974) pp. 97-115.
- FORD, E.B. Ecological genetics (London : Methuen, 1971).
- FOREY, P.L. (ed.) The evolving biosphere (Cambridge and British Museum Natural History : Cambridge University Press, 1981).
- FUTUYAMA, D.J. Evolutionary biology (Sunderland : Sinauer, 1979).
- GARSTANG, W. Larval forms and other zoological verses (Oxford : Blackwell, 1951).
- GHISELIN, M.T. "A radical solution to the species problem" Syst. Zool. 23 (1974) pp. 536-544.
- GIRAY, E.F. "An integral approach to the species problem" Br. J. Ph. of Sc. 27 (1976) pp.317-328.
- GOULD, S.J. Ontogeny and phylogeny (Cambridge Mass. : Harvard University Press, 1977).
- GOULD, S.J. Ever since Darwin (New York : Norton, 1977).
- GOULD, S.J. "The art of storytelling" New Scientist, Nov. 1978, p. 530.
- GOULD, S.J. "Species are not specious" New Scientist, August 1979, p. 374.
- GOULD, S.J. and ELDRIDGE, N. "Punctuated equilibria : the tempo and mode of evolution reconsidered" Paleobiology 3 (1977) pp. 115-151.

- GOULD, S.J. and LEWONTIN, R.C. "The spandrels of San Marco and the panglossian paradigm : a critique of the adaptationist programme" Proc. R. Soc. Lond. B205 (1979) pp. 581-598.
- GRANT, V. "The plant species in theory and practice" in The species problem Mayr, E. (ed.) (Washington D.C. : American Association for the Advancement of Science, Pub. 50, 1957) pp. 39-80.
- GRANT, V. Organismic evolution (San Francisco : Freeman, 1977).
- GREEN, M. "Aristotle and modern biology" in The understanding of Nature, Green, M. (Dordrecht : Reidl, 1974).
- GREEN, M. "Reducibility : another side issue?" in The understanding of nature Green, M. (Dordrecht : Reidl, 1974).
- GREEN, M. and MENDELSON, E. (eds.) Topics in the philosophy of biology (Dordrecht : Reidl, 1976).
- GREGG, J.R. "Taxonomy, Language and reality" The American Naturalist 84 (1954) pp.412-435.
- GREGG, J.R. and HARRIS, F.T.C. (eds.) Form and strategy in Science (Dordrecht : Reidl, 1964).
- HALDANE, J. The philosophical basis of biology (London, 1931).
- HARRÉ, R. and MADDEN, E. Causal Powers (Oxford : Blackwell, 1975).

- HEMPEL, C.G. Aspects of Scientific explanation and other essays in the philosophy of science (London: Collier Macmillan, 1965).
- HOLM, E. The biology of flowers (Harmondsworth : Penguin Books, 1978).
- HOLSINGER, K.E. "The nature of biological species" Ph. of Sc. 51 (1984) pp.293-307.
- HULL, D.L. "The effects of essentialism on taxonomy - two thousand years of stasis" Br. J. Ph. of Sc. 15 (1964/5) pp. 314-326 and pp. 1-18.
- HULL, D.L. "Morphospecies and biospecies : a reply to Ruse" Br. J. Ph. of Sc. 20 (1970) pp. 280-282.
- HULL, D.L. "A population approach to scientific change" Science 182 (1973) pp. 1121-1124.
- HULL, D.L. Philosophy of biological sciences (Englewood Cliffs : Prentice-Hall, 1974).
- HULL, D.L. "Reduction in genetics - doing the impossible" in Logic, methodology and philosophy of science IV Suppes. P. et al. (eds.) (1973) pp.619-35.
- HULL, D.L. "Are species really individuals?" Syst. Zool. 25 (1976) pp. 174-191.
- HULL, D.L. "The ontological status of species as evolutionary units" in Fundamental problems in the special sciences Butts, R.E. and Hintikka, J. (eds.) (Dordrecht : Reidel, 1977) pp. 91-102.
- HULL, D.L. "A matter of individuality" Ph. of Sc. 45 (1978) pp. 335-360.

- HULL, D.L. "The limits of cladism" Syst. Zool. 28
(1979) pp. 417-438.
- HULL, D.L. "The principles of biological classification
: the use and abuse of philosophy" PSA 2
Asquith, P. and Griere, R. (eds.) (Lansing
Michigan : PSA, 1980).
- HULL, D.L. "Units of evolution : a metaphysical essay"
in Philosophy of evolution Harré, R. and
Jenson, U. (eds.) (London : Harvester Press, 1981)
pp. 23-40.
- HULL, D.L. "Kitts and Kitts and Caplan on species"
(discussion) Ph. of Sc. 48 (1981) pp. 141-152.
- JARDINE, N. "A logical basis for biological
classification" Syst. Zool. 18 (1969) pp. 37-52.
- JENSON, U.J. and HARRÉ, R. (eds.) The philosophy of
evolution (Brighton: Harvester Press, 1981).
- KAHANE, H. "Thomason on natural kinds" Nous IV
(1970).
- KITCHER, P. "Species" Ph. of Sc. 51 (1984)
pp.308-333.
- KITTS, D.B. and KITTS, D.J. "Biological species as
natural kinds" Ph. of Sc. 46 (1979) pp. 613-622.
- KÖRNER, S. (ed.) Explanation (New Haven : Yale
University Press, 1975).
- KREBS, C.J. Ecology : the experimental analysis of
distribution and abundance (New York : Harper and
Row, 1972).

- KRIPKE, S.A. "Naming and necessity" in Semantics of natural languages Davidson, D. and Harman, G. (eds.) (Dordrecht : Reidel, 1972) pp.253-355 and 763-767.
- LEHMAN, H. "Are biological species real?" Ph. of Sc. 34 (1967) pp. 157-167.
- LEHMAN, H. "Reply to Munson" Ph. of Sc. 37 (1970) pp. 125-130.
- LEIBNIZ, G.W. Nouveaux essais sur l'entendement humain (1765).
- LEWONTIN, R.C. "The units of selection" Annual Review of Ecology and Systematics Vol. 1 Johnston, R.F. et al. (eds.) (California : Annual Reviews Inc., 1970).
- LEWONTIN, R.C. The genetic basis of evolutionary change (New York : Columbia University Press, 1974).
- LEWONTIN, R.C. "Sociobiology - a caricature of Darwinism" PSA 2 Suppe, F. and Asquith, P. (eds.) (Lansing Michigan : PSA, 1976).
- LEWONTIN, R.C. "Adaptation" Scientific American 237 (1978) pp. 157-169.
- LOCKE, J. Essay concerning human understanding Yolton, J.W. (ed.) (London : Dent and Sons, 1965).
- MACKIE, J.L. Problems from Locke (Oxford : Clarendon Press, 1976).

- MACKIE, J.L. "The law of the jungle : moral alternatives and principles of evolution" Philosophy 53 (1978) pp. 455-464.
- MANSER, A. "Neo-Darwinsim : a discussion" Theoria to Theory 13 N^o3 (1979), p. 197ff
- MAYNARD SMITH, J. The theory of evolution (Harmondsworth : Penguin, 1962).
- MAYNARD SMITH, J. "The evolution of behaviour" Scientific American 239 (1978) pp. 136-145.
- MAYR, E. "Species concepts and definitions" in The species problem Mayr, E. (ed.) (Washington D.C. : American Association for the Advancement of Science 50, 1957) pp. 1-22.
- MAYR, E. "Difficulties and importance of the biological species concept" in The species problem Mayr, E. (ed.) (Washington D.C. : American Association for the Advancement of Science 50, 1957) pp. 371-388.
- MAYR, E. Animal species and evolution (Cambridge Mass. : Harvard University Press, 1963).
- MAYR, E. Principles of systematic zoology (New York : McGraw Hill, 1969).
- MAYR, E. Evolution and the diversity of life (Harvard : Belknap Press, 1976).
- MAYR, E. "Evolution" Scientific American 239 (1978) pp. 38-47.
- MAYR, E. The growth of biological thought : diversity, evolution and inheritance (Cambridge Mass. : Harvard University Press, 1982).

- MEGLITSCH, P.A. "On the nature of species" Syst. Zool. 3 (1954) pp. 49-65.
- MELLOR, D.H. "Natural kinds" Br. J. Ph. of Sc. 28 (1977) pp. 299-312.
- METTLER, L.E. and GREGG, T.G. Population genetics and evolution (Englewood Cliffs : Prentice-Hall, 1969).
- MIDGLEY, M. Beast and man (London : Harvester Press, 1978).
- MUNSON, M. "Biological species : Mr Lehman's thesis" Ph. of Sc. 37 (1970) pp. 121-124.
- ODUM, E.P. Fundamentals of ecology (Philadelphia, P.A. : W.B. Saunders, W. 1971).
- PATTERSON, C. Evolution (London : British Museum Natural History, 1978).
- PIANKA, E.R. Evolutionary ecology (New York : Harper and Row, 1974).
- PLATTS, M. "Natural kind words and rigid designators" PAS LXXXII (1981/1982) pp. 103-114.
- PRATT, V. "Biological classification" Br. J. Ph. of Sc. 23 (1972) pp. 305-327.
- PRATT, V. "Numerical taxonomy - a critique" J. Theor. Biology 36 (1972) pp. 581-592.
- PROCTOR, M. and YEO, P. The pollination of flowers (London : Collins, 1973).
- PUTNAM, H. "Is semantics possible?" (1970) in Mind, Language and reality 2 Putnam, H. (Cambridge : Cambridge University Press, 1975) pp. 139-152.

- PUTNAM, H. "The meaning of meaning" (1975) in Mind, language and reality 2 Putnam, H. (Cambridge : Cambridge University Press, 1975) pp. 215-271.
- QUINE, W.V. From a logical point of view (New York : Harper and Row, 1963).
- QUINE, W.V. "Natural kinds" in Essays in Honour of C.G. Hempel Rescher, N. (ed.) (Dordrecht : Reidl, 1969).
- ROTHSCHILD, M. "The rabbit flea and hormones" Endeavour 24 (1965) pp. 162-168.
- ROTHSCHILD, M. and FORD, B. "Hormones of the vertebrate host controlling ovarian regression and copulation of the rabbit flea" Nature 211 (1966) pp.261-266.
- RUSE, M. "Definitions of species in biology" Br. J. Ph. of Sc. 20 (1969) pp. 97-119.
- RUSE, M. "The species problem : a reply to Hull" Br. J. Ph. of Sc. 21 (1971) pp. 369-371.
- RUSE, M. The philosophy of biology (London : Hutchinson University Library, 1973).
- RUSE, M. Sociobiology - sense or nonsense? (Dordrecht : Reidl, 1979).
- RUSE, M. Darwinism defended (Mass. : Addison Wesley, 1982).
- SAARINEM, E. (ed.) Conceptual issues in ecology (Dordrecht : Reidl, 1980).

- SCHWARTZ, S.P. (ed.) Naming, necessity and natural kinds (Ithica and London: Cornell University Press, 1977).
- SIMPSON, G.G. "The species concept" Evolution 5 (1951) pp. 285-288.
- SIMPSON, G.G. Principles of animal taxonomy (New York : Columbia University Press, 1961).
- SMITH, V.E. (ed.) Philosophical problems in biology (New York : St John's University Press, 1966).
- SOBER, E. "Evolution, population thinking and essentialism" Ph. of Sc. 47 (1980) pp. 350-383.
- SOBER, E. "Significant units and the group selection controversy" PSA 2 Asquith, P. and Griere, R. (eds.) (Lansing Michigan : PSA 1980).
- SOBER, E. "Evolutionary theory and the ontological status of properties" Philosophical Studies 40 (1981) 147-176.
- SOBER, E. "Sets, species, and evolution: comments on Philip Kitcher's 'Species'" Ph. of Sci. 51 (1984) pp. 334-341.
- SOBER, E. and LEWONTIN, R.C. "Artifact, cause and genic selection" Ph. of Sc. 49 (1982) pp. 157-180.
- SOKAL, R.R. and SNEATH, P.H.A. Principles of numerical taxonomy (London : W.H. Freeman and Co., 1963).
- SOLOMON, M.E. Population dynamics (London : Edward Arnold, 1969).

- SONNEBORN, T.M. "Breeding systems, reproductive methods, and species problems in protozoa" in The species problem Mayr, E. (ed.) (Washington D.C. : American Association for the Advancement of Science 50, 1957) pp. 155-324.
- THOMASON, R. "Species, determinates and natural kinds" Nous 3 (1969) pp. 95-101.
- THOMPSON, W.R. "The status of species" in Philosophical problems in biology Smith, V.E. (ed.) (New York : St. John's University Press, 1966).
- TIENSON, J. "Can things of different natural kinds be exactly alike?" Analysis 37 (1977) pp. 190-197.
- VAN DE GOHM, R. Fascinating animal facets (London : John Gifford, 1975).
- VARLEY, G.C., GRADWELL, G.R. and HASSELL, M.P. Insect population ecology (Oxford : Blackwell Scientific Publication, 1973).
- WADE, M. "Group selection among laboratory populations of Tribolium" Proc. Nat. Acad. Sc. USA. (1976).
- WALTERS, S.M. "Angiosperm taxonomy" New Phytol. 60 (1961) pp. 74-84.
- WHITE, G.B. "Semispecies, sibling species and superspecies" in The evolving biosphere Forey, P.L. (ed.) (British Museum Natural History : Cambridge University Press, 1981) pp. 21-28.

- WHITE, M.J.D. Modes of speciation (San Francisco :
Freeman, 1978).
- WIGGINS, D. Sameness and substance (Oxford :
Blackwell, 1980).
- WILSON, E.O. Sociobiology : the new synthesis
(Cambridge Mass. : Belknap, 1975).
- WILSON, E.O. and BOSSERT, W.H. A primer of population
biology (Sanford Conn. : Sinauer Associates,
1971).
- WOALOFF, Z. The upsurges and recessions of the desert
locust plagues.
- WOODGER, J.H. The axiomatic method in biology (London
and New York : Cambridge University Press, 1937).
- WOODGER, J.H. Biological principles (London :
Routledge and Kegan Paul, 1948).
- WOODGER, J.H. Biology and language (Cambridge :
Cambridge University Press, 1952).
- ZEMACH, E.M. "Putnam's theory on the reference of
substance terms" J. Phil. 73. (1976) pp.116-127.