descent, even though both may have an adaptive basis: similarity among closely related species may be selectively maintained. When attempting to interpret comparative evidence, it is also important to distinguish the selective forces responsible for the origin of character states from those responsible for their maintenance in contemporary populations. Many comparative tests are based on optimality models, and complement the testing of adaptationist ideas by experimentation, which is often impractical.

2

Why worry about phylogeny?

'Comparative biologists may understandably feel frustrated upon being told that they need to know the phylogenies of their groups in great detail, when this is not something they had much interest in knowing. Nevertheless phylogenies are fundamental to comparative biology; there is no doing it without taking them into account' (Felsenstein 1985*a*, p. 14).

'Ought we, for instance, to begin by discussing each separate species—man, lion, ox, and the like—taking each kind in hand independently of the rest, or ought we rather to deal first with the attributes which they have in common in virtue of some common element of their nature, and proceed from this as a basis for the consideration of them separately?' (Aristotle, *De partibus animalium*).

2.1 Introduction

Living organisms can tell us a lot about their evolutionary history. Indeed, our estimates of phylogenies would be much the same in the absence of a fossil record. This chapter explains why an assessment of phylogenetic relationships is a prerequisite for a successful comparative analysis. In particular, closely related species share many similarities in addition to those of relevance to any particular comparative question. Such similarities can confound comparative studies. If we had a sample of bird and mammal species, for example, and wanted to know why some species have feathers, we might notice that the feathered species lay eggs and have beaks while those species with teeth and fur produce live young. As far as we know, these differences are not adaptively related, but if each species in our sample was used as an independent point for statistical analysis, we should find strong associations between having feathers and beaks and laying eggs. But a phylogenetic reconstruction of this case would reveal that the characters in question had each evolved just once in these groups. This is why we must worry about phylogeny: phylogenies help us to identify *independent* evolutionary events, and it is independent events that statistical tests rely on. This theme will recur throughout.

After describing how a knowledge of phylogenetic relationships can be used in comparative analyses, we shall discuss the biological foundations

for phylogenetic history being retained in contemporary phenotypes. This will lead to an examination of the biological reasons why closely related species are so similar to each other. In Chapters 4 and 5 we provide a statistical account of phylogenetic similarity to complement the biological perspective given here.

2.2 Correlation, causation, phylogeny, and confounding variables

The correct use of phylogenetic information can help distinguish cause from effect in comparative relationships, and also eliminate many potential confounding or third variable explanations. Furthermore, if the same correlations between character states can be shown to exist in several independently evolving lineages, this means the traits have tended to evolve in a correlated fashion and explanations associated with phylogenetic history are unlikely to apply.

2.2.1 Distinguishing cause and effect

Comparative studies relating either phenotype to environment or phenotype to phenotype among contemporary species are inevitably based on correlational evidence. But, as common sense and most elementary statistical textbooks tell us, correlation is not causation. Consider two characters that can each exist in one of two states. For example, butterfly larvae may be palatable ($P+$) or unpalatable ($P-$), and they may be solitary ($S+$) or gregarious ($S-$). Suppose we find that larvae from palatable species tend to be solitary, so that character state $P+$ is associated with character state $S+$, then by paying attention to phylogenetic history, we can begin to unravel causation. The association between $P+$ and $S+$ may have arisen because (1) $P+$ causes $S+$; because (2) $S+$ causes $P+$; or because (3) both $P+$ and $S+$ are caused by some third variable. A good phylogenetic tree with specified ancestral character states allows us to distinguish directions of causality: if $P+$ always appears before $S+$ in a phylogeny and we can rule out other causal influences, then the direction of causality is established (Ridley 1983a; Chew and Robbins 1984).[4] This approach has been used to investigate, for example, displays and the evolution of polygyny in birds (Winterbottom 1929), the evolution of patterns of parental care in fish (Gittleman 1981), and the evolution of gregariousness and aposematic coloration in lepidopterans (Sillén-Tullberg 1988).

[4] We are assuming here that there are no time lags in the system. For example, a third character could change, bringing about an immediate response of $P+$ and then a lagged response of $S+$.

2.2.2 Removing the influence of confounding variables

The problem of confounding variables is likely to be reduced but not necessarily eliminated by searching for the same relationships in different lineages (Clutton-Brock and Harvey 1979). On the whole, closely related species are more similar than distantly related species in morphology, behaviour, and ecology. If closely related species share a character state, then the chances are that they will share a whole lot more too. Consider a comparison among species belonging to 2 distantly related genera, say 10 species of Peromyscus mice and 10 species of Drosophila fruit flies. Differences among the mice or among the flies are likely to be swamped by differences between the two groups. If species are treated as independent points for analysis, we would find significant associations and correlations between almost any pair of characters we examined: diet, body weight, leg number, presence or absence of wings, clutch size, lifespan and so on. Such relationships are unlikely to be informative in our search for the adaptive significance of cross-taxonomic variation.

However, rather than making comparisons between genera, we might instead look within genera. (For didactic purposes, we are assuming that our phylogeny is incomplete and the true relationships among species within genera are unknown, which is not actually true for Peromyscus and Drosophila.) Comparisons within genera can, of course, deal only with characters that actually vary within genera, like diet, body weight, clutch size and lifespan. However, when they can be made (e.g. Read 1987), such comparisons are particularly informative because they automatically hold constant all the variables that are shared by congeners (see Møller and Birkhead in Harvey 1991).

2.2.3 When patterns differ among taxa

Cross-species comparisons can mask interesting patterns in the data (Clutton-Brock and Harvey 1984). It is frequently the case that correlates of variation in some taxa differ from those in other taxa, and we shall meet examples in the next section. However, on occasion it seems that relationships between variables at one taxonomic level are not the same as those at another: the same patterns may be repeated in different taxa, but vary according to the rank of the taxon being considered! An extreme example is given by Huey (1987): the relationship between variability in body temperature and thermal performance breadth (the range of body temperatures through which lizards' sprint speeds exceed some arbitrary criterion) is positive within a number of genera but negative across genera. Another example (which we shall question in Chapter 6), is the suggestion that brain mass increases less for a given change in body mass among adults of more closely related species of vertebrates than it does across adults of more distantly related species (Lande 1979; Martin and Harvey 1985; Pagel

and Harvey 1989a). For example, the exponent relating brain to body mass among species within genera is often said to lie between 0.2 and 0.4 (Gould 1975; Lande 1979), whereas among species from different orders it is typically between 0.55 and 0.75 (Martin 1983; Harvey and Bennett 1983).

The patterns in the two examples described above would have been missed if phylogenetic relationships were not studied. If such phylogenetically related patterns are commonplace, we must be very careful to take full account of phylogenetic relationships in comparative studies. One pattern that we can be sure *is* commonplace is similarity among closely related species, but the processes responsible for that similarity are less often considered.

2.3 Three reasons why phylogenetically related species are similar

How has evolutionary history come to be recorded in contemporary phenotypes? At least three processes have been involved which we term *phylogenetic niche conservatism*, *phylogenetic time lags*, and *different adaptive responses*. We consider each in turn below, and illustrate them as problems that comparative analyses must face by drawing an analogy between comparative and experimental studies in Box 2.1. Comparing phenotypes of extant species living in known environments is like analysing the results of a temporally nested experiment when records of early treatments and responses to them have been lost.

2.3.1 Phylogenetic niche conservatism

The first process leading to similarity among closely related species is adaptive, and is a consequence of vacant niches having been invaded by those available species that were best suited to occupy them. For example, if a new area of coniferous forest appeared adjacent to grassland, lakes, and deciduous forest, it is more likely that it would have been invaded by species of, say, birds and insects from the deciduous forest than from the other two habitats. Fish would not stand a chance in the new terrestrial habitat, and birds adapted to grassland would probably lose in competition with those from deciduous forests. Through time, the birds from the deciduous forest would, no doubt, become better adapted to the new coniferous habitat and diverge phenotypically from their ancestors. But they would still be birds, and they would retain the lifestyle of birds. They would not become insects, partly because insects would be occupying the insect niche. This is the principle of phylogenetic niche conservatism: past and present phenotypes of a lineage are likely to have occupied similar environments. This is a purely adaptationist reason for why phenotypically similar species are likely to be close phylogenetic relatives (Grafen 1989).

Box 2.1. An experimental analogue for comparative studies

2nd factor	1	2	1	1	2	2	2	2
1st factor	A	B	C	D	E	F	G	H
Environment	a	b	c	d	e	f	g	h
Phenotype								
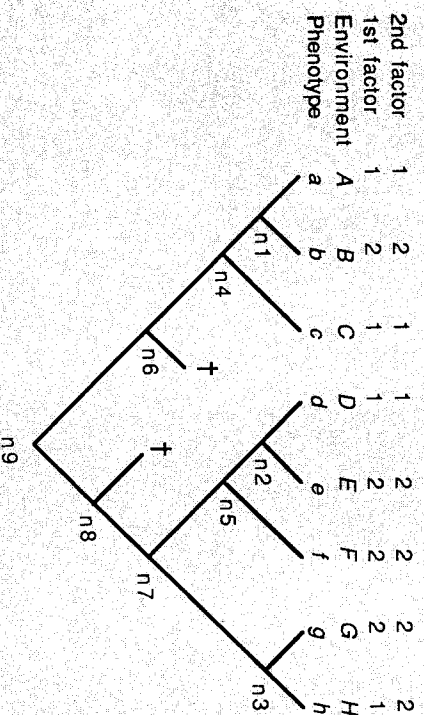
An analogy between (1) phenotypic evolution under a range of environments, and (2) response of individuals to a nested sequence of experimental treatments.

1. Contemporary phenotypes a to h are found in environments A to H. The ancestral species marked at nodes n1 to n9 existed when lineages divided. Some lineages went extinct (†). Because historical information on phenotypes and environments is lacking, both must be reconstructed.

2. The experimental analogue begins by subjecting a large sample of individuals to the same treatment at time n9. The individuals are then divided sequentially into groups and subgroups repeatedly but after varying intervals of time. Between divisions, the individuals in each group or subgroup are subjected to the same sequence of treatments which differs from that received by other individuals in other groups. The experimentalist keeps no historical record of the treatments received by the different individuals. Because historical information on treatments and responses is lacking, both must be reconstructed.

Knowing the structure of the tree (the sequence in which lineages split) we can use contemporary phenotypes and environments (treatments) to help in that reconstruction (this will be the topic of Chapter 3). Further, because extant phenotypes contain information about their evolutionary history, the comparative method must identify phylogenetic correlates in order to distinguish them from the effect of current environments on current phenotypes. Bearing in mind the analogy between phylogeny and a nested experiment, the effect of history on phenotype can be summarized through five generalizations.

1. Each environment consists of many selective factors, or, equivalently, each treatment consists of many factors. Levels of two factors are shown in the figure, but contemporary and historical environments differ on many other non-independent factors. Factors 1 and 2 might be measures of temperature (hot, cold) and humidity (wet, dry), but other factors such as whether food sources are clumped or not are ignored.

2. Factors tend to covary across environments or treatments. For example, the level of factor 1 is a good predictor of the level of factor 2. (This results in the problem of *confounding variables* discussed earlier in this chapter (Section 2.2); a relationship between variation in a phenotypic character and an environmental factor may be caused by another, possibly unrecorded, factor).

3. Past environments or treatments for a lineage tend to be similar to present environments. For example, n3 is likely to have had level 2 of factor 2 because phenotype g does. As far as the experiment is concerned, this would mean that the past treatments on a sample were similar to subsequent treatments. For the evolutionary analogue, it means that organisms tend to occupy similar habitats to those occupied by their ancestors. (This may be because, when new ecological niches open up, those species inhabiting the most similar existing environments are best adapted to invade the new ones. This is *phylogenetic niche conservatism*: closely related species may be phenotypically similar to each other in part because they are likely to inhabit similar environments *for historical reasons*. Unrecorded factors in the environments of close relatives are likely to be more similar to each other than are unrecorded factors in the environments of distant relatives.)

4. Past environments or treatments may leave their marks on contemporary phenotypes. For example, the environment for n7 may have been influential in moulding phenotype d. Furthermore, random changes resulting from neutral evolution by genetic drift or some change in experimental phenotypes that did not result from specified treatments may be retained. (This is the problem of *phylogenetic time lags*: it is possible that a character state observed on a contemporary phenotype represents an adaptation to factor(s) in some past environment. The non-selective version of time lags is genetic drift or neutral evolution: species that have shared longer periods of phylogenetic history may still have similarities that accumulated as a consequence of genetic drift. We shall illustrate this process in Chapter 5, Section 5.2 and Fig. 5.4.)

5. The response of a lineage to a treatment (environment) depends, to some extent, on its phenotype when it entered that regime. For example, phenotypes a and d have similar levels of factors 1 and 2 but, if they differed phenotypically at n1 and n2, they might respond differently to factors 1 and 2 and move towards different equilibrium phenotypes. (*Different adaptive responses* to similar selective forces are a problem facing many comparative studies: two types of organisms may have responded to the same environment in different ways.)

There are two components to the concept of phylogenetic niche conservatism: (1) the species most likely to invade a vacant niche is the one in an adjacent environment that occupies the most similar niche; and (2) species are restrained from moving into new niches in large part because those niches are already occupied by other taxa that are well adapted to the niches and are better competitors for the limiting resources. Evidence for the general importance of phylogenetic niche conservatism may actually be provided by the sporadic occurrence of adaptive radiations: the absence of competitors that occupied adjacent niches in ancestral environments often provides the clue to understanding an adaptive radiation that followed a species' invasion of a new habitat. Darwin's finches on the Galápagos Islands, from which other land birds were absent, provides a typical example (Grant 1986).

2.3.2 Phylogenetic time lags

The second historical process involved in phenotypic diversity is phylogenetic time lags. A trait could have evolved in a common ancestor of several extant species, either by natural selection or by genetic drift. The trait will ultimately be lost provided that (1) suitable genetic variance is present or arises by mutation, and the costs of retaining the trait are not outweighed by its benefits in the contemporary environment, or if (2) pleiotropic gene effects are involved so that selected changes in another character lead to reduction in the focal character.

Phylogenetic time lags do not provide as important a problem to comparative studies as we might think. Related species may express traits that are of little or no adaptive significance, and which certainly do not serve the function they had in the past. The vermiform appendix of humans and the remnants of hip bones in cetaceans are cases in point. Our aim is to explain taxonomic diversity, and such organs usually vary in their state of development among higher-level taxa. If we look across mammals, we find that herbivores have a large vermiform appendix (the caecum) whereas carnivores do not, and terrestrial mammals have hips whereas whales do not. In such cases, the comparison can point to the functional significance of the trait of interest. The important point is that the correct comparison must be made. If we find an apparently functionless trait, a search for why the trait is there. It is not always necessary to seek comparison with distant relatives. For example, the flight motor neurons of flightless grasshoppers, which have been inherited from flying ancestors, are now smaller than the equivalent neurons of flying grasshoppers (Dumont and Robertson 1986).

Intimate knowledge of the biology of a species would be necessary to demonstrate that a trait is, in fact, of no functional significance. There are

many examples of traits taking on different functions (Gould and Vrba 1982). This means that if some members of a taxon have a trait that can be shown to serve a particular function, it does not necessarily follow that the same trait serves the same function in other members of the taxon. For example, on occasion the kea *Nestor notabilis*, a New Zealand parrot, uses its beak to rip through the skin of dead sheep and feed on the fat beneath. Closely related parrots use their kea-like beaks to feed on seeds and fruit (Futuyma 1979). As we shall see below, different selective forces may go on to mould the same character.

2.3.3 Different adaptive responses

The third way in which history is recorded in contemporary species is through different adaptive responses. The methods used in later chapters of this book seek similar adaptive responses to similar selective pressures, recognized as instances of parallel or convergent evolutionary change. However, one important limit to correlated evolutionary change concerns the phenotypic similarity of the species being compared. Animals of similar phenotype are likely to evolve similar responses to the same selective force, whereas different phenotypes may respond differently. For example, in response to a threat from predators, distasteful animals might evolve warning coloration while palatable species would become cryptic (Harvey *et al.* 1982; Guilford 1985). In a similar vein, when faced with the threat of predation, large animals may stand and fight thus being selected for even larger size, whereas small animals may escape down burrows and as a consequence are selected to be even smaller (Edmunds 1974; Simms 1979; Ralls and Harvey 1985). Such differences can set phylogenetic limits to the generality of many comparative trends.

Adaptive responses lie behind many historical explanations of biological diversity just as they are at the root of many micro-evolutionary processes. Distantly related species occupying similar niches may remain phenotypically dissimilar, while closely related species may show parallel or convergent evolution. As we shall see below, the concept of different evolutionary responses to similar selective forces unites several biological perspectives on the problem of why closely related contemporary species tend to be phenotypically similar.

Different characters respond to similar forces

In order to browse from trees, giraffes have evolved long necks while some other species of mammals have evolved the ability to climb trees. The adaptive route taken may be influenced by phylogenetic history. It may also constrain or otherwise influence the subsequent direction of evolutionary change. For example, in response to increased predator pressure, terrestrial browsers can evolve even larger body sizes, but this route may

be closed to arboreal browsers which must often be small enough to feed from terminal twigs without breaking them (Clutton-Brock and Harvey 1983). They may therefore evolve a nocturnal lifestyle with accompanying changes in their visual apparatus. This is essentially the phenomenon of an adaptive landscape having separate adaptive peaks (Wright 1932). There are many well-documented cases of different characters having responded to similar selective forces. Simpson (1967) cites the case of carnivorous mammals in which different teeth in the lower jaw have become adapted for meat shearing: the fourth premolar in the wolf *Canis*, the first molar in *Oxyaena*, and the second molar in *Hyaenodon*.

As Gould and Lewontin (1979) have emphasized, selection uses whatever variation is available, and if the variation is heritable a character will evolve. For example, male bovids have strong horns for combat over mates, whereas cervids use antlers. Cross-species comparisons within each of those families of mammals demonstrate expected relationships between the size of these costly structures and the extent to which the species is polygynous (Clutton-Brock *et al.* 1980; Packer 1983). However, comparisons of horn size and antler size with measures of polygyny across all mammals would not reveal the strong patterns found within the two families. Indeed, males of polygynous species in at least one order, the primates, have developed neither horns nor antlers, but enlarged canines (Leutenegger and Kelley 1977; Harvey *et al.* 1978).

The evolution of horns, antlers, teeth, and other weapons has been accompanied by both the evolution of different fighting strategies and defence of appropriate areas of the body. As a consequence, species differences in the location of dermal shields and areas of thickened skin only make sense in the context of differences in fighting behaviour and weaponry (Jarman 1988). Again, one adaptive route influences the direction of subsequent evolutionary change, a topic we shall need to return to below.

Studies of structural antigenic and genetic changes in haemagglutinin which accompany adaptation of an influenza virus to being cultured in hens' eggs provide a good example of alternative genetic mutants appearing to provide similar adaptive responses. When genetically identical isolates of the A(H1N1) virus were propagated in eggs, one of three antigenically distinct variants not present in the inoculum soon appeared in each egg and spread to fixation. Identical antigenic variants were not always genetically identical, although in every case HA1 amino acid substitutions were located in the vicinity of the receptor binding site (Robertson *et al.* 1987).

Different forces mould the same character

Just as different characters may respond to meet the same selective pressure, so the same character may respond to different selective

pressures. A careful redefinition of the function of character states can sometimes reveal unrecognized similarities, as we saw with the beaks of hawks, shrikes, and shrike-tits in Chapter 1. But this will not always be the case. The forward pair of pentadactyl limbs in mammals provides an obvious example (Darwin 1859, p. 434): 'What can be more curious than that the hand of a man, formed for grasping, that of a mole for digging, the leg of the horse, the paddle of the porpoise, and the wing of the bat, should all be constructed on the same pattern and should include the same bones, in the same relative positions?'.

Different degrees of response

Different taxonomic groups may even produce different degrees of response to similar selective pressures. For example, genetic variance allowing the evolution of a particular adaptation may occur in one taxon but not another. Compare sex determining mechanisms in the hymenoptera and fruit flies. Hymenopterans have haplo-diploid sex determination with fertilized eggs developing into females and unfertilized eggs into males. Under conditions of regular inbreeding or local mate competition, the optimum strategy for a mother is to produce broods with an excess of daughters (see Section 1.6.1). Hymenopterans adapt their sex ratios accordingly (Hamilton 1967), as mothers can choose whether to fertilize any particular egg as it is laid (e.g. Gerber and Klostermeyer 1970). However, like mammals, *Drosophila* has chromosomal sex determination with XX individuals developing into females and XY into males, and it may be that here strongly biased sex ratios cannot easily evolve (Maynard Smith 1980). For example, attempts to bias the sex ratio by selection experiments have usually failed (e.g. Toro 1981; Toro and Charlesworth 1982), and when adaptive sex ratio variation can be detected among species with chromosomal sex determination, it is not so extreme as among the hymenoptera and other haplo-diploid taxa (Clutton-Brock 1986; Clutton-Brock and Iason 1986; Bull and Charnov 1988).

We do not need to compare such phylogenetically distant relatives as those from different orders or classes to find different degrees of response to selection. For example, the extent to which thermal sensitivity of sprint speeds evolves genetically to match activity body temperatures seems to differ among iguanid genera (van Berkum 1986). At a lower taxonomic level still, geographic variation in morphometric measures of a single species, the pocket mouse *Perognathus goldmani*, is more closely allied with phylogenetic relatedness among karyotypically defined races than with those environmental variables which are 'standardly employed in attempts to determine factors underlying patterns of geographic variation in morphology' (Straney and Patton 1980, p. 896). But as Straney and Patton stress, and as is usually the case in such fine-grained comparisons,

the similarities may result from unmeasured selective forces that are more similar in the niches occupied by the more closely related races. Without a detailed genetic analysis, the results of controlled selection experiments, and appropriate observational studies of animals in the field, it is not possible to determine the cause of these and other similar patterns (see also Grant 1986, p. 183). Nevertheless, the probability that even different genetic races of the same species will not respond in precisely the same way to the same selective forces should always be borne in mind when interpreting imperfect comparative relationships.

Key innovations and developmental constraints

The topic of different responses to the same selective force subsumes two well-discussed biological perspectives on evolutionary change. The first is the concept of key innovations, and the other is developmental constraints. We mention these here, albeit briefly, because they have generated their own fairly voluminous literatures that bear on our theme. From time to time, a change occurs in a phenotype that allows a new range of viable variants to evolve. As a consequence, a new adaptive radiation can arise, either because the derived forms containing the new characteristic displace old forms from their niches or because the new characteristic is associated with higher rates of speciation or cladogenesis. Futuyma (1986, p. 439) provides a useful review of these areas and puts the matter in a nutshell when he writes that '(developmentally) integrated systems are likely to display a limited, recurring repertoire of variations, giving rise therefore to parallel evolution and to atavistic variants that reveal in a recapitulatory way the ancestral foundations of the developmental program'. A new mutation producing a key innovation may release the ancestral phenotype from some developmental constraint, thus setting the scene for a new adaptive radiation.

In a careful analysis of the pharyngeal bones and associated musculature of cichlid fishes and their relatives, Liem (1973, 1980) has probably pinpointed such a key innovation. Cichlids have undergone adaptive radiations in African lakes despite competition from species belonging to several other fish families. The success of cichlids results in large part from an evolved diversity of feeding mechanisms. In relatives of cichlids, the pharyngeal bones hold prey items but cannot manipulate them. A small shift in position of a single muscle attachment in a common ancestor of cichlids, possibly caused 'by a very simple change in ontogenetic mechanism' (Liem 1973, p. 439), may have reversed the muscle's function from one of abduction to adduction of the lower pharyngeal jaw. This was then followed by secondary changes that led to the pharyngeal bones being able to manipulate as well as to hold prey items. As a consequence, the premaxillary and mandibular jaws which had previously been constrained

to serve the dual functions of collecting and manipulating food were freed to evolve along new routes that did not involve food manipulation. Furthermore, Liem (1980) goes on to show how an anatomical decoupling of the maxilla and premaxilla in cichlid fishes has allowed greater flexibility of potential feeding movements. For example, cichlids have five ways to protrude the upper jaw whereas their close relatives have just one.

Lauder (1981) has focused on how we might demonstrate that particular derived morphological features will trigger the evolution of phylogenetic lineages with parallel patterns of morphological change (transformations), resulting in arrays of terminal taxa with similar phenotypic ranges (relations). He argues that so-called transformations and relations may be demonstrated to be repeatable by showing how the same transformations and relations have occurred in different monophyletic groups, each containing the same key morphological feature (See Fig. 2.1). The hypothesis that the key feature is responsible for the historical consequences can be tested by comparing the transformations and relations among monophyletic taxa, some of which contain the key feature and others of which do not.
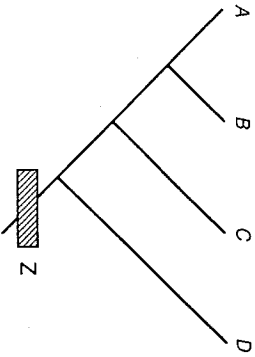

Fig. 2.1. Z marks a morphological change in an ancestral species. A, B, C, and D are terminal taxa that each inherit the new character state. Transformational studies examine changes in phenotype along the paths linking Z with the different terminal taxa. Relational studies examine the diversity of terminal taxa in the monophyletic group containing Z. (After Lauder 1981).

It is even possible to show the same transformations and relations occurring in a single monophyletic group. For example, the various routes to upper jaw protrusion in cichlid fishes discussed above may have been followed independently by adaptive radiations in different African lakes. Lauder's discussion offered a different and potentially useful phylogenetic

perspective to comparative analyses for, as he presented it, Lauder considered only intrinsic features. That is, he was not concerned with how phenotypes evolve in response to external selective pressures (after all, several different types of upper jaw protrusion in cichlid fishes may be adaptively equivalent). Comparative biologists often relate phenotypes to extrinsic factors in the environment, but Lauder asked whether the origin of particular phenotypic novelties might inevitably result in the evolution of other predictable phenotypic changes. Environmental change may have selected for the particular feature in the first place but, once that feature evolved, it may have influenced strongly the course taken by subsequent evolution.

Lauder's approach does not mean that we should exclude extrinsic factors from historical analyses (see Liem and Wake 1985). Similar historical patterns may be detected following particular key innovations, but those changes may only be properly understood with reference to selective factors operating in the external environment (i.e. extrinsic factors). Take the example of the repeated adaptive differentiation of leaves into tendrils, hooks and spines (Hutchinson 1969). We could analyse separate phylogenies structurally in terms of transformational and relational patterns, but a biologically comprehensive understanding would include a consideration of the selective forces, such as predation and the need for climbing plants to reach the top of the canopy, which were operating when those structures evolved. Similarly with cichlid fish radiations in African lakes: presumably the particular feeding behaviours and associated morphologies that evolve in any radiation will have been in part determined by available food sources.

Irreversible evolution

Finally, some evolutionary routes may preclude return with the result that, when ancestral environments reappear, ancestral adaptations do not re-evolve (or at least do not re-evolve with facility). Groups of related species may thereby end up in the evolutionary equivalent of black holes from which there is no easy return. This topic of irreversible evolution is reviewed by Bull and Charnov (1985) and by Harvey and Partridge (1987). Godfray (1987) provides an instructive, if gruesome, example. Species of the Braconid hymenopteran genus *Apanteles* lay their eggs in lepidopteran caterpillars. More than half of 276 species for which Le Masurier (1987) could find data are solitary, with a single young feeding in its host. Many of the solitary species have long piercing mandibles which are used to kill fellow parasitoids in the same host. The other species are gregarious with typically 12–26 young per host, but occasionally up to 1200. Why, despite the availability of suitably sized hosts, do very few species of *Apanteles* lay broods of 2–11 eggs? Godfray's population genetic models demonstrate

that genes for fighting should spread, and thus murderous mandibles should evolve, whenever competition for resources in a host gets intense. Once such mandibles have evolved, mothers are selected to lay just a single egg in a host because only one young can survive however many eggs are laid. If the environment changes and hosts grow larger over evolutionary time, the production of solitary aggressive young may remain the evolutionarily stable strategy. Indeed, in the simplest models considered by Godfray, the condition for genes for tolerance invading a population of fighters involves an Allee effect (individuals must have a higher fitness as one of a group than when alone). If Godfray's explanation for the dearth of parasite species laying few eggs is correct, we might expect: (1) a correlation between host and parasite biomass in gregarious species; (2) only solitary parasites to occupy small hosts; and (3) both solitary and gregarious species to occupy larger hosts. All three predictions hold (Godfray 1987). Furthermore, when large-bodied hosts are compared, the biomass of gregarious species per host is more than ten times that of solitary species (Le Masurier 1987).

Other examples of evolutionary routes along which it is easier to travel one way than the other include the transition between inbreeding and outbreeding. Once individuals in an inbred population begin to outbreed, recessive deleterious mutations will accumulate and inbreeding depression can become a potent force preventing the subsequent evolution of inbreeding. Currently, we lack a unifying framework that might help predict where we might find other cases of irreversible evolution (see Bull and Charnov 1985).

2.4 Afterwords

Although the comparative approaches that we shall be describing in Chapters 4 to 6 of this book generally seek evidence for similar phenotypic responses to similar selective forces, it should now be clear why that is not always what happens (see also Bock 1977, 1980). Most biological laws are limited in their generality and exceptions abound but, as the many examples cited in this book suggest, we believe that Bock (1980, p. 225) is throwing the baby out with the bathwater when he writes 'that the existence of these exceptions means that the comparison method of judging adaptations is not lawlike and hence invalid'! We have seen how different adaptive responses and time lags can result in imperfect correlations between character states and environments, but appropriate choice of taxa for analysis will usually help to unravel the factors involved. Phylogenetic niche conservatism, on the other hand, is more likely to lead to statistical problems: speciose taxa can bias statistical measures, such as

correlation and regression, and degrees of freedom will be overestimated when species are used as the units for analysis.

If comparative studies are to explain the diversity among species, the roles of phylogenetic conservatism, phylogenetic time lags, and the diversity of adaptive responses must all be assessed. A rough measure of the extent to which evolutionary history has moulded a character is provided by comparing very closely related species living in different environments. If the variation among species in a character is high so that closely related species have evolved different phenotypes, evolutionary history has probably been of little importance in preventing change.

2.5 Summary

The careful use of phylogenetic relationships can help distinguish cause from effect and control for the influence of confounding variables in comparative studies. Closely related species tend to be phenotypically similar to each other as a consequence of at least three different biological processes: phylogenetic niche conservatism, phylogenetic time lags, and similar adaptive responses. Statistical degrees of freedom are easily inflated if niche conservatism and time lags are not taken into account when analysing comparative data, whereas different adaptive responses among phylogenetic lineages are best recognized by an appropriate choice of taxa for comparison.