Higher taxonomic groups – their usefulness for the ecological interpretation of ancient plant remains

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Summary

Ancient plant remains potentially provide evidence for the investigation of past human land-use and the reconstruction of past vegetation. To interpret ancient plant remains in these terms, it is necessary to understand the ecological preferences of plant species. This thesis addresses two problems associated with using the ecological preferences of species to interpret ancient plant remains: (a) The ecological preferences of plant species may change through time, and (b) many ancient plant remains can only be identified to higher taxonomic groups, but it is often not known whether the species within a higher taxonomic group have similar or different ecological preferences.

The functional attributes (ecological preferences) of species from 172 genera and 15 families were measured, and the variation of the functional attributes within these higher taxonomic groups and across taxonomic levels was calculated. The results indicate which attributes are most and least likely to be similar for all the species in a higher taxonomic group, and in which particular groups the attributes are most and least variable. If an attribute varies little within a higher taxonomic group, then (a) attribute values for the species in that group are unlikely to have changed much over time, and (b) the attribute value of any ancient plant remains identified to that group, but not to species, could be predicted from the mean attribute value of all the species in the group. The significance of taxonomic inaccuracies for calculations of attribute variation is also assessed.

Finally, it is demonstrated that the functional attribute values of genera can be substituted for some species attributes in modern studies relating the functional attributes of weed species to agricultural regime. This indicates that attribute values for genera can, in some circumstances, be used to provide functional attribute values for unspeciated material in assemblages of ancient plant remains.

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Chapter 1 – Introduction

1.1 Ancient plant remains and ecology

Plant ecology is used by archaeobotanists to investigate aspects of the past on the basis of plant macrofossils and microfossils. Using this evidence, it is possible to investigate past agricultural practices and other human land-use, and to reconstruct past vegetation on both local and regional scales. In order to interpret ancient plant remains in ecological terms, it is necessary to understand the ecological preferences of the species in question. Many plant species are particular in their ecological requirements, so different modern ecological conditions are characterised by different floras. If modern ecological conditions can be distinguished in terms of their floristic composition, then it follows that the species composition of an assemblage of ancient plant remains is potentially a good indicator of past ecological conditions. Unfortunately, however, there is no direct way of measuring the *past* ecological preferences of plant species, so archaeobotanists and palynologists have to rely on ecological data based on *modern* examples of the species represented in the archaeological record. Thus, the ecological interpretation of ancient plant remains is always based upon analogy with the ecological preferences of modern plant populations.

Although the most useful modern ecological data for the interpretation of ancient plant remains relate to species, many such remains can only be identified to higher taxonomic groups (groups of related species at different hierarchical levels). This thesis explores the ecological variability of higher taxonomic groups of plants with two aims:

1. To determine what useful ecological inferences can and cannot be drawn from ancient plant remains identified to higher taxonomic groups (but not to species), and to target higher taxonomic groups from which few useful ecological inferences can be drawn for research into more precise taxonomic identification of their fossilised remains.

2. To determine which present-day ecological preferences of plant species are reliable indicators of the ecological preferences of the same species in the past.

The structure of this thesis is as follows. This chapter begins with a review of the types of past ecological conditions that can be investigated using different plant remains, and why this is relevant to archaeology. This is followed by a consideration of some problems that are general to all ecological interpretations of ancient plant remains and of the potential for using data for the ecological variability of higher taxonomic groups to address these problems. Chapter 2 considers various methods for the classification of plants, in particular the FIBS technique for plant functional classification, and discusses the potential for ecological specialisation in higher plant groups. Chapter 3 discusses the different sources of ecological data that are used in the interpretation of ancient plant remains, including the ARCHFIBS method on which this thesis is based. Chapter 4 covers the methods used to (a) measure the ecological characteristics of species, (b) assess the accuracy of plant taxonomic classifications, and (c) to analyse the variation of ecological characteristics within higher taxonomic groups. Chapter 5 presents the results of the taxonomic assessment, and Chapter 6 presents the results of the analyses of variation. Chapter 7 investigates the potential for using the ecological characteristics of higher taxonomic groups in place of species characteristics in ecological studies. Chapter 8 summarises the results and draws some final conclusions.

In this thesis, the term 'archaeobotany' refers only to the study of plant macrofossils that are associated in some way with humans. These macrofossils consist of seeds, leaves and other plant elements that can easily be seen with the naked eye. 'Palynology' refers to the general study of plant microfossils, usually pollen but also spores. The term 'ancient plant remains' is used when both macrofossils and microfossils are being referred to.

1.1.1 Plant macrofossils and the ecology of crop fields and other human land-use contexts

Crop field ecology is of archaeological interest because it is potentially a good indicator of one of man's primary economic activities: agriculture (e.g. Hillman 1973, 1981, 1984, 19991; M. Jones 1981, 1988; Wasylikova 1981; G. Jones 1992; van der Veen 1992). Husbandry techniques such as ploughing, weeding, watering, and fertilising all have a direct effect on the ecology of a field - for instance, two fields, one fertilised and the other unfertilised but otherwise identical, would be expected to be ecologically distinct as a result of their different nutrient levels. If husbandry techniques partially determine ecological conditions, and these ecological conditions can be distinguished in terms of their floristic composition, then this floristic composition is potentially an indicator of the husbandry techniques employed. It follows, therefore, that ancient remains of crop field floras can be used to reconstruct past crop field ecology, and that from this it may also be possible to reconstruct past husbandry techniques and the agricultural systems of which they are a part.

The charred remains of cereal and legume crops are recovered in significant quantities from many archaeological sites, and it may seem that these remains would provide good evidence of past crop field ecology. Unfortunately, however, crop plants are generally quite poor ecological indicators (Behre and Jacomet 1991). Crops species tend to be ecologically flexible, and when deliberately sown may grow (albeit not optimally) in conditions that do not reflect their ecological preferences. The ecological behaviour of ancient wheat species, for instance, is poorly understood but experimental work suggests that there is considerable variation even within individual species (Davies and Hillman 1988). Davies and Hillman (1988) have shown that different populations of emmer wheat react significantly differently in experiments on the effect of flooding on crop growth and yield. They suggest that simplistic stereotypes of the ecological behaviour of primitive wheats may be quite misleading, and that these species can be both ecologically and physiologically very flexible. This ecological flexibility is perhaps unsurprising given that wheat and all the other major grain crops are today grown under a

wide variety of different agricultural and ecological conditions, and over very broad ranges (Wilsie 1962; de Rougemont 1989; Zohary and Hopf 1994).

Although crop species are not good sources of ecological evidence, the weeds that grow with them often are. Because crop weeds are not deliberately sown, they tend to be found in ecological conditions that are particularly favourable for their growth. Arable weed species vary in their ecological amplitude, but for many species this is relatively narrow. Consequently, the weed floras of ecologically distinct fields are likely to be significantly different. Because the ecology of a crop field is directly affected by the husbandry techniques with which it is managed, this means that it should be possible to distinguish differently managed fields (e.g. fertilised and unfertilised) in terms of their weed floras. Many weed seeds enter the archaeological record in charred form with the grain crops that they infested, and these form the best source of archaeobotanical evidence for reconstructing crop field ecology and crop husbandry practices. As a result, much archaeobotanical research has focused on investigating and developing the potential of this evidence (e.g. G. Jones et al. 1995, 1999, 2000; Charles et al. 1997, 2002; Bogaard et al. 1998, 1999, 2001 for ecological methodology) (e.g. Hillman 1973, 1981, 1991; G. Jones 1992 for ethnoarchaeological studies) (e.g. M. Jones 1981, 1988 for archaeobotanical syntheses).

Although crop fields are the agricultural contexts most often associated with plant macrofossil evidence, these plant remains can also be good evidence of quite different agricultural contexts. For instance, Behre and Jacomet (1991) draw together evidence from a number of studies (Körber-Grohne 1967; van Zeist 1974; Behre 1976, 1981, 1985) of non-carbonised plant macrofossils from the salt marshes of Germany and the Netherlands that indicate the ecology of land exploited for hay. Ecological indicator species identified in the macrofossil remains of hay from different sites demonstrated that a wide range of environments from exposed salt marshes to sheltered fresh water areas were being exploited

1.1.2 Ancient plant remains and vegetation reconstruction

1.1.2.1 Local vegetation reconstruction

Plant macroremains can also be used to reconstruct the local vegetation and ecological conditions in habitats other than crop fields. For the most part, the sorts of macroremains that provide evidence of crop field vegetation (charred weed seeds) differ considerably from those that provide evidence for other localised stands of vegetation (waterlogged seeds and other plant parts), and these differences will be considered in detail in Chapter 3. For the present, it is only necessary to understand that the waterlogged remains of wild plants are often preserved more or less *in situ* both in human settlement sites and within the wider environment (Green 1976, 1982; Wasylikova 1986; Behre and Jacomet 1991).

The (usually) waterlogged macroremains of non-crop plants recovered from human settlements can be used to reconstruct some of the ecological conditions pertaining in the settlements themselves (e.g. Hall *et al.* 1980; G. Jones *et al.* 1991). For example, some early Medieval pits excavated in London contained remains of plants typical of waste places, gardens and other disturbed ground, and these plants seem likely to have been growing in the vicinity of the pits (G. Jones *et al.* 1991). Waterlogged contexts on settlement sites often appear to have functioned as cess pits and dumps for household waste (e.g. Hall *et al.* 1980; G. Jones *et al.* 1991), so they may also provide plant macrofossil evidence of household activities and diet. It should be noted, however, that the interpretation of *in situ* wild plant remains can be rather limited and circular. For instance, wild plant remains preserved in a ditch are likely to be indicative of the ecological conditions typical of ditches.

Waterlogged macroremains of wild plants preserved outside settlements are most useful for establishing the presence of particular species in a given locality (Godwin 1975). Consequently, these remains are sometimes studied as complements to fossil pollen assemblages, where they are used to provide detail about the local components of the vegetation (Wasylikova 1986).

1.1.2.2 Large-scale vegetation reconstruction

Whilst plant macrofossils are usually suitable evidence for reconstructing local vegetation and ecological conditions, particularly those that directly reflect human activity, fossil pollen is most suited to a different type of vegetation reconstruction. Pollen can be transported over long distances before being deposited, making fossil pollen evidence unique in the breadth of its geographical coverage (Faegri and Iversen 1989 pp. 27-31; Moore *et al.* 1991 pp 182-184). In addition, fossil pollen assemblages may represent deposition over long periods of time, and so they provide good evidence for temporal changes in vegetation (Moore *et al.* 1991 pp. 185-191). As a result, fossil pollen can be used to reconstruct vegetation on large geographical and temporal scales, but is less well suited to detailed studies of local vegetation.

Fossil pollen research has often concentrated on the reconstruction of very broad regional patterns of vegetation change, particularly forest history (e.g. Godwin 1975; Davis 1983; Huntley and Birks 1983; Delacourt and Delacourt 1987). On a simple level, this sort of research is pertinent to archaeology because it illustrates the changing vegetational contexts in which past societies functioned. More importantly, however, knowledge of the ecological preferences of the species that constitute the vegetation allows palynologists to interpret vegetational changes in terms of ecological changes, particularly climate change (e.g. H. J. B. Birks 1981; Prentice 1986). Thus, pollen is an important source of evidence for reconstructing one of the fundamental ecological factors that affect human society.

Pollen is, however, also a source of evidence for human influence on the environment. During the Holocene, human activities such as forest clearance and agriculture have had a strong influence on vegetation patterns, albeit on a generally more local scale than climate. Consequently, much palynological research has been directed at identifying small-scale human-influenced vegetation types such as pasture or cultivated land from a fossil pollen record that is often dominated by forest plants (e.g. Iversen 1941, 1949; Behre 1981; Behre and Jacomet 1991; Gaillard *et al.* 1992, 1994; Hicks 1992; Hicks and Birks 1996).

1.2 General problems regarding the ecological interpretation of ancient plant remains

There are a variety of different approaches to the ecological interpretation of ancient plant remains, but three problems are common to all of these: 1) taphonomic processes result in assemblages of ancient plant remains that may not accurately reflect the composition of past plant communities; 2) the ecological preferences of plant species may change through time and across space; 3) many ancient plant remains can only be identified to higher taxonomic groups, but it is often not known whether the species with a higher taxonomic group have similar or different ecological preferences. Each of these problems will be considered in turn.

1.2.1 Taphonomic processes

Taphonomic processes can be seen as filters which come between living plant communities and assemblages of ancient plant remains. Each filter alters the composition of the plant material in some way, so that the composition of the assemblage of ancient remains may differ to varying degrees from the composition of the living community.

The many different taphonomic processes that affect the composition of assemblages of ancient plant remains can be separated into three basic categories: pre-depositional, depositional, post-depositional (Clarke 1973). The processes included within these categories are significantly different for plant macroremains and pollen, so these different types of ancient plant remains will be considered separately.

1.2.1.1 Plant macrofossil taphonomy

There are a number of means by which plant macroremains can be preserved, and different taphonomic processes are likely to have acted on remains preserved by different means. This consideration of plant macrofossil taphonomy will, therefore, be divided according to the main preservation types of the remains.

Charring is one of the commonest processes by which plant macroremains are preserved. Under certain conditions, high temperatures cause plant

material to be converted to elemental carbon in a manner that more or less preserves the original form of the material (Wilson 1984; Boardman and G. Jones 1990; Hubbard and al Azm 1990). Because this process is dependent on heat, charred plant remains are predominantly associated with human settlements (Green 1982). Of the full range of plants found in any settlement, those that are routinely deliberately burnt (fuel-plants) or processed in some way in the vicinity of high temperatures (food-plants) are most likely to be preserved by charring (Green 1982).

Human actions are responsible for the majority of pre-depositional taphonomic processes that affect the types of plant remains that are generally preserved by charring. For crop plants, these are the processes that transform the living plant community into agricultural products and by-products (G. Jones 1983). These might include the weeding and harvesting of the crop; its transportation to a settlement or other agricultural work area; and the separation of weeds, straw and chaff from the desired grain by methods such as winnowing, threshing and sieving (Hillman 1981, 1984; G. Jones 1984). In addition, crops grown separately may be mixed together, and those grown together (for instance if barley and wheat were sown in the same field) may be separated out (G. Jones and Halstead 1995).

These processes may be the same for some of the plants preserved by charring in animal dung used for fuel, particularly if livestock have been fed grain crops (Halstead and Jones 1989; G. Jones 1998). Other plants present in dung fuel may have been processed and selected by humans to produce hay, leaf fodder, or silage; selected by the feeding animal; or added to the dung before burning (Anderson and Ertag-Yaras 1998; Charles 1998). An animal's digestive system will act as a strong taphonomic filter between the plants it eats and those that survive to be charred in its dung, and this taphonomic process differs between animals (Anderson and Ertag-Yaras 1998). The pre-depositional processes for wood used as fuel are also dependent on human action. Wood may be deliberately managed whilst growing, then deliberately cut and processed, or, at the other extreme, natural wind-fall wood may simply be gathered and transported to the settlement.

Depositional taphonomic processes cause the plant remains that survive the pre-depositional stages to be incorporated into archaeobotanical deposits, and charring is itself one of these processes. Although charring is thought of as a preservation process, under many circumstances high temperatures are destructive of plant material (Wilson 1984; Boardman and Jones 1990), and fragile plant parts such as non-woody stems and leaves are often destroyed rather that preserved. Seeds are among the most robust parts of a plant, however, and so are relatively likely to survive charring within a narrow band of temperatures (Wilson 1984; Boardman and G. Jones 1990; Hubbard and al Azm 1990). Charred fuel-plant remains consist largely of fragments of wood (charcoal) and seeds from burnt animal dung. Charred food-plant remains consist largely of the seeds and other dense elements of cereal and legume plants and the weeds that were harvested and processed with them (Behre and Jacomet 1991). Although many other types of plants are cooked and eaten, most are exploited primarily for their leaves, roots or tubers, and these soft elements are relatively unlikely to be preserved by charring.

Whereas fuel-plants are intended to be burnt, food-plants are more likely to be inadvertently charred during cooking or drying. The charred remains of any of these processes may be deliberately discarded as refuse, or may simply be trampled into the ground, and are thus incorporated into the archaeological record. In more exceptional circumstances, destructive fires may cause large quantities of stored plant material to be charred at once (e.g. G. Jones *et al.* 1986). If the storage facilities are abandoned after the fire, then this charred material may be preserved *in situ.*

Once plant material has been incorporated into the fossil record, post-depositional taphonomic processes begin to act on it. Unlike much of the original plant material, carbon is resistant to destruction by microbes, so charred plant remains can survive for long periods of time even in conditions with high microbial activity (Evans 1978). Indeed, charred plant macroremains suffer very little post-depositional change other than the effects of alternate wetting and drying, which can destroy the structure of carbonised material. All plant macrofossil assemblages, however, may be affected by the mixing of

deposits as a result of bio-turbation, geological reworking or human disturbance.

The other common process by which plant macroremains are fossilised is waterlogging, which occurs when plant remains are incorporated into waterlogged deposits such as bogs, wells and lakes.

Waterlogged remains from human settlement sites are likely to include food refuse that will have experienced pre-depositional processes similar to those of charred macroremains. Other plant remains brought to settlement sites by people (such as those used for medicine, tanning, and flooring) are also commonly preserved by waterlogging (e.g. G. Jones *et al.* 1991), and these will have undergone different pre-depositional processes that separate the used plant material from the living plant community. In contrast to charred remains, however, assemblages of waterlogged plant macroremains tend to contain a significant amount of material deposited by natural (as opposed to human) agencies (Behre and Jacomet 1991). Much of this material is likely to consist of plants that were growing in the immediate vicinity of the waterlogged context (Green 1976, 1982; Behre and Jacomet 1991), and which have therefore undergone very little in the way of pre-depositional processes.

Of the full range of plant material used by people at a settlement site, only a fraction is likely to be deposited into contexts that will result in its preservation by waterlogging. Some of this may be deliberately dumped as refuse, or as faeces if the context was used as a cess pit, and some is likely to find its way into waterlogged contexts by natural processes (Hall *et al.* 1980; G. Jones *et al.* 1991). In addition to plants utilised by people, weeds growing in the immediate vicinity of settlement site waterlogged contexts can simply fall in and be preserved *in situ* (Green 1976, 1982; Behre and Jacomet 1991). In natural contexts, deposition from very local plants is important, but birds and other animals may introduce material from further afield (Behre and Jacomet 1991) and, in large depositional contexts such as lakes, water-transported material may also be added (Greig 1976). The depositional processes for waterlogged plant macroremains are, therefore, often particularly difficult for the archaeobotanist to determine (Greig 1976; Hall *et al.* 1980).

Waterlogged remains tend to be subject to more post-depositional alteration than charred remains, although this is dependent on the degree of waterlogging. Permanently waterlogged environments are essentially anaerobic, and so exclude the microbes that quickly destroy dead plant tissues (Evans 1978). Partially waterlogged environments, such as those with a fluctuating water table, are only intermittently anaerobic, and so allow some microbial activity and the resulting decay of plant tissues. In permanently waterlogged conditions, therefore, more or less total preservation of plant tissues, including relatively fragile elements such as leaves, buds and catkins (Tomlinson 1985, 1991), is possible. In partially waterlogged environments, however, the presence of some microbial activity means that only denser elements such as seeds commonly survive (Green 1976, 1982).

Plant macroremains can also be fossilised by mineralisation, desiccation and freezing, and recorded as impressions in material such as pottery and mud-brick. Each of these processes of preservation are much less common than charring or waterlogging (Green 1982), however, so their taphonomic processes will not be considered here.

1.2.1.2 Pollen taphonomy

Fossil pollen differs from most plant macrofossils in that it is predominantly preserved in natural (rather than man-made) sediments, and arrived there through natural processes (rather than through the direct interference of people) (Faegri and Iversen 1989; Moore *et al.* 1991). In addition, all fossil pollen consists of the remains of a single part of the plant, whereas plant macrofossils may consist of a variety of plant parts. The function of a pollen grain is to transport male genetic material to the stigma of a flower of the appropriate species, but the majority of pollen grains fail to reach their target and it is the remains of these 'wasted' grains that form the fossil pollen record (Moore *et al.* 1991 p. 181).

The pre-depositional processes for fossil pollen are particularly complex. Any pollen which germinates or which fails to reach a context suitable for its preservation is effectively filtered out of the fossil record. This is significant because there is considerable variability between species in the quantity of

pollen produced and the means by which it is dispersed (Faegri and Iversen 1989 pp. 11-31; Moore *et al.* 1991 pp. 181-184), and this results in some species having a much better chance of being represented in fossil pollen deposits than others. There are, in fact, three basic strategies of pollen dispersal from the parent plant, each of which has different taphonomic implications: self-pollination, animal-pollination and wind-pollination.

Self-pollinating plants produce very little pollen, and only a small fraction of this is released into the atmosphere and thus dispersed away from the parent plant (Faegri and Iversen 1989 p. 12). As a result, self-pollinating plants are effectively filtered out of the fossil pollen record. Some animal pollinated plants are extremely specialised, with pollen being passed only to a particular animal when it follows a particular pattern of behaviour (Faegri and Iversen 1989 p. 12). These species release very little pollen into the atmosphere and, as a result, are poorly represented in the fossil pollen record. Other animal-pollinated species produce large quantities of pollen, much of which is released directly into the atmosphere and widely dispersed (Faegri and Iversen 1989 pp. 12-13), and these species are more likely to be represented. Lastly, wind-pollinated plants generally release very large quantities of pollen directly into the atmosphere, and rely on wind-currents to carry some of it onto the flowers of other plants of the same species (Faegri and Iversen 1989 pp. 13-14). Plants of this category are by far the most likely to be represented in fossil pollen deposits. Indeed, some wind-pollinated taxa such as *Pinus* produce such huge quantities of pollen that they are represented in the fossil pollen record at levels that considerably exaggerate their importance in the original vegetation (Faegri and Iversen 1989 p. 14).

Pollen deposition is predominantly a natural process. Pollen that is released into the atmosphere and carried away from the plant by air currents falls to the surface after a while, or is incorporated into atmospheric water droplets and falls as rain (Moore and Webb 1978 pp. 100-101; Faegri and Iversen 1989 31-36). It should be noted, however, that quite different depositional processes are relevant to pollen assemblages from archaeological sites. In these contexts, a considerable amount of pollen is likely to have been deposited as a result of human activity (Faegri and Iversen 1989 p. 178). One modern study

found an average of 0.5 million pollen grains per gram of house dust, but very little pollen in the indoor air (O'Rourke and Lebowitz 1984). This strongly suggests that pollen inside buildings is predominantly deposited from the feet and bodies of people and animals.

Thus, the pre-depositional and depositional taphonomic processes of pollen dispersal result in fossil pollen assemblages that are extremely biased sub-samples of the original plant communities: some species are effectively excluded from the pollen record, whilst others are significantly over represented. These same processes also necessarily result in pollen deposits of very mixed origin. Pollen can be transported over very long distances, and there are records of pollen being found as much as 600km from its nearest possible source of origin (Bassett and Terasmäe 1962). In general, however, the natural limit of pollen dispersion is around 50-100km (Faegri and Iversen 1989 p.29), and much pollen is deposited only a few kilometres from its source (Lowe and Walker 1984). It is possible to produce models estimating the relative input of plant communities at different distances from a particular pollen site (e.g. Tauber 1965), but there is no way of distinguishing which species belong to which communities.

The outer wall, or exine, of a pollen grain is constructed from an extremely resistant substance called sporopollenin, which is much more readily preserved than the inner portions of the grain (Faegri and Iversen 1989 p. 221). Nevertheless, pollen exine can be destroyed both by oxidation and by the invertebrates and microbes that eat the cytoplast (Faegri and Iversen 1989 p. 221; Moore *et al.* 1991 pp. 169-170). As for waterlogged plant macroremains, therefore, the post-depositional preservation of pollen grains is best in anaerobic sediments from which microbes and other destructive organisms are excluded (Moore *et al.* 1991 p. 10). There is a variety of such sediment types, but those most often sampled for fossil pollen evidence are peat bogs and lake bottoms. In partially waterlogged environments there will be some microbial activity, so pollen grains will be less well preserved. If pollen is transported after its original deposition, for instance in river water, then its state of preservation may also be affected by erosion (Moore *et al.* 1991 p.170). In addition, pollen-bearing contexts may become mixed as a result of

bio-turbation, geological action, or the movement of water through the sediments (Birks and Birks 1980 pp. 183-187; Moore *et al.* 1991 pp. 14-26), and these processes may result in the loss of some material and the addition of material from different sources.

1.2.1.3 Taphonomy summary

The end result of all these processes, whether for plant macroremains or for pollen, is that the composition of almost any studied assemblage of ancient plant remains will be considerably removed from the composition of the living vegetation from which it originated. Only in the most exceptional circumstances does an assemblage of ancient plant remains closely reflect the full composition of a single living plant community. As an example of this for plant macrofossils, two charred assemblages from Bovenkarpsel and Twisk in the Netherlands each appear to represent the *in situ* preservation of a single freshly harvested, unprocessed, grain crop and its weeds (Buurman 1979, 1987). For pollen, H.J.B Birks (1970) analysed a moss layer trapped in silt deposits from Loch Fada, Isle of Skye, and concluded that it was the remains of a moss-dominated community that had been washed into the loch during a flood and buried more or less intact. Pollen sampled from the moss seemed to essentially represent that local moss-dominated community. These are rare examples, however, and in general it is impossible to be sure how many different plant communities are represented in a fossil assemblage, or how completely they are represented.

In addition to the true taphonomic processes, the sampling and retrieval methods used by archaeobotanists and palynologists to extract plant fossils from their sediments of deposition act as final filters between living plant communities and the studied assemblage. Although only a fraction of the available plant fossil evidence is usually extracted from any sampling site, the retrieval processes differ from the true taphonomic processes in that they are (ideally) controlled to result in representative samples of the full population of preserved evidence.

1.2.2 Ecological preferences of plant species

Any method for the ecological interpretation of ancient plant remains is, of necessity, based upon analogy with the ecological preferences of modern plants. It is, however, the case that modern and ancient populations of the same species do not necessarily share the same ecological preferences. Perhaps the clearest examples of this are species which today are arable weeds, but which are likely to have existed in different ecological niches in pre-agricultural contexts (G. Jones 1992; Küster 1991; Sukopp and Scholz 1997). If a modern species is not exclusively an arable weed, but also occurs in a natural (non-agricultural) habitat, then it may be that this was its original habitat. For example, *Chenopodium polyspermum* and *Chenopodium album* are both modern arable weeds that also occur in damp, riverside habitats, and the latter are thought likely to be their original habitats (Küster 1991; Sukopp and Scholz 1997). With the arrival of farming in Europe during the Neolithic, these and other indigenous species may have undergone evolutionary changes in their ecological preferences that enabled them to invade the new arable habitats (Küster 1991). Alternatively, however, the ecological preferences of such species may have remained essentially the same but the new agricultural habitats were sufficiently similar to the species' original habitats to 'satisfy' those preferences (riverbanks and arable fields are both environments that experience considerable disturbance, for example).

Overall, changes in the ecological preferences of plant species are extremely difficult to detect. The crucial point is that such changes *could* have taken place in any species, but may not have done. It is worth noting, however, that many species are represented fairly consistently through time in assemblages of ancient plant remains that seem to represent similar ecological conditions. For instance, some species occur regularly in archaeobotanical crop weed assemblages over long periods of time, and these species remained common in arable contexts until the widespread use of herbicides began in the middle of the twentieth century (Holzner 1978; M. Jones 1988). This seems to suggest that, whilst species' ecological preferences can change, many may have been more or less ecologically stable over significantly long periods. The arable environment encompasses considerable variation,

however, so long-term arable weeds may have been stable in only some of their ecological preferences (e.g. for disturbed conditions), whilst some of their other preferences may have changed quite radically (e.g. for moisture or soil pH).

In addition, many plant species have evolved adaptations to different ecological conditions in different parts of their range (Stace 1989 p. 168). The various 'ecotypes' of such species are distinct genetic races and are also differentiated by other characters, which are often morphological, but which may also be chemical or physiological (Etherington 1975 pp. 270-272; Stace 1989 p. 168). For instance, upland ecotypes of *Festuca ovina* have a much lower calcium requirement than lowland ecotypes of the same species (Snaydon and Bradshaw 1961). For the most part, different ecotypes cannot be distinguished morphologically from their fossil remains (Birks and Birks 1980 p. 236). Consequently, if ecological data for modern species that include different ecotypes are to be applied to ancient plant remains, the data need to take account of the possible variation in adaptation (Birks and Birks 1980 p. 236). In many cases however, the ecological datasets on which interpretations of ancient plant remains are based (see Chapter 3) refer only to the most characteristic types of particular species (Behre and Jacomet 1991).

The existence of different ecotypes is a problem for applying modern ecological data to the past and also for the application of ecological data across biogeographical boundaries. Thompson *et al* (1993) tested the significance of the latter problem by comparing ecological data for species in Central Europe (Ellenberg 1974) with similar data for the same species collected during vegetation surveys undertaken in Central England (Grime *et al.* 1988; Grime and Lloyd 1973; Hodgson and Band unpublished described in Hodgson 1986). Although there were differences between the two geographical regions in the type of data collected, Thompson *et al* (1993) concluded that the ecological characteristics of Central European plant populations are reasonable predictors of the characteristics of British populations of the same species. This suggests that it is reasonable to apply ecological data for plant species across some biogeographical boundaries, but

caution certainly needs to be exercised when applying data between areas that are ecologically very different.

1.2.3 Identification

Floras and other guides to the identification of complete living plants use a wide variety of different features to define individual species. It is unsurprising, therefore, that identifying species on the basis of the very fragmentary evidence that survives the taphonomic processes described above is not always possible. This is partly an artefact of the relatively low identification potential of individual plant elements viewed in isolation, and partly because of the damage done to those elements by the processes of fossilisation.

This is a significant problem for the ecological interpretation of ancient plant remains because higher taxonomic groups tend to have much greater amplitude of ecological preferences than do individual species. The breadth of ecological preferences varies for different higher taxonomic groups, and in many cases is not known in detail. If an archaeobotanical assemblage contains many taxa that cannot be identified to species, then it currently has little potential as a source of evidence for past ecological conditions.

The particular problems of identifying plant remains to species differ significantly for plant macroremains and pollen, so these will be considered separately.

1.2.3.1 Plant macrofossil identification

The plant elements that are most often preserved as charred and waterlogged macrofossils are seeds, fruits and their associated structures; more fragile elements such as leaves, stalks, buds and catkins may also be preserved by waterlogging. The potential of these individual elements to be identified to species is extremely variable, even when they are in their fresh state. The species of some higher taxonomic groups are particularly difficult to distinguish on the basis of their seeds alone. For instance, it is quite common for genera of the Fabaceae family to include some species that cannot be distinguished on the basis of seed morphology, and even members of *different* Fabaceae genera may have extremely similar seed morphology (Butler 1991).

This is exacerbated by the potential for phenotypic plasticity in some Fabaceae species: when growing with *Lens culinaris* (lentil), *Vicia sativa* (vetch) may develop populations that mimic the lentil crop and produce lenticular seeds (Rowlands 1959; Butler 1991). Notwithstanding such examples, however, a great many plant species *can* be identified from their seeds, and most genera include some such species.

Of the plant elements that are usually only preserved by waterlogging, buds and catkins are often diagnostic of individual species when in their fresh state (Tomlinson 1985, 1991). Leaves can be diagnostic at a variety of different taxonomic levels from species to class, but identification is hindered by the fact that many taxa have morphologically very variable leaves (Hickey 1971). Stems are generally not identifiable to species (Tomlinson 1985, 1991).

Whilst it is not always possible to identify individual plant elements to species in their fresh state, the identification potential of fossilised material may be considerably lower. It has already been shown that only seeds and a few other dense plant elements commonly survive charring, but it is also the case that those elements that do survive have less identification potential than their living counterparts. For instance, *Galium* species often have diagnostic cell patterns in their seed coat, or testa. In well preserved charred *Galium* seeds this testa may be more evident than in fresh seeds, but charring often destroys or damages the testa, so the archaeobotanical remains of *Galium* species are often identified only to the genus level (Tomlinson and Hall 1995).

Because charring may be destructive of fine details, charred seeds are usually identified primarily on the grounds of their general morphology. Charring can, however, cause severe distortion of both seed size and shape, which may make accurate identification on morphological grounds impossible (Wilson 1984; Boardman and Jones 1990; Hubbard and al Azm 1990). On the whole, however, charred seeds can routinely be identified to the genus level and often to species.

Waterlogging is a much less destructive process than charring, so waterlogged seeds often retain many of the diagnostic features of their living counterparts, including any fragile outer coverings. Consequently, waterlogged seeds are potentially easier to identify than charred seeds. They may however

be rather swollen and distorted, and many will have undergone some decomposition, and this may make identification on morphological grounds difficult (Körber-Grohne 1991). On the other hand, slight decomposition (like charring) can expose epidermal cells that are often highly diagnostic (Wasylikova 1986; Körber-Grohne 1991). Other waterlogged remains such as leaves and stems are often very fragmentary, and this considerably lowers their identification potential (Tomlinson 1985, 1991).

In plant macrofossil studies, remains that cannot be speciated are often simply identified to higher taxonomic groups, usually genus or family, but they can also be identified to 'grouped types' that include more than one species or genus. In plant macrofossil analysis such type names are usually used when a seed cannot be identified to a single species, but a genus-level identification would be unnecessarily broad. For instance, in his guide to the identification of Near Eastern grass seeds, Nesbitt (2000) often subdivides genera into a number of types, each comprised of a few species that have morphologically indistinguishable seeds. More rarely, a grouped type will cross higher taxonomic boundaries. For instance, because the seeds of the closely related genera *Vicia* and *Lathyrus* are so similar (Butler 1991), identifications of 'Vicia/Lathyrus type' are common in the archaeobotanical literature (Tomlinson and Hall 1995).

Ecological interpretations of plant macrofossil assemblages are based predominantly on those taxa that have been identified to species. Taxa identified to higher taxonomic groups or types are only usually included if the ecological characteristics of all species in the group are believed to be very similar. For instance, in an assemblage of charred macroremains from the medieval site of Gasselte in the Netherlands, of the 50 weed taxa identified, 31 (62 %) were species (van Zeist and Palfenier-Vergter 1979). A further 10 taxa were included in the site's ecological interpretation, however: 4 were identified to species, but with the possibility of error acknowledged, 4 were identified to types that included only two species, and 2 were identified to genera. By the ecological system (phytosociology) used to interpret the assemblage, these identifications were sufficient to classify the taxa ecologically and allow a detailed interpretation (van Zeist and Palfenier-Vergter 1979). In circumstances

where very few taxa in an assemblage can be identified to species, however, the potential for ecological interpretation is currently extremely limited. For instance, from an assemblage of charred macroremains from the Syrian Neolithic site Ramad, of the 60 non-crop taxa identified, only 12 (20 %) were firmly identified to species, and many of the rest were identified to higher taxonomic groups or quite widely defined types (van Zeist and Bakker-Heeres 1982). Consequently the only ecological interpretations of this material were the classification of some of the taxa as probable field weeds, and the suggestion that the crops were autumn sown. The problems encountered in identifying this particular assemblage were in part due to a paucity of reference material for the flora of the area (van Zeist and Bakker-Heeres 1982), and this should be recognised as an additional factor that can hinder the identification of both plant macroremains and pollen.

1.2.3.2 Pollen identification

The most serious problem for pollen identification is that individual species rarely have morphologically unique pollen grains. Indeed, it is not unusual for all the species of a genus or family to share the same pollen morphology. For this reason, all pollen grains are categorised into 'types', each of which has equivalent morphological status, that is, each type includes all the species that share a particular pollen morphology, and no others (Bennett 1994). These types, rather than species, are the basic unit of identification in palynology (Bennett 1994).

As for plant macrofossil types, the taxonomic status of pollen types is variable (Bennett 1994). Many types coincide exactly with taxonomic groups. For instance, in the British flora, the species *Ranunculus arvensis*, the genus *Veronica*, and the family Rubiaceae all have pollen types unique to themselves (Bennett 1994). In other cases, nearly all the species in a genus or family are of one pollen type, but there are also a small number of exceptional species in the group that have their own pollen type(s). The British pollen type '*Rubus* undifferentiated', for instance, includes all the native *Rubus* spp. except *Rubus chamaemorus*, which has its own pollen type (Bennett 1994). Finally, it is also possible for pollen types to cross taxonomic boundaries. In some instances

this simply means that two complete taxonomic groups share a pollen type. For example, the British 'Alchemilla-type' comprises all the native species of the closely related genera *Alchemilla* and *Aphanes* (Bennett 1994). Other cross-taxa pollen types are more complicated, however. The British 'Cerastium type', for instance, contains all the native *Cerastium* spp., all the native *Stellaria* spp. except *S. holostea*, plus *Myosoton aquaticum* and *Moenchia erecta* (Bennett 1994). Overall, pollen types tend to include more species than plant macrofossil types, and are often equivalent to family level identifications.

The pollen of different plant taxa is distinguished by a number of morphological features, all of which are part of the outer wall, or exine of the grains (Moore *et al.* 1991 pp.67-78). Because the pollen exine is the part that survives fossilisation (Faegri and Iversen 1989 p. 221), this means that fossilised pollen is potentially as readily identifiable as living pollen. This is in contrast to plant macrofossils, many of the diagnostic features of which do not readily survive fossilisation, even when preservation conditions are good. Overall, however, pollen grains can usually be identified with less taxonomic precision than plant macrofossils, and most fossil pollen studies include a high proportion of pollen types that represent higher taxonomic groups or that cross taxonomic boundaries. For instance, in a study of pollen from the French Holocene deposit of Marais des Baux, of the 59 pollen types identified, only 15 (25%) were species types (Andrieu-Ponel *et al.* 2000). 20 (34%) were genus types, 18 (31%) were types that did not precisely correspond with taxonomic groups, and 6 (10%) were family types. The very high degree of taxonomic uncertainty in pollen identifications is perhaps the greatest hindrance to the ecological interpretation of fossil pollen spectra. A single pollen type could include species indicative of a variety of different ecological conditions, or, indeed, one good ecological indicator and a range of ecologically more flexible species (Behre 1981; Hicks 1988; Gaillard *et al.* 1992; Hicks 1992). For instance, grass species are potentially excellent ecological indicators, but most pollen studies only distinguish between 'Poaceae (wild type)' and 'Poaceae (cereal type)' pollen. Of the domesticated grasses, only *Secale* (rye) and *Zea* (maize) can be identified to genus (Faegri and Iversen 1989 p. 184).

In order to interpret fossil pollen assemblages, therefore, palynologists tend to decide which species are 'most likely' to be represented by pollen types in particular circumstances. For instance, the British 'Jasione montana type' potentially includes the species *Jasione montana* and *Wahlenbergia hederacea*, but in Shetland, where *Wahlenbergia* is thought unlikely to have ever occurred, this type is usually reduced to include only *Jasione montana* (Bennett 1994). In most cases, such decisions are based on the present ecology and distribution of the species that could be represented by each pollen type (e.g. Behre 1981; Hicks 1988). Evidently, there is a considerable amount of subjectivity involved in selecting the 'most likely' species on these grounds, although Behre strangely suggests that this subjectivity "may even be advantageous, if based on the author's solid knowledge of the ecology of the species and the landscape in question." (Behre 1981 p.226). The assumption that a species' modern ecological preferences are relevant to the past may, however, be entirely unjustified, so this 'advantage' is surely illusionary.

Reducing pollen types to the 'most likely' species in this way is, therefore, circular reasoning: an assumed ecological context is used to reduce pollen types to species, then the ecological tolerances of these same species are used to reconstruct the local ecology. Evidently, such reasoning will always serve to reinforce the original assumptions made about the ecological context, which may have been quite inaccurate, so ecological interpretations based on such reasoning should be treated with great caution.

1.3 The relevance of higher taxonomic groups to these problems

The previous section identified three fundamental problems with the application of ecological data for modern plant species to assemblages of ancient plant remains. In this thesis, ecological data relevant to higher taxonomic groups will be used to address the last two problems: those associated with identifying ancient plant remains to species and to applying modern ecological data to the past. Ecological data for higher taxonomic groups do not address the problems associated with taphonomic processes,

and taphonomic issues will only be considered again where they are relevant to the other problems.

As mentioned above, in the current state of research most data on the ecological preferences of plants refer to individual species rather than to higher taxonomic groups. Consequently, if ancient plant remains are not identified to species, then they have little potential as a source of evidence for past ecological conditions. Nevertheless, as will be explained in the next chapter, there is significant evidence that plant higher taxonomic groups often exhibit some level of ecological specialisation (e.g. Stebbins 1974; Grime *et al.* 1981; Grime 1984, 1985; Hodgson 1986; Hodgson and Mackey 1986; Díaz and Cabido 1997; Westoby 1998). If the species within a higher taxonomic group vary little in their ecological preferences, then useful ecological inferences can be drawn from ancient plant remains that are identified to that higher group but not to species. On the whole, however, there is currently little information to suggest precisely which ecological preferences are relatively unvarying in which higher taxonomic groups.

In both palynology and archaeobotany, considerable research is directed towards new techniques for identifying material to species (or as low a taxonomic group as possible). For instance, scanning electron microscopy has been used extensively to define criteria for the identification of Fabaceae genera and species from micro-features of the seed testa (Butler 1988, 1991, 1996). For palynology, it has been claimed that recent improvements in the precision of taxonomic identifications have lead to "nearly all major developments in our understanding of the patterns and processes of late Quaternary vegetational history." (H.J.B Birks 1994 p.107). These improvements in taxonomic precision are partly due to the production of comprehensive modern pollen reference collections and accurate pollen Floras, but also to technical developments in microscopy. Such research is very time consuming and costly, however, and the use of SEMs and other specialist equipment is likely to be beyond the financial resources or expertise of many archaeologists and palynologists. If useful ecological inferences can be drawn from ancient plant remains identified to higher taxonomic groups that are unvarying in many of their ecological preferences, the need for new

identification criteria for such groups is not great. Instead, higher taxonomic groups from which few ecological inferences can be drawn should be targeted for such research.

The other problem that will be addressed using ecological data for higher taxonomic groups is that the ecological preferences of modern species are not necessarily the same as the ecological preferences of species in the past (Birks and Birks 1980; Küster 1991; Jones 1992). Higher taxonomic groups are relevant to this problem because an ecological characteristic that is relatively unvarying within a higher taxonomic group is likely to have undergone little independent evolution since the species in that group diverged from their common ancestor (Stebbins 1972, 1974). Consequently, modern measurements of that ecological characteristic are likely to be relevant to the past, both for the individual species and for the group as a whole. As before, however, there is currently little information to suggest precisely which ecological characteristics for which taxonomic groups have been relatively stable through time.

Chapter 2 – Ecological background

In the first part of this chapter a number of different plant classification systems are discussed. All of these all are considered further in this thesis, though emphasis is placed on plant functional classifications, in particular the FIBS (Functional Interpretation of Botanical Surveys) technique. The second part of the chapter considers the ecological significance of higher taxonomic groups, in particular the potential for phylogenetic conservatism in higher plant groups.

2.1 Plant classification

2.1.1 Taxonomic classifications

Plants (and other organisms) may be classified in many different ways, but the most familiar scientific systems consider how similar or different to each other plants are, based on the present state of a range of characters. These systems are usually referred to as taxonomic classifications or taxonomies. There are many schools of taxonomic classification, but these fall within two broad categories that can be termed 'phenetic taxonomies' and 'phylogenetic taxonomies' (Stace 1989 p. 11).

2.1.1.1 Phenetic taxonomies

Phenetic taxonomies are generally based on a wide range of characters which are traditionally morphological, but, increasingly today, may be anatomical, chemical, cytological or a mixture of these (Stace 1989 p. 11). The plants are arranged hierarchically, with very similar species being grouped into a genus, similar genera into a family, and so on. *The International Code of Botanical Nomenclature* (Greuter *et al.* 2000) defines the standard plant hierarchy on which most contemporary phenetic taxonomies are based. This hierarchy is the classificatory basis of scientific Floras such as the *Flora Europaea* (Tutin *et al.* 1968; 1972; 1976; 1980; 1993) and *New Flora of the British Isles* (Stace 1997). Table 2.1 shows the full hierarchy of ranks as

recognised by the *International Code,* but, in this thesis, only the ranks 'species', 'genus', and 'family' are generally applied.

Despite the guidelines of the *International Code* (Greuter *et al.* 2000), there are no absolute criteria by which groups within a phenetic taxonomic hierarchy are defined (Cronquist 1968 pp. 28-32; Stace 1989 pp. 187-192). Traditionally, taxonomists have defined groups based on a combination of established custom and personal judgement of the discontinuities of variation in plant characters. Because some taxonomists prefer to emphasise the differences between characters (the so-called 'splitters'), and others the similarities (the 'lumpers'), this means that there can be considerable differences even between classifications based on the same characters (Stace 1989 p.189). Even within a single phenetic classification, there is no strict comparability between groups at the same taxonomic level (Cronquist 1968 pp. 28-32; Stace 1989 pp. 187-192). For instance, the genus *Leitneria* contains only a single species (*L. floridana*), and so encompasses very little phenotypic variation, whereas the genus *Senecio* contains over 2000 species, and so encompasses a great deal of phenotypic variety (S. Jones and Luchsinger 1987 p. 60). In response to the very subjective nature of taxonomies reliant on personal judgement, Sokal and Sneath (1963; Sneath and Sokal 1973) developed a system of 'numerical taxonomy'. This system applies cluster analysis to large sets of binary phenotypic characters of taxa (often, but not necessarily, species) (Stace 1989 pp. 43-52). Unfortunately, although numerical taxonomy defines clusters of taxa objectively, subjective methods are still used to equate these clusters with the different taxonomic ranks. Consequently, even numerical taxonomy results in groups at a single taxonomic level varying considerably in size and degree of diversity (Stace 1989 p. 49).

Phenetic taxonomies are intended primarily to be predictive. For instance, if a particular plant is known to be a member of the grass family (Poaceae) it is possible to predict aspects of its morphology, anatomy and chemical characteristics even if that plant has not been previously investigated (Stace 1989 p.10). Because closely related taxa have such characteristics in common, phenetic taxonomies also tend to reflect the evolutionary relationships of taxa and are commonly used as a guide to such relationships.

Although evolutionary history and relatedness are taken into account in the construction of most phenetic taxonomies (S. Jones and Luchsinger 1987 p. 55), phenotypic differences and tradition tend to take precedence over evolutionary relatedness when defining taxonomic groups (Harvey and Pagel 1991 p. 52; Sivarajan and Robson 1991 pp. 110-111). In truth, therefore, phenetic taxonomies "provide only a somewhat muddy reflection of evolution" (Cronquist 1968 p. 15).

2.1.1.2 Phylogenetic taxonomies (phylogenies)

Phylogenetic taxonomies, in contrast, are constructed for the specific purpose of determining the evolutionary relationships and history of a group of taxa (Stace 1989 p. 11). Intentionally phylogenetic taxonomies based on the phenotypic features of extant taxa and (to a much lesser extent) fossil plants have been constructed since the late nineteenth century (S. Jones and Luchsinger 1987 pp. 26-34). The modern school of phylogenetics, however, grew out of Hennig's proposed rules for accurately reconstructing evolutionary relationships from characters in which a 'primitive' and 'advanced' state can be recognised (Hennig 1966). More recently, the development of molecular systematics – the use of DNA and RNA to infer evolutionary relationships among taxa – has greatly facilitated the study of phylogenetics (Harvey and Pagel 1991 p. 65; Soltis and Soltis 1998; Judd *et al.* 2002 p. 105-106).

As for phenetic taxonomies, phylogenies are based upon similarities between taxa, but it is a fundament of phylogenetics that these similarities must be a direct result of character inheritance through evolutionary descent. Modern phylogenies are constructed by methods similar to those of 'numerical taxonomy' (see above, Section 2.1.1.1.) (Stace 1989 p. 52). That is, various characters of a group of taxa are observed and divided into distinct character states, and the resulting dataset is subject to a form of cluster analysis. For modern phylogenetic analyses, however, it is necessary to determine which states of any character are derived from a recent ancestor (advanced character states) and which are inherited from a more distant ancestor (primitive character states) (Stace 1989 p. 53; Judd *et al.* 2002 pp. 17-21). A group of taxa that share an advanced state of a particular character are

considered to be more closely related to each other than they are to taxa that have a primitive state of that character.

The output of a phylogenetic analysis is a diagram in which taxa are grouped in clusters, or 'clades', that reflect their evolutionary relationships. For instance, Figure 2.1 shows a simple phylogenetic 'cladogram' reflecting the character states of fruits in three members of the Rose family (Rosaceae) (after Judd *et al.* 2002 p. 4). All three taxa have fruits called drupes – fleshy fruits containing a stony seed. Compared to cherries, however, blackberries and raspberries both have an advanced state of this character in which numerous small fruits are clustered together to form a compound fruit. This indicates that blackberries and raspberries are more closely related to one another than either are to cherries. In the cladogram, therefore, blackberries and raspberries have their own clade, which is nested within a larger clade that also includes cherries. In a true phylogeny, each clade must be monophyletic – that is, it must contain all the descendents of a single common ancestor (Judd *et al.* 2002 p. 4).

Once created, phylogenetic cladograms may be used as the basis for classifying taxa. Because a phylogeny is similar in structure to a hierarchy (in which small groups are nested within large groups) it is common to base phylogenetic classifications on the same hierarchical system on which phenetic taxonomies are based (Judd *et al.* 2002 p. 35) (see Table 2.1). Although this system of classification has the advantage of familiarity, there are considerable problems involved in fitting the complexity of an extensive phylogenetic cladogram into the arbitrary ranks of the phenetic hierarchical system (Stace 1989 pp. 56-58; Judd *et al.* 2002 pp. 35-36). In general, phylogenetic groups are assigned the name and rank of the phenetic taxonomic groups they most resemble in species composition, with the proviso that phylogenetic groups assigned to the same rank should not be assumed to be similar in age or amount of character variation (Judd *et al.* 2002 p. 36). Some phylogenetic researchers feel that assigning groups to arbitrary ranks causes confusion in evolutionary studies (e.g. Eriksson *et al.* 1998), and they favour adopting a purely phylogenetic taxonomy in which taxa are grouped but not ranked (Stace 1989 pp. 56-58; Judd *et al.* 2002 p. 36). Although a code of rules for building

purely phylogenetic classifications has been drafted (Cantino and de Queiroz 2000), it is not yet in operation, and such classifications seem unlikely to come into common usage until the phylogenetic relationships between taxa are more fully understood, and more familiar to the scientific community, than at present.

It is important to note that, although modern phylogenies are more accurate reflections of evolutionary relatedness than phenetic taxonomies, they should be treated as hypotheses rather than statements of fact (Silvertown and Dodd 1996). One reason for this is the difficulty of determining which character states are advanced and which are primitive (Stace 1989 pp. 53-54; Judd *et al.* 2002 pp. 17-22). If the character states are wrongly diagnosed, then the resulting phylogeny will be erroneous. Other problems are caused if characters have evolved in a parallel or convergent fashion, or have reversed direction so that an advanced character-state reverts to a primitive one (Judd *et al.* 2002 pp. 22; Stace 1989 pp. 59). As a result of these processes, a number of different phylogenies can often be proposed from a single data set, and determining which phylogeny is correct is probably the most contentious area of phylogenetics (see Stace 1989 pp. 59-60 for reviews of these issues; Judd *et al.* 2002 pp. 17-25).

2.1.2 Ecological classifications

Although taxonomic classifications often include ecological information as notes appended to the species descriptions, such information is generally of a very limited nature and is rarely used in the construction of taxonomies (Stace 1989 p. 173). Other classification systems, however, are intended specifically to categorise species either according to ecological criteria or in a manner that directly reflects ecological conditions.

2.1.2.1 Phytosociology (syntaxonomic classifications)

Phytosociology is a method for describing and classifying vegetation in terms of hierarchically defined plant communities. This method was developed principally by researchers in Zürich and Montpellier, and the phytosociological tradition has remained particularly strong in continental Europe (e.g. Braun-Blanquet 1936; Braun-Blanquet *et al.* 1952; Oberdorfer 1954; Hüppe and

Hofmeister 1990) compared to Britain, although it is the basis of the recent *National Vegetation Classification* of British plant communities (Rodwell 1991a, b, 1992, 1995, 2000). The general approach of the Zürich-Montpellier School was formalised by Braun-Blanquet (Braun-Blanquet 1928) and this 'Braun-Blanquet approach' (Westhoff and van der Maarel 1973) remains the basis of many phytosociological classifications.

To build these classifications, vegetation types are described by recording species presence and abundance in a series of vegetation stands. Wherever possible, details of the local ecological conditions are also recorded and environmental samples collected and analysed (Westhoff and van der Maarel 1973 pp. 638-639). Earlier practitioners used tables and various visual aids to consider the floristic similarities and dissimilarities between vegetation stands, and from this to define phytosociological communities (Westhoff and van der Maarel 1973 pp. 643-654), but there is now a strong reliance on multivariate statistics to perform this task (e.g. Rodwell 1991a, b, 1992, 1995, 2000). Once the communities have been defined, they are characterised according to whatever ecological information is available (Westhoff and van der Maarel 1973 p.645). Thus, although a phytosociological community (or syntaxon) is considered to be a reliable *expression* of the ecological conditions in which it occurs, it is defined independently of these conditions.

Phytosociological communities are organised into a hierarchical classification system that is akin to the taxonomic hierarchy (Westhoff and van der Maarel 1973 p. 626; Stace 1989 p. 172). The basic unit of the hierarchy is the 'association', which corresponds in function to the species in the taxonomic hierarchy. Associations are grouped into alliances, alliances into orders, orders into classes, and classes into divisions.

Phytosociological classifications have been used in a wide variety of scientific disciplines, including archaeobotany, as an aid in the ecological interpretation of vegetation data (Westhoff and van der Maarel 1973 p. 681). Indeed, from early in the development of this approach to plant classification, it was recognised that:

> "the really valuable element in the phytosociological method might be not so much the hierarchical definition of plant associations, as the meticulous

sampling of homogenous stands of vegetation on which this is based, and the possibility of using this to provide a multidimensional framework for the presentation and study of ecological problems." (Rodwell 2000 p. 3).

2.1.2.2 Autecology and functional classifications

In contrast to phytosociology, which treats whole plant communities as a unit, autecology generally deals with the ecology of individual species. Whereas phytosociological studies simply include descriptions of the environment in which species (and their communities) tend to grow, autecological studies directly relate species to their environment and attempt to explain *why* they are there. Autecological data can be obtained from field surveys and observations or from laboratory-based experimental programmes.

Perhaps the best-known autecological data are Ellenberg's tables of indicator values (commonly known as Ellenberg numbers) for some 2000 Central European plant species (Ellenberg 1950, 1974; Ellenberg *et al.* 1992). These numbers provide quantitative estimates of the relationship of each species to six major climatic and edaphic variables: light availability, temperature, continentality, soil moisture, soil pH and nitrogen availability. The Ellenberg numbers are predominantly derived from observations of the field distribution of species in a given area, and so act as surrogates for the actual field measurements of, and species preferences for, the relevant environmental variables, although later versions of the tables also include some data derived from experimental work (Thompson *et al.* 1993).

Another commonly used large autecological dataset, the *Comparative Plant Ecology* (Grime *et al.* 1988), covers fewer species and a smaller geographical range than the Ellenberg numbers (273 common British vascular plant species), but includes standardised data for a greater variety of ecological characters. These include life form, nuclear DNA amount and chromosome number, germination characteristics, geographical distribution and gregariousness. These data consist of original field and laboratory measurements plus information compiled from a wide variety of published sources (Grime *et al.* 1988 p. 6).

Due partly to the influence of A. R. Clapham (e.g. Clapham 1956), the autecological approach to plant ecology has (with the exception of Ellenberg)

been particularly strong in Britain compared to continental Europe (Grime *et al.* 1988 p. 1). Traditionally, the majority of autecological work has dealt with only small numbers of species, or even single species published as monographs. Even co-ordinated autecological accounts such as the *'Biological Floras'* published in the *Journal of Ecology* each deal with a single species and are not sufficiently standardised to allow the simple comparison of species on a broad scale (Grime *et al.* 1988 p. 6). Not all plant autecological studies, therefore, are relevant to a discussion of classification. In recent years, however, there has been a considerable movement in ecology towards the collection of standardised 'functional' autecological data for many species from a given environment or geographical region, and the subsequent classification of these species into 'functional groups'.

Most plant taxonomists (both phenetic and phylogenetic) have avoided basing their classifications on characters that have well-defined functions because these are likely to have undergone strong evolutionary selection (Stace 1989 p. 182). Such selection may result in convergent evolution, parallel evolution or very rapid divergence of taxa, all of which cause the possession of shared functional characters to be a poor measure of overall relatedness (Stace 1989 p. 182). Because *ecologically* functional characteristics are amongst those generally excluded from taxonomic processes, although the species within taxonomic groups are similar in many morphological and other respects, they may be adapted to quite different ecological conditions.

'Functional classifications', however, are based on autecological characters that have a known functional relationship with particular ecological conditions. They group plants (and other organisms) according to their adaptation to the environment rather than how morphologically similar or evolutionarily related they are. Functional classifications have a long pedigree; Theophrastus produced a sophisticated system for plants as early as c. 300 BC (Gitay and Nobel 1997), suggesting, for instance, "that we should classify in some cases simply by size, and in some cases by comparative robustness or length of life." (Hort 1916 p. 27). Some botanical functional classifications are in fact quite

familiar, terms such as tree, shrub and herb; annual, biennial and perennial all define functional classes (Westoby and Leishman 1997).

Like phytosociological classifications, functional classifications ultimately allow the complexity of an ecosystem to be reduced to a relatively small number of groups of known ecological significance (Simberloff and Dayan 1991; Westoby 1998). Under both systems, species are replaced as the basis of analysis by generalised groups of taxa that share a particular relationship to the environment. Although the analysis of generalised ecological data (as opposed to data relevant to individual species) has its detractors (e.g. Harper 1982; Grubb 1985), it is widely recognised to be a realistic method of analysing the fundamental aspects of complex ecosystems. Because contemporary functional classifications are based on detailed autecological data that have the potential to explain *why* a group of species occupies a particular environment, they are far superior in this respect to phytosociological classifications which are based on data that essentially state *where* groups of species will grow.

2.1.2.2.1 Plant functional attributes and functional types

The autecological characters on which functional classifications are based are generally referred to as 'traits' or 'functional attributes', and functional attribute is the term that will be used throughout this thesis. In essence, a functional attribute is any characteristic that may have adaptive significance for a plant, and for which there is measurable variation between taxa in state, size or number (Semenova and van der Maarel 2000). The various plant functional classification schemes are based on a range of different attributes, depending on the vegetation studied and the questions asked. Most schemes, however, use physiological, life-historical and biochemical attributes that respond in a known way to resource availability and environmental disturbance (Grime *et al.* 1997a; Shugart 1997).

In order to simplify the complexity of nature, functional classification schemes generally aim to sort the different attributes into groups. The basis for forming these attribute groups is the idea that, although plant species vary widely in their functional attributes, this variation is not random - species that

are similar in one attribute are likely to be similar in a range of co-adaptive attributes (Grime *et al.* 1997b; Westoby and Leishman 1997). For instance, plants in dry, nutrient poor habitats tend to have evolved tough, long-lived leaves *and* short canopies. Species are, therefore, assigned to functional groups based on commonly recurring combinations of attributes that reflect ecological conditions.

The contemporary approach to functional groups began with Root's (1967) work on bird 'guilds' in which he defined a guild as: "a group of species that exploit the same class of environmental resources in a similar way. This term groups together species, without regard to their taxonomic position, that overlap significantly in their niche requirements." (Root 1967 p. 335). Root saw the guild as having a position in functional classifications comparable to that of the genus in taxonomic classifications (Root 1967). Many terms other than guild have since been used for these groups, including 'syndrome' (e.g. McIntyre *et al.* 1999) and 'strategy' (e.g. Grime *et al.* 1988). Following the general term used in contemporary plant ecology (e.g. papers in Smith *et al.* 1997), however, these groups will be referred to as 'functional types' throughout this thesis.

There are also many different definitions of functional types, depending on how they are intended to be used. Gitay and Noble (1997) review many of the different definitions, and conclude that they can be divided into two broad groups: one in which species are grouped on the basis that they use the same resources, and another in which species are grouped by their response to some sort of disturbance. These groups can then be subdivided according to whether or not the species use the same resource in the same way, or respond to the disturbance by the same mechanism (Gitay and Nobel 1997). In essence, however, a functional type is a non-taxonomic classification leading to a grouping of organisms that have similar functional attributes.

There are many plant functional classification schemes in existence, some developed for application in particular regions or habitats, and some intended for much wider, even global, application. As an example of a functional classification scheme developed for habitat-specific application, Boutin and Keddy (Boutin and Keddy 1993) grew 43 species of North American wetland

plants under laboratory conditions, and measured 19 attributes (most of them functional) of these plants at particular juvenile developmental stages. A further 7 attributes were measured for adult plants of the same species growing in the wild. Various statistical techniques were applied to the resulting data set, and these distinguished four functional groups, each of which was related primarily to plant response to light conditions. The authors suggested that knowledge of these functional groups could be used to predict the effects on wetland floras of various environmental perturbations resulting from farming and land development (Boutin and Keddy 1993). For other examples of functional classification intended for habitat-specific application, see the habitat based chapters in Smith *et al* (1997).

As an example of a functional attribute scheme intended for global application, Westoby (1998) developed a scheme based on only three functional attributes (specific leaf area, canopy height and seed mass) which he believes are fundamental trade-offs controlling plant strategy in any environment. These attributes can be relatively simply and consistently measured for all higher plant species from any location. The functional type of each species is determined by its position in a triplot with axes corresponding to the functional attributes. Because this scheme incorporates few functional attributes, it is not appropriate for the detailed ecological investigation of particular habitats. The simplicity of the scheme makes its application on a world-wide scale realistic, however, and this would greatly facilitate study of vegetation dynamics under global change (Westoby 1998). For other examples of functional classifications intended for wide application see Raunkiaer (1934), Grime (1979) and Díaz and Cabido (1997).

2.1.2.2.2 FIBS – the Functional Interpretation of Botanical Surveys

The scheme employed in this thesis (and the wider archaeobotanical project of which it is a part) is called FIBS (Functional Interpretation of Botanical Surveys). FIBS was developed at the Unit of Comparative Plant Ecology (UCPE) at the University of Sheffield (Hodgson 1991; Hodgson *et al.* 1993, unpub a and b; Grime *et al.* 1997a) for use in conservation and land management, and was subsequently adapted for archaeobotanical application

thanks to a collaboration of the UCPE with a team from the Department of Archaeology and Prehistory, University of Sheffield (Charles *et al.* 1997, 2002; Bogaard *et al.* 1998, 1999, 2001; Hodgson *et al.* 1999; Hoppé 1999; G. Jones *et al.* 2000).

FIBS was designed as a procedure for analysing functional changes in the floristic composition of vegetation, particularly those brought about by changes in land use (Hodgson *et al.* unpub.-a). The method grew out of Grime's plant strategy theories (Grime 1974, 1979) and the autecological data collected for the volume *Comparative Plant Ecology* (Grime *et al.* 1988). Because FIBS is a tool for application in practical land management, it is simpler and easier for the non-specialist to apply than many systems of functional analysis. To this end, the three basic tenets of the method are (Hodgson *et al.* unpub.-a):

1. Attributes must be both quick and easy to measure and ecologically useful (i.e. functional).
2. Although the attributes may be fairly crudely measured, each measurement must be roughly equivalent for each species. This can be achieved by measuring only robust, well-grown plants that represent the potential of species under good conditions, rather than the response of individual plants under varying conditions.
3. To ensure accuracy, vulnerability to a particular ecological factor should, where possible, be assessed by a number of independent attributes.

The basis of the method is quadrat survey of the vegetation in question, with different survey techniques being appropriate to different research objectives (Hodgson *et al.* unpub.-a). A variety of functional attributes is then measured for each of the species identified in the survey, following the three tenets listed above. For the data analysis, the species names are replaced by their values for each of the functional attributes and the vegetation is characterised according to these attributes.

The FIBS technique was first tested by analysing changes that had occurred in the semi-natural grasslands of Central England in the 25 years between 1965 and 1990 (Hodgson *et al.* unpub.-b). Vegetation surveys carried out in 1965 were replicated in 1990 and, for the FIBS analysis, the characteristics of

the vegetation in both surveys were assessed according to various functional attributes of the species. The two surveys were then compared to look for changes over time in the representation of functional attributes at the various survey sites.

Central England has one of the most intensively studied floras in the world, and the changes in land-use that had taken place over the 25 years were already known. Thus it was possible to predict the functional changes in the vegetation that would result from each change of use. Despite the fact that the survey data used had been collected for a different purpose, the results of the FIBS analysis were entirely consistent with the predicted results (Hodgson *et al.* unpub.-b). This proved that species respond to changes in land use in a manner that can be detected by even quite crudely measured functional attributes, and that the FIBS method is suitable for detecting those changes.

A second test of the method (Hodgson 1991) applied FIBS to four phytosociological sub-communities of calcareous grassland, as defined by the (then unpublished) National Vegetation Classification (NVC) (Rodwell 1992). The principle functional characteristics of each sub-community were identified from the functional attributes of the communities' best-represented species. When the characteristics identified by FIBS were compared to the NVC ecological characterisations of the same communities (based on extensive field knowledge of the vegetation types), they showed good correspondence.

FIBS can, therefore, be used to compare vegetation in different situations, whether geographical or temporal. Providing the adaptive nature of the measured attributes are well understood, FIBS can also be used to predict how the vegetation will react to different land management regimes. This makes it a useful technique for environmental management, and is also the key to its modification for use in archaeobotany. The archaeobotanical application of FIBS will be outlined in Chapter 3.

2.2 Ecological significance of higher taxonomic groups

In the following sections, the terms 'taxonomy' and 'taxonomic group' are used in a manner that implies phenetic taxonomic classifications are an accurate reflection of phylogenetic relatedness. Although this is not necessarily

true (see Sections 2.1.1.1 and 2.1.1.2), these terms are used because (in the absence of any alternative) many of the studies mentioned below have used phenetic taxonomic classifications as approximations of true phylogeny.

2.2.1 Phylogeny and ecology

Definitions of functional types often stress their independence from taxonomy and phylogeny, and refer to them as 'non-phylogenetic classifications' (e.g. Gitay and Nobel 1997). Whilst this makes it clear that phylogenetic relatedness is not a defining feature of functional types, it also gives the impression that functional and phylogenetic classifications are always unrelated. Given that functional attributes are necessarily adaptive, this seems unlikely to be the case, indeed "one wonders why the groups are not allowed or supposed to be phylogenetic" (Semenova and van der Maarel 2000 p. 918).

Some ecological specialisations, such as the nitrogen fixing capability of the Fabaceae, have long been recognised within plant higher taxonomic groups. Until relatively recently, however, few plant ecologists have explicitly investigated the connection between phylogeny and ecology, perhaps because characters of known ecological significance are rarely used to define plant taxonomy (Grime and Hodgson 1987; Stace 1989 p. 173). It was Stebbins' pioneering work on the evolution of flowering plants that first formalised a theory of ecological specialisation in plant higher taxonomic groups (Stebbins 1971, 1972a, b, 1974).

2.2.2 Stebbins and the theory of evolutionary canalisation

The principle of 'genetical uniformitarianism' is fundamental to evolutionary research (Stebbins 1972a; 1974 pp.13-14). This principle states that: "the processes of evolution ... have operated in the past essentially as they do now, even though the genotypes and phenotypes upon which they operated, as well as the environmental conditions that created selection pressures, were different." (Stebbins 1972 p.8). If this is the case, then the process of adaptive radiation, which is the primary basis of diversification in modern populations and species, was also responsible for the diversification of the populations that

gave rise to modern genera and families. Thus, the characteristics that differentiate higher taxonomic groups are quantitatively greater than, but not qualitatively different from, those that differentiate contemporary species and populations (Stebbins 1972b; 1974 p.14).

Stebbins suggested that this constancy of evolutionary process enables adaptive characters to be strongly conservative within higher taxonomic groups (Stebbins 1972a, 1974). He developed this idea into the 'hypothesis of evolutionary canalisation', which he summarised as "the tendency for populations to respond adaptively to new environments in ways that are determined by characteristics acquired as a result of previous adaptive radiations." (Stebbins 1974 p. 23). In other words, the future direction of evolution is strongly influenced by previously acquired adaptive characteristics.

This hypothesis depends upon three major principles (Stebbins 1974 pp. 23-33):

1. **Selective inertia.** The intensity of selection that is needed to establish a new adaptive gene combination or mutation is much greater than that required to maintain or modify an adaptive mechanism, once it has been acquired. (In fact, it would be more accurate to say that progressive diversifying selection requires *some* selective pressure, whereas stabilising selection merely requires the absence of 'counter selection' pressures.)

2. **The conservation of organisation.** This is the *consequence* of selective inertia. Once a complex, organised structure or process has become an essential adaptive element of a successful taxon, unless this element experiences strong selective pressure, its essential features are likely to be conserved in the evolutionary descendants of that taxon.

   According to Stebbins, this principle has two evolutionary implications. Firstly, it explains how random fluctuations in the environment interact with random mutations and gene combinations to produce a progressive increase in the complexity of organisms. Once an organism has acquired a complex adaptive structure, mutations or new gene combinations that destroy or weaken that structure are more likely to be eliminated

(presumably because they impair the plants performance and thus its chance of reproducing) than those that modify the structure without adversely affecting it. The complex structure, once acquired, thus serves as the basis for further complexity.

Secondly, it explains why the essential features of some complex structures are often peculiar to particular families or genera, and occur in those groups with considerable consistency. As an example, Stebbins cites the very distinctive petal structure of the family Fabaceae (legumes) (Stebbins 1974 p. 25). The flowers of all Fabaceae species have five petals, one broad 'standard' petal at the top, two narrower wings at the sides, and two lower petals that are joined by a 'keel' that conceals the reproductive organs. This complex flower structure was probably built up in the ancestral taxa of the Fabaceae over a succession of intermediate stages, involving long-term high selective pressure. That particular selective pressure is extremely unlikely to be acting on all the thousands of evolutionary descendent species of those ancestral taxa, and yet, the distinctive flower structure is maintained throughout the Fabaceae family.

3. **Adaptive modification along the line of least resistance**. Although there are many possible pathways for adaptation to a particular environmental situation, the pathway taken is likely to be influenced by the innate, genetically controlled pattern of development that exists in the population at any stage of its evolution. In other words, the simplest, and therefore most likely, evolutionary pathway will be that which requires the fewest changes to be made to existing and successful complex structures. This is the 'line of least resistance'.

   An example of this principle given by Stebbins (Stebbins 1974 pp. 31-33) considers the response to selection for increased seed production in a sunflower. The sunflower has a 'composite flower' formed from many florets, and the individual florets each produce only a single seed. An increase in the number of seeds per floret would involve a drastic reorganisation of floral development. Increase in the number of florets per 'composite flower', however, requires a relatively simple increase in the amount of cells that produce floral growth (floral meristem) before the stage

of plant development at which the florets are differentiated. This second option involves the fewest changes to an existing and successful complex structure, and is the way seed production in sunflowers has been increased by plant breeders.

Taken together, these three principles suggest that the direction of any new adaptive selection will be influenced to some degree by the adaptive state of the ancestral taxa. Consequently, groups of closely related species (higher taxonomic groups) may retain some of the functional adaptations of their ancestral taxa in common, and thus be adapted to similar environments. If this is the case, then some higher taxonomic groups should correspond well with some functional groups. It should be remembered, however, that adaptive features of an ancestral taxon can be retained by its descendents long after the selective pressures that were required to establish them have ceased to exist (Stebbins 1974 pp. 35-36). In such cases, more recent selective pressures may cause the descendent species to be adapted to a variety of different environments. It is, therefore, possible for the species in a higher taxonomic group to have *previously* adaptive features in common, and yet not to share any *currently* adaptive features (i.e. functional attributes).

2.2.3 Ecological specialisation in higher taxonomic groups

Stebbins' theories regarding evolutionary canalisation were a strong influence on the work of the Unit of Comparative Plant Ecology (UCPE), University of Sheffield. Members of the UCPE undertook a number of influential studies investigating the ecological specialisation of plant families in the Sheffield region. Hodgson (1986) found evidence for a connection between family membership, species abundance in different habitats, growth rate, seed size and germination behaviour. This connection held up even when the families included a mixture of annual and perennial species, and species with different geographical origins. Grime *et al* (1981) had previously also found that seed and germination characteristics are related to taxonomy. To gauge the extent to which these specialisations could be due to the retention of complex ancestral characters, Hodgson and Mackey (1986) investigated possible taxonomic constraints on the ecological modification of seed size.

They found that features of floral morphology and embryology act to constrain seed weight, and that these complex characters are generally conservatively expressed within the families studied. Perhaps most surprisingly, Grime even found evidence of ecological adaptations common to the regional representatives of an entire taxonomic division, the Pteridophytes (ferns and their allies) (Grime 1985).

Overall, these UCPE studies showed that higher taxonomic groups often exhibit some level of ecological specialisation, at least on a regional scale, and that in some cases this is related to the retention of complex characters. This confirmed that evolutionary canalisation is relevant to contemporary ecological adaptations, and gave credence to Stebbins' hypothesis at a time when such ideas generally had little support amongst ecologists (Hodgson 1986).

The recent increase in functional ecological studies has brought to light many more examples of ecological specialisations in higher taxonomic groups (e.g. Givnish 1987; Herrera 1992; Díaz and Cabido 1997; Díaz *et al.* 1998), and it is now widely accepted that functional attributes are often not independent of phylogeny. It is worth noting, however, that some local correlations between functional attributes and phylogeny fall apart when considered on a wider geographic scale (Grime 1984). It is also clear that such correlations are usually very group specific – a functional attribute that is very stable in one taxonomic group may be very variable in another group at the same taxonomic level (Grime 1984; Hodgson and Mackey 1986; Westoby 1998). Going back to the definition of functional types, it seems that the phrase 'non-phylogenetic classification' is indeed inappropriate. It would be more accurate to follow Root's early definition and say that functional groups are defined "without regard to their taxonomic position" (Root 1967 p. 335).

2.2.4 Phylogenetic conservatism

The focus of Section 2.2 has been on the tendency for new adaptations to be partially determined by the adaptive state of ancestral taxa. Although, Stebbins himself referred to this as 'evolutionary canalisation' (Stebbins 1974), the terms 'constraint' or 'phylogenetic constraint' frequently replace this in the literature. A representative example of this is Grime's (1984) statement that:

> "at various stages in the evolution of plants specialisations have occurred which continue to exercise surprisingly persistent constraints upon the ecology of contemporary families, tribes, genera and species" (Grime 1984 p. 22).

Some ecologists, however, object to the term 'phylogenetic constraint' (e.g. Miles and Dunham 1993; Ackerly and Donoghue 1995; Westoby 1999). The primary objection is that the term, whilst rarely defined in ecological studies, is assumed to have particular theoretical implications. In general it is taken to imply that a species has been under selective pressure to modify a particular attribute, but has been restricted from doing so as a result of its evolutionary history (Miles and Dunham 1993; Westoby 1999). The term is, however, also used to imply that attributes have been retained in a group of related species simply because of a lack of selective pressure (Westoby 1999). In both cases, the term constraint reflects Stebbins' particular theories of ecological specialisation(Stebbins 1972b, 1974) (see Section 2.2.2). In the first case, Stebbins' principle of 'adaptive modification along the lines of least resistance' accounts for particular attributes remaining unchanged when a species experiences directional selective pressure (Stebbins 1974 pp. 31-33). In the latter case, constraint has implications very similar to the principles of 'selective inertia' and 'conservation of organisation' (Stebbins 1974 pp. 23-31).

It has been some thirty years since the publication of Stebbins' hypothesis of evolutionary canalisation (Stebbins 1972b, 1974) and, unsurprisingly, there are now alternative theories to explain the retention of particular attributes through evolutionary lines (e.g. Harvey and Pagel 1991 pp. 38-48; Miles and Dunham 1993; Westoby 1999). 'Phylogenetic niche conservation' is a well-established alternative theory which suggests that, because ancestor species have an assemblage of attributes that make them well fitted to particular ecological conditions, their descendants are likely to be most successful when they exploit similar ecological conditions (Westoby 1999). As a result, natural selection favours the retention of the ancestors' attributes in most of the descendent lineages. In evolutionary terms, this seems to be a fundamentally different explanation to 'evolutionary canalisation' because it explains the retention of attributes in terms of continuing functional adaptation to a stable environment rather than the channelling of adaptations to a changed environment. For Westoby (1999), the term phylogenetic constraint is not

appropriate to this theory, so indiscriminate use of the term to describe ecological specialisations in higher taxonomic groups would implicitly exclude niche conservation as a possible explanation.

It could be argued, however, that there are underlying similarities between the theories of evolutionary canalisation and phylogenetic niche conservation, and that there are elements of constraint involved in both. Following the theory of evolutionary canalisation, a species is not prevented from adapting to changed ecological conditions, but the *direction* of its adaptation is influenced (constrained) by previously acquired adaptive attributes (Stebbins 1974 pp. 31-33). According to the theory of phylogenetic niche conservation, a species' existing adaptive attributes make it so well suited to a particular set of ecological conditions that natural selection tends to maintain those attributes in its descendants (Westoby 1999). It seems reasonable to say that the descendent species are, therefore, 'constrained' as to the ecological conditions in which they can live. In either case, the adaptive state of the ancestor species has an influence that could be termed 'constraint' upon the adaptive state of its evolutionary descendants.

There has been much heated debate over the significance for comparative biology of different explanations of the non-independence of functional-attributes and phylogeny (e.g. Ackerly and Donoghue 1995; Harvey *et al.* 1995a, b; Rees 1995; Westoby *et al.* 1995a, b, c). For the purpose of this thesis, however, it is important to identify ecological specialisations in higher taxonomic groups, rather than to explain or control for them. Because the term 'constraint' is sometimes considered to have particular interpretative significance, I will be following Westoby (Westoby *et al.* 1995b; Westoby 1999) in using the term 'phylogenetic conservatism' instead, thus identifying specialisations without suggesting the mechanism by which they came about.

Chapter 3 – The use of ecological data in the interpretation of ancient plant remains

Despite the problems outlined in Chapter 1, data on the ecological preferences of modern plant species remain the best evidence for the ecological interpretation of ancient plant remains. Two branches of plant ecology, phytosociology and autecology, are the primary sources of these data, but specially conducted field surveys also contribute. This chapter will discuss these different sources of ecological data, including the ARCHFIBS method on which this thesis is based.

3.1 Indicator species and broad groups of species

Before discussing the advantages and disadvantages of the various sources of ecological data that are used in archaeobotanical interpretation, it is useful to consider some general points concerning the use of indicator species or broad groups of species for the identification of past ecological conditions.

3.1.1 Indicator species

Interpretative approaches based on indicator species use knowledge of the behaviour of modern plants to identify those species that are most closely associated either with particular ecological conditions, or with particular plant communities (Birks and Birks 1980 p.233-237; Behre 1981). Where those species are found in assemblages of ancient plant remains (be they plant macrofossil or pollen assemblages), they are assumed to indicate the existence of the same conditions or communities in the past. Although the term 'indicator species' is commonly used in both plant macrofossil and pollen analyses, it is worth noting that the indicators used in palynology should more accurately be described as 'types'.

Unfortunately, relatively few plants have sufficiently precise ecological or community characteristics for them to be used as indicator species (Ellenberg 1950; Westhoff and van der Maarel 1973). It follows, therefore, that relatively

few of the species represented in any archaeobotanical assemblage are likely to be useful indicator species. As a result, when using this method, only a small fraction of the available archaeobotanical evidence contributes to the interpretative process. The indicator species method, therefore, provides quite precise ecological information for a restricted number of species.

3.1.2 Broad groups of species

Rather than basing ecological interpretations on the characteristics of just a few species, an alternative method is to apply data compiled from modern ecological studies to *all* the speciated material in an assemblage of ancient plant remains (Birks and Birks 1980 p. 237; G. Jones 1992; van der Veen 1992). This is potentially advantageous because ecological interpretations based on large numbers of species are relatively secure compared to those based on only a handful of species. However, standardised ecological data that are available for large numbers of species are often not very precise (G. Jones 1992), so the resulting interpretations may be rather general.

Although the problems described in Chapter 1 are relevant to *all* ecological interpretations of archaeobotanical material, they may be to some extent mitigated by basing interpretations on broad groups of species rather than a handful of indicator species. Although individual species (including indicator species) may change their ecological preferences through time, it is unlikely that broad groups of species will all have changed their preferences in the same direction (G. Jones 1992; van der Veen 1992 p. 109; Hodgson *et al.* 1999). Thus, any general patterns suggested by evidence from broad groups of species are likely to be reliable, even if some individual species have not been stable through time. Compared to the indicator species method, therefore, interpretations based on broad groups of species make less of an assumption that the modern ecological preferences of species were also possessed by those species in the past. The greater precision of the indicator species method may, therefore, be more apparent than true.

3.2 Phytosociology

As explained in Section 2.1.2.1, phytosociology is a method for describing and classifying vegetation in terms of hierarchically defined plant communities. Phytosociological communities are defined in terms of their floristic composition, and each community is considered to be a reliable *expression* of the ecological conditions in which it occurs (Westhoff and van der Maarel 1973). Most species can occur in a range of phytosociological communities, but some are essentially restricted to a single community and are usually described as that community's 'character species'.

There are two approaches to the application of phytosociology to ancient plant remains (G. Jones 1992), both of which rely on the presence of character species in plant macrofossil or pollen assemblages. Character species are the 'indicator species' of phytosociology, so both phytosociological approaches described here are essentially indicator species approaches. These two approaches can be termed the 'community approach' and the 'ecological approach'.

3.2.1 The 'community approach'

The community approach assumes that the character species of an archaeobotanical assemblage can be used to identify the phytosociological community or communities from which the assemblage came. The past vegetation is then reconstructed in terms of these communities. For instance, Greig (1988) classified pollen and macrofossil evidence from various periods of British history and prehistory in terms of its phytosociological communities, and used this as evidence for the existence of particular phytosociological grassland communities in the past. Based on archaeobotanical crop-weed evidence, Knörzer (1971) went a step further and produced a phytosociological classification (called the *'Bromo-Lapsanetum antiquorum'*) for the now extinct plant community that was formed when various weed species invaded the new crop field habitats during the Neolithic.

There are however, a number of serious problems with the community approach to using phytosociology in archaeobotanical interpretation. Firstly,

phytosociological character species of one community can also occur in other communities, in which case it is impossible definitively to equate a species in the archaeobotanical record with a particular phytosociological community (M. Jones 1988; Behre and Jacomet 1991; Küster 1991; van der Veen 1992 p. 105). In archaeobotany, the usual solution to this problem is to assume that character species are representative of either the community in which they usually occur, or that which seems most likely in the given context (van Zeist 1974). As with choosing the most likely species to be represented by pollen types, the latter method employs circular reasoning – an assumed ecological context is used to link a character species to a particular community, then the ecological preferences of that community are used to reconstruct the local ecology.

It is, however, often the case that samples of ancient plant remains contain character species of a number of different phytosociological communities, and that these communities are typical of a variety of different ecological conditions (Behre and Jacomet 1991; Hillman 1991; van der Veen 1992 p. 104). For instance, stored grain from Neolithic lakeshore settlements in Switzerland contains seeds of weed species that, in modern phytosociological terms, are characteristic of a mixture of arable, ruderal, grassland and forest communities (Behre and Jacomet 1991). Such phytosociologically ambiguous assemblages can be interpreted in two very different ways (van der Veen 1992 p. 104). The simplest interpretation is that taphonomic processes have caused material from different plant communities to be mixed together in a single assemblage. Rather than representing a single community therefore, the remains are interpreted as representing a variety of different communities (e.g. van Zeist and Palfenier-Vergter 1979; van Zeist 1981).

The alternative interpretation is that modern phytosociological communities are not necessarily relevant to the past. It has already been explained that individual plant species may change their ecological preferences through time, and it is perhaps even more likely that the composition of plant communities will change. Plant communities may change through time either due to changes in the ecological preferences of individual species, or because the migration of species through space brings about new combinations of species

in an environment and breaks apart existing combinations. For example, when species from various 'natural' communities moved in to exploit the new arable field environments that appeared in Europe during the Neolithic, they formed new plant communities that had no exact analogue in the earlier vegetation (Küster 1991).

Thus, the assumption that modern plant communities are necessarily analogous to the plant communities of the past is not always justified. Some modern plant communities will be quite recently evolved entities, and so have no equivalent in the past; and some past plant communities will have been modified over time, and so have no equivalent in the present (M. Jones 1981, 1988; Hillman 1984; Moore 1990; Behre and Jacomet 1991; Küster 1991). Such communities are known as non-analogue communities. A phytosociologically ambiguous archaeobotanical assemblage can, therefore, be interpreted as representing a single non-analogue community rather than a mixture of different communities (e.g. Hillman 1981; van der Veen 1987 p. 104). Evidently, if a community has no modern analogue by which to determine its ecological characteristics, then this renders it extremely difficult to interpret in ecological terms. The problems associated with this particular assumption are only relevant to interpretative techniques that require the matching of modern and ancient plant communities, and the reliance of the community approach to phytosociology on this assumption is one of its fundamental weaknesses.

Unfortunately, there is no sure way of determining whether an assemblage of ancient plant remains contains character species of a number of different phytosociological communities because the remains of different communities have become mixed together or because the assemblage represents a non-analogue community. The increasing evidence for the non-comparability of modern and past plant communities is sufficient, however, for some archaeobotanists to suggest that the 'community approach' to phytosociology is wholly inappropriate to the interpretation of archaeobotanical assemblages (Havinga 1964; G. Jones 1992; van der Veen 1992 p. 108).

There is also a geographical problem associated with the community approach to phytosociology: species may occur in different communities in

different parts of their range, so the species composition of plant communities is not necessarily geographically stable (Westhoff and van der Maarel 1973; Holzner 1978). A single species may be a character species for community *A* in one area and for community *B* in another area (Westhoff and van der Maarel 1973), so it is not always justifiable to use character species to identify communities across biogeographical boundaries.

3.2.2 The 'ecological approach'

The 'ecological approach' to the application of phytosociology to ancient plant remains uses phytosociological character species to indicate the presence of particular ecological conditions rather than particular phytosociological communities (G. Jones 1992). Phytosociological character species have quite particular ecological preferences (Holzner 1978), and all the character species of a community share those preferences to a greater or lesser degree. Character species can, therefore, be used to indicate the presence of ecological conditions that are favourable to the community as a whole without assuming that the community will have been constant over time. Thus, the great advantage of the 'ecological approach' over the 'community approach' is that it does not rely on the assumption that the species compositions of phytosociological communities are stable through time.

In practical terms, the 'ecological approach' is best applied to character species of the higher phytosociological units, such as classes and alliances (G. Jones 1992). The character species of the lowest phytosociological unit, the association, are likely to be the most specific in their ecological requirements, but have the distinct disadvantage that they are often limited in their geographical relevance (Westhoff and van der Maarel 1973; Holzner 1978; G. Jones 1992). The character species of higher phytosociological units, on the other hand, tend to be consistent in their ecological preferences over a relatively wide geographical area (Westhoff and van der Maarel 1973), making them more suitable for practical application. These character species are less specific in their ecological requirements than those of lower units, but they are nevertheless effective indicators of quite broad ecological conditions (G. Jones 1992). As long as species in assemblages of ancient plant remains are

classified by higher phytosociological units, therefore, this approach is relatively free of the geographical uniformitarian problems associated with the community approach.

The 'ecological approach' to phytosociology is most explicitly employed by Glynis Jones in her study of crop husbandry at the Bronze Age site of Assiros, Greece (G. Jones 1992). In this study, species in samples of ancient crop weed are classified by the modern phytosociological classes Chenopodietea and Secalinetea, and the samples are interpreted according to the broad ecological characteristics of these classes. It is not, however, assumed that the species composition of the modern phytosociological groups can be used to reconstruct the complete plant communities of the ancient fields. Similar methods are used, albeit less explicitly in many other archaeobotanical applications of phytosociology (e.g. van Zeist and Palfenier-Vergter 1979; Willerding 1980; Wasylikova 1981).

3.3 Autecology

In contrast to phytosociology, which is the study of whole plant communities, autecology is the study of the ecology of individual species (see Section 2.1.2.2). Although there are many published sources of autecological data (e.g. Grime *et al.* 1988; the many 'Biological Floras' published in the *Journal of Ecology*), because Heinz Ellenberg's tables of indicator values (Ellenberg numbers) cover some 2,000 species in a systematic manner (Ellenberg 1950, 1974; Ellenberg *et al.* 1992), his is the autecological approach that has most often been applied to assemblages of ancient plant remains.

For archaeobotanical applications, Ellenberg numbers are generally used to construct 'eco-diagrams': bar graphs showing the number of species (or number of seeds of species) in an assemblage for each indicator value of Ellenberg's six ecological variables (e.g. van Zeist 1981; Wasylikova 1981; van Zeist *et al.* 1986; van der Veen 1987). Although 'eco-diagrams' were envisioned as a means of inter-site comparison of ecological conditions (Willerding 1978, 1980a), different authors have included different categories of plant (e.g. all herbaceous species in the assemblage, only segetal and ruderal species, only species in particular phytosociological groups) in their

eco-diagrams, which makes inter-site comparisons difficult (van der Veen 1992 p. 105). Also, not all Ellenberg's ecological factors are always included in the eco-diagrams. Van Zeist *et al* (1986) used eco-diagrams to compare environmental conditions at three medieval sites in the Netherlands (Passe, Odoorn and Gasselte). Because they felt that temperature, continentality and light conditions would not vary between sites close to one another, they only included Ellenberg numbers for the edaphic factors (van Zeist *et al.* 1986 p. 271). Whilst this makes sense for the comparison of the three sites in question, it does limit the potential for comparisons with other sites further afield. Despite such inconsistencies, however, the eco-diagram has proved to be a valuable tool for the interpretation of past ecological conditions.

In a detailed approach to the archaeobotanical use of Ellenberg numbers, van der Veen (1992 pp. 116-143) applied discriminant and cluster analyses to the Ellenberg numbers and other autecological data for weed species in samples of carbonised crop remains from Prehistoric sites in north-east England. Multivariate analysis of the species composition of the samples had shown them to be divided into two groups, each characterised by different crops and weeds (van der Veen 1992 pp. 11-116). The subsequent autecological analysis suggested that the two groups of samples were ecologically distinguished primarily by the soil preferences of the weed species and by the tillage methods practised. Because tillage has a strong effect on soil type, the differences between the weed samples were interpreted as being due to differences in crop husbandry regime practised at the various sites from which the samples came (van der Veen 1992 p.143).

Ellenberg numbers (and other autecological approaches) have, however, been used less often in archaeobotanical interpretation than phytosociological data, and have most often been used only as a compliment to phytosociology, rather than being preferred to it (van der Veen 1992 p. 105). This is unfortunate because autecological approaches have a number of general advantages over phytosociology when applied to the interpretation of ancient plant remains. Firstly, autecology tends to provide more detailed ecological information than phytosociology. Phytosociology is primarily a method for defining plant communities; the ecological meaning of these communities is

only a secondary consideration (Westhoff and van der Maarel 1973 p.645). As a result, the ecological content of phytosociological studies can be rather low. For instance, the survey on which the phytosociological classification of British plant communities is based included very little field sampling of ecological material, and the ecological information included in the reports is very variable in both quality and quantity (Rodwell 1991a, b, 1992, 1995, 2000). In contrast, autecological studies tend to contain relatively detailed information on the relationship of species to a range of environmental factors, and this sort of information is of particular value for the ecological interpretation of ancient plant remains (van der Veen 1992 p. 108).

A second advantage of an autecological system such as Ellenberg's is that it provides ecological data for a great many species rather than just a handful of indicator species. This means that, in the archaeobotanical and palynological application of autecology, all speciated taxa in an assemblage can potentially contribute to its ecological interpretation (van der Veen 1992 p. 108). As explained in Section 3.1.2, this is advantageous because ecological interpretations based on large numbers of species are relatively secure and do not overly rely on the assumption that the modern ecological preferences of species were also possessed by those species in the past. Many species have quite wide ecological amplitude, however, and so will add little to the ecological interpretation of an assemblage of plant remains.

Although the Ellenberg's numbers provide relatively detailed ecological data compared to phytosociology, they cover only six environmental factors and are derived primarily from field observations rather than measurements or experimentation (Thompson *et al.* 1993). Many other autecological sources (e.g. the *Biological Floras* of the Journal of Ecology) contain much more extensive and objective data. However, such detailed autecological sources have tended to treat only small numbers of species in a systematic manner (Hodgson 1990), which limits their application to the study of ancient plant remains. The quantity of detailed autecological data available for large groups of species and its accessibility to the non-specialist is improving, however (Hodgson 1990), and so archaeobotanists and palynologists increasingly have the opportunity to draw upon this data for the ecological interpretation of

ancient plant remains. Section 3.6 will deal with a new archaeobotanical approach to the use of *functional* autecological data.

3.4 Limitations of approaches based on field observations

Both phytosociology and Ellenberg's particular approach to autecology are based primarily on field observations. Perhaps the most fundamental limitation of these approaches is that field observations are not sufficient to indicate which ecological variables actually determine a species' occurrence in a particular environment (Charles *et al.* 1997). In any environment, plants are affected by a multiplicity of different ecological variables (such as light, moisture and nutrient availability, predation etc.), all acting in concert. Although all plants are able to tolerate some environmental variation, if the intensity of just one of these variables is too much for a given plant to cope with, then it will be absent from that environment (Daubenmire 1974). Because each plant is affected by so many different ecological variables, it is very difficult to establish precisely which variables determine a species' presence or absence in a particular environment from field observations alone. For instance, many calcifuge plants (plants usually found on non-calcareous soils) are sensitive to both the nutrient deficiency and the droughts that are typical of calcareous soils (Thompson *et al.* 1993). Field observations would be sufficient to note a species' absence from these soils, but would not be sufficient to establish whether both nutrient status and water availability determine that absence or just one of those factors.

Field observations, therefore, are suitable for determining *where* a species is found, but not *why* it is there (Charles *et al.* 1997). Consequently, archaeobotanical interpretations based on field observations can be inexact. For instance, in the interpretation of ancient crop weed assemblages, it is often unclear which aspects of the arable environment (water or nutrient availability, sowing time of the crop, degree of shade etc.) determined the composition of the weed flora (Charles *et al.* 1997). In the absence of this knowledge, the same archaeological weed evidence has been interpreted as evidence for husbandry practices as diverse as sparse cultivation (Willerding 1980b), spring sowing (Wasylikova 1981) and garden-type agriculture (G. Jones 1992).

In addition, just as some ancient plant communities have no analogue in the present (see Section 3.2.1), it is also probable that some ancient *environments* have no present-day analogue (Hillman 1991; G. Jones 1992). The species composition of non-analogue environments must have been influenced by combinations of environmental factors that do not occur in the present (Charles *et al.* 1997). In order to reconstruct non-analogue environments from archaeobotanical evidence, therefore, it is necessary to disentangle the various environmental factors that can affect species composition and reassemble them in different combinations. Because field observations provide no easy means of disentangling different environmental factors, they cannot readily be used to reconstruct ecological conditions for which there is no modern analogue.

3.5 Specially conducted vegetation surveys

In addition to using existing sources of ecological data, archaeologists and palynologists can conduct vegetation surveys designed to determine the floral composition of particular present-day environmental contexts. The species composition of these contexts can then be compared with assemblages of ancient plant remains. If samples of ancient plant remains have very similar species composition to the surveyed contexts, then this suggests that they represent similar ecological conditions.

A team of archaeobotanists from the Department of Archaeology and Prehistory at the University of Sheffield (G. Jones *et al.* 1995, 1999; Palmer 1998; Charles *et al.* 2002) has been conducting vegetation surveys to determine the species composition of crop fields under a variety of different agricultural regimes. The first of these vegetation surveys was carried out in fields around the town of Borja in northern Spain, where the agricultural system includes the use of traditional flood irrigation (G. Jones *et al.* 1995). To test whether or not weed floras could be used as indicators of irrigation and dry farming, the flora of fields receiving different levels of irrigation from dry to regularly flooded was recorded (G. Jones *et al.* 1995). For each field, the weed survey was conducted along a transect, ten quadrats were placed along the transect and the species presence in each quadrat was recorded. In addition

to location and irrigation regime, a variety of other ecological information was recorded for each quadrat. Correspondence analysis (ter Braak 1986, 1987) of the survey data showed that the weed floras of the fields clearly corresponded with the different levels of irrigation.

Subsequently, similar vegetation surveys have been conducted by the Sheffield team of the weed floras of a variety of other agricultural regimes. A survey carried out in Irbid, Jordan, demonstrated that cereal fields managed under different crop rotation regimes could be clearly distinguished on the basis of their weed floras (Palmer 1998). Vegetation survey of the weed floras associated with pulse crops in Evvia, Greece, demonstrated that crops cultivated on a garden-scale and a field-scale could be distinguished on the basis of the weed floras of the plots (G. Jones *et al.* 1999). In order to test the applicability of the results of this study to different contexts, a second survey of weed floras associated with garden- and field-scale cultivation was carried out, this time in Asturias, Spain (Charles *et al.* 2002). Figures from these studies are presented in Chapter 7, where they will be discussed in more detail.

A Swedish team has been using specially conducted vegetation surveys in an ongoing study of the relationship between modern vegetation and human land-use in southern Sweden (Berglund *et al.* 1986; Gaillard *et al.* 1992, 1994; Broström *et al.* 1998). This project is aimed primarily at finding ways of identifying different types of land use (cultivated fields and variously managed grasslands) in assemblages of fossil pollen. Consequently, the different vegetation types were surveyed on the basis of their representation in pollen samples rather than by recording the presence of whole plants. For each vegetation type, an area as far away from other vegetation as possible was chosen, and $10m^2$, $20m^2$, $50m^2$ and $100m^2$ quadrants were centred on this area. Pollen was collected from 10 moss polsters sampled from within each quadrant (Berglund *et al.* 1986). Correspondence analysis of the data showed that the composition of the pollen samples corresponded reasonably well with the different land use of the sampling sites (Gaillard *et al.* 1994). Figure 3.1 is a correspondence analysis plot showing modern pollen samples classified according to whether their sites were grazed or mowed and pollarded (Gaillard *et al.* 1994). Grazed sites are mainly located towards the bottom of the plot,

and mowed sites towards the top. This means that these types of land-use each produce distinctive pollen spectra, and so it may be possible to find analogues for them in fossil pollen sequences.

3.6 ARCHFIBS - a new autecological approach using functional attributes

It is evident from the preceding discussion that there are many problems associated with applying contemporary ecological approaches to the identification of past ecological conditions. Nevertheless, the ecological preferences of modern plant species are the best available source of information on the ecological conditions of the past. For this source to be exploited to its full potential, archaeobotanists need a method that can identify the ecological principles underlying species distribution (Charles *et al.* 1997).

Once such method is the 'FIBS' approach to plant functional analysis (Hodgson 1991; Hodgson *et al.* 1993, unpub a and b; Grime *et al.* 1997), the archaeobotanical application of which has been called 'FIBS in archaeobotany', or 'ARCHFIBS' for short (Charles *et al.* 1997, 2002; Bogaard *et al.* 1998, 1999, 2001; Hodgson *et al.* 1999; Hoppé 1999; G. Jones *et al.* 2000). To recap briefly, FIBS is an autecological approach based upon the idea that species tolerant of a particular ecological factor tend to have a suite of functional attributes in common, and can be grouped together as a particular functional type. Different functional types should, therefore, be characteristic of different ecological conditions. The technique was designed to analyse the functional changes in floral composition that are brought about by changes in land-use (Hodgson *et al.* unpub.-a). Consequently, it should also be capable of analysing the functional differences between weed floras of crops under different agricultural regimes. This possibility has now been tested, and proved to be true, by a number of ARCHFIBS studies.

The weed survey carried out at Borja, Spain (G. Jones *et al.* 1995) (see Section 3.5) demonstrated that weed floras are potentially good indicators of different levels of irrigation and dry farming. A number of functional attributes thought to be relevant to differences in irrigation level were measured for the

weed species recorded in the original Borja quadrat surveys (Charles *et al.* 1997). The functional attribute data were used to interpret the correspondence analyses that distinguished the differently irrigated fields in terms of their weed floras. Three of the functional attributes measured (SLA - specific leaf area, canopy height and presence/absence of a persistent seed bank) showed clear patterning in relation to irrigation level.

In addition, discriminant analyses were used to indicate which functional attributes best discriminated between fields under different levels of irrigation (Charles *et al.* 1997). In this analysis, five of the functional attributes measured (specific leaf area, canopy height and diameter, stomatal density, root diameter) were strongly correlated with the discriminant function distinguishing irrigation levels. When the resulting discriminant functions were used to reclassify fields into irrigation groups, all the fully irrigated and dry-farmed fields were correctly reclassified.

This initial study showed the utility of FIBS for distinguishing husbandry practices based on the functional attributes of weed floras. Following the success of the Borja study, the ARCHFIBS method has also been successfully applied to the weed floras of a number of different agricultural regimes. The weed survey carried out at Irbid, Jordan (Palmer 1998) demonstrated that cereal fields managed under different crop rotation regimes could be clearly distinguished on the basis of their weed floras. Functional attributes relating to the duration and quality of the period of plant growth, the capacity of plants to regenerate under conditions of high disturbance, and to drought tolerance and avoidance were measured for the weed species recorded in the weed survey (Bogaard *et al.* 1999). When these functional attribute data were used to interpret the correspondence analysis distinguishing fields under different crop rotation regimes, a total of eight attributes showed patterning in relation to crop rotation regime (canopy height and diameter, DMC – leaf dry matter content, leaf thickness and width, flowering period, vegetative spread and epidermal cell wall undulation). In discriminant analysis, the same eight functional attributes were strongly correlated with the discriminant functions distinguishing the different crop rotation regimes. When the discriminant functions were used to reclassify fields into one or other of the rotation regime

categories, 83% of the were correctly reclassified as belonging to either 3- or 2-year rotation regimes.

The weed survey from Evvia, Greece, demonstrated that the difference between crops cultivated on a garden-scale and a field-scale could be distinguished on the basis of the weed floras of the plots (G. Jones *et al.* 1999). A variety of functional attributes were measured for the weed species recorded in the weed survey (Jones *et al.* 2000). When the functional attribute data were used to interpret the correspondence analysis distinguishing plots at different cultivation intensity, nine attributes showed patterning in relation to cultivation intensity (canopy height, diameter and dimension, leaf weight and area per node, leaf area:thickness, flowering period, vegetative spread, and stomatal distribution). In discriminant analysis, fourteen attributes were correlated with the discriminant functions distinguishing the different levels of cultivation intensity. When the discriminant functions were used to reclassify plots into 'intensity groups', 77% of the plots were reclassified into the correctly reclassified.

Not all the ARCHFIBS studies are based on data from specially conducted weed surveys, however. A study of crop sowing time (Bogaard *et al.* 2001) was based on a published German phytosociological dataset (Hüppe and Hofmeister 1990). This study therefore differs from the earlier ARCHFIBS studies in that the unit of analysis is the summarised information on a whole phytosociological association rather than an individual field or garden plot; the species data take the form of an abundance value for each species rather than the number of survey quadrats in which the species was present; and the species themselves are character species of phytosociological communities rather than those recorded as present in the surveyed fields (Bogaard *et al.* 2001). Correspondence analysis of the phytosociological dataset showed a clear separation of the weed associations of autumn- and spring-sown crops (Bogaard *et al.* 2001). Functional attributes were measured for the 90 character species from the phytosociological associations included in the study. When these data were used to interpret the correspondence analysis distinguishing associations with different crop sowing times, eight attributes showed patterning in relation to sowing time (life history, germination time,

flowering period, canopy height and dimension, leaf area and weight per node, and leaf area:thickness). The discriminant analysis for this study was very successful: nine functional attributes were correlated with the discriminant functions distinguishing different sowing times (flowering period, germination time, endopolyploidy, canopy height and diameter, leaf weight per node, leaf area:thickness, SLA and DMC). When the discriminant functions were used to reclassify associations according to the sowing time of their crops, 97% were reclassified correctly.

Each of these studies demonstrated that FIBS could be used to determine functional differences between the weed floras associated with a variety of different present day agricultural regimes. In each case, the functional attributes that characterise the agricultural regime under consideration were identified. This enables the application of the method to archaeobotanical assemblages where the agricultural regimes applied to crops are unknown. In this respect ARCHFIBS has a number of advantages over interpretative techniques that rely on data from field observations. As mentioned above, any ecological method based on field observations is suitable for addressing the question of where a species is found, but not why it is there (Charles *et al.* 1997). Because ARCHFIBS uses measurements of *functional* attributes in place of fields observations, however, it is capable of determining which attributes of the plant determine its presence in a particular location, and why. For instance, in the Borja study the species found in the irrigated fields tended to have high specific leaf area and tall canopies (Charles *et al.* 1997). Both attributes are associated with high productivity (in this case caused by increased water availability) and it is this ecological variable that seems to be dominant in determining the species composition of the irrigated fields.

Equally significantly, ARCHFIBS allows the results of analyses based on modern weed surveys to be applied to *completely different* sets of species, including archaeobotanical assemblages. In effect, the method identifies relationships between functional attributes and ecological conditions, rather than species and ecological conditions. This means that ecological conditions associated with one set of species sharing a particular suite of functional

attributes should also be associated with another set of species sharing the same suite of attributes.

Thus ARCHFIBS potentially meets the two fundamental requirements that have been identified for the archaeobotanical application of weed survey data:

> "(1) The 'translation' of species which characterise particular husbandry regimes into functional attributes that can be applied to a different group of species; (2) an understanding of the biological significance of attributes which 'explains' the association of particular species with particular husbandry regimes and so allows an informed judgement of the relevance of the modern analogue to particular times and places in the past." (Charles *et al.* 1997 p.1159).

The potential to meet the first of these requirements has been tested in the most recent ARCHFIBS study of present-day agriculture (Charles *et al.* 2002). The Evvia study described above (G. Jones *et al.* 1999), identified a suite of functional attributes that distinguish between the weed floras of intensively and extensively farmed pulse crops, and the Germany study (Bogaard *et al.* 2001) identified a suite of attributes that distinguish between autumn- and spring-sown crops. To test whether or not these suites of functional attributes would also distinguish the weed floras of intensively farmed crops of a different type, and in a different geographical area, a weed survey was undertaken of intensively farmed spelt wheat plots in Asturias, northern Spain (Charles *et al.* 2002).

The functional attributes found most useful for distinguishing different levels of cultivation intensity and different sowing times in the earlier studies were also measured for the species recorded in the Asturias weed survey (Charles *et al.* 2002). Discriminant functions that had been successfully used to reclassify the Evvia fields in terms of cultivation intensity and the German associations in terms of sowing time were also used to classify the Asturias cereal plots on the basis of the functional attributes of their weed species. Using the discriminant functions for the Evvia study, all the cereal plots from Asturias were correctly classified as gardens. Using the discriminant functions from the German study, the Asturias plots were either classified as autumn-sown or were ambiguously classified. This result was consistent with the sowing time in Asturias which is spread from late autumn to winter. Together, these results indicate that the suites of functional attributes identified to

distinguish intensive and extensive cultivation in Evvia, and crop sowing time in Germany, can indeed be applied to other geographical areas and crop types (Charles *et al.* 2002). This bodes well for the application of functional attribute data measured for modern species to the identification of past agricultural practices from archaeological weed assemblages.

Finally, it should be noted that ARCHFIBS has the potential to interpret the floras of non-analogue environments: if the species in an archaeobotanical assemblage prove to have a suite of normally unassociated functional attributes in common, then this may be evidence for ecological conditions that have no modern analogue. Such assemblages may, of course, also be the result of the mixing of material due to taphonomic processes.

Chapter 4 - Methods

This chapter covers two distinct sets of methods. The first part deals with the field and laboratory methods used to produce functional attribute data for the species. The second part deals with the methods used to analyse these data.

4.1 Field and laboratory methods

All the field and laboratory methods, except for the choice of taxa to study, are based on those of the FIBS project of the Unit of Comparative Plant Ecology (UCPE), University of Sheffield (Hodgson 1991; Hodgson *et al.* 1993, unpub a, b) and the ARCHFIBS project of the Department of Archaeology and Prehistory, University of Sheffield (Charles *et al.* 1997, 2002; Bogaard *et al.* 1998, 1999, 2001; G. Jones *et al.* 2000).

4.1.1 Choosing the taxa

The choice of which taxa to study was directed by the two principle aims of the thesis, both of which concentrate upon higher taxonomic groupings of plants:

1. To determine what useful ecological inferences can and cannot be drawn from ancient plant remains identified to higher taxonomic groups (but not to species), and to target higher taxonomic groups from which few useful ecological inferences can be drawn for research into more precise taxonomic identification of their fossilised remains.
2. To determine which present-day ecological preferences of plant species are reliable indicators of the ecological preferences of the same species in the past.

It was not possible to measure functional attributes of enough species adequately to represent the full range of plant taxonomic levels (see Table 2.1) within the constraints of this thesis, and so taxa were chosen to represent the levels to which ancient plant remains are commonly identified: species, genus and family. Plants collected specifically for this project belong to ten

angiosperm (flowering plant) families, each represented by at least three genera and fifteen species. Multiple collections of species from different locations were made whenever possible, with the aim of collecting each species at three locations.

Genera (and consequently their families) were chosen with the aid of the Archaeobotanical Computer Database for the British Isles, which lists and quantifies all the species recorded as plant macrofossils in Britain up until 1991 (Tomlinson and Hall 1995a, b). A genus was preferred for study if it included either a large number of species that are found in the archaeobotanical record, or at least one species that is very common in the archaeobotanical record. For the final choice, preference was given to collecting families and genera whose fossil remains are difficult to identify to species. For each genus, only species that are common in the archaeobotanical record were initially targeted for collection, and other species were added if and when they were encountered in the field.

For all but one of the target families, the dataset used for this thesis includes species from genera in addition to the three target genera. A small number of these additional species were collected and measured by the author, but proved not to belong to the target genera. The majority, however, were collected (and their functional attributes measured) as part of previous ARCHFIBS studies (Charles *et al.* 1997, 2002; Bogaard *et al.* 1998, 1999, 2001; Hoppé 1999; G. Jones *et al.* 2000). The ARCHFIBS database generated by these studies also includes functional attribute data for five additional families that are represented by at least three genera, and the species from these untargeted families were also included in the dataset used for this thesis.

Table 4.1 lists all the species collected for this thesis from the ten target families and from the five additional families. Data from the Archaeobotanical Computer Database for the British Isles (ABCD) (Tomlinson and Hall 1995a, b) have been included as an indication of which taxa are common in the archaeobotanical record, and which families and genera tend to have fossil remains that are difficult to identify to species.

All but two of the target genera, *Adonis* (Ranunculaceae) and *Verbascum* (Scrophulariaceae), fit the preferred selection criteria of including a large number of species that are found in the British archaeobotanical record and/or at least one archaeologically common species. The family Ranunculaceae was targeted for collection because of the commonness in the archaeobotanical record of the genus *Ranunculus* (Tomlinson and Hall 1995a). Although *Ranunculus* spp. are very common in the British archaeobotanical record, and *Thalictrum* spp. are also moderately common, other Ranunculaceae genera are not (Tomlinson and Hall 1995a). In addition, most British Ranunculaceae genera have only a small number of rather locally distributed species (Stace 1997) that could prove difficult to collect given a limited timescale and budget. Whilst the genus *Adonis* is not common in Britain, it is relatively common in southern Europe and the Middle East, both archaeobotanically (M. Charles pers. comm.) and in the modern flora (Tutin *et al.* 1993), and so could be collected from outside Britain. For these reasons, *Adonis* was chosen as the third target Ranunculaceae genus.

The family Scrophulariaceae was targeted for collection because of the commonness in the archaeobotanical record of the genus *Veronica* (Tomlinson and Hall 1995a). Although *Scrophularia* spp. are also moderately common in the British archaeobotanical record, other Scrophulariaceae spp. are not (Tomlinson and Hall 1995a). Also, like Ranunculaceae, most British Scrophulariaceae genera have only a small number of rather locally distributed species (Stace 1997). The genus *Verbascum* was, therefore, chosen as the third target Scrophulariaceae genus simply because a number of its species are locally common in the main collection areas.

It can be seen from Table 4.1 that the family Poaceae includes 5 target genera rather than the usual three. This is because the genus name *Bromus* is used differently in the Archaeobotanical Computer Database for the British Isles (ABCD) (Tomlinson and Hall 1995a, b) and in the taxonomies used in this thesis (see Section 4.2.1.1). In the ABCD, *Bromus* includes species that in the *New Flora of the British Isles* (Stace 1997), and therefore also in this thesis, are considered to be members of the genera *Anisantha* and *Bromopsis*. Because the taxonomic systems used in this thesis were not fully defined until

after collections were begun, some species that had originally been considered to belong to *Bromus* were later assigned to *Anisantha* or *Bromopsis*.

The family Polygonaceae includes 4 target genera for similar reasons. In this case, the genus name *Polygonum* is used differently in the ABCD (Tomlinson and Hall 1995a, b) and in the taxonomies used in this thesis. In the ABCD, *Polygonum* includes species that in the *New Flora* (Stace 1997), and in this thesis, are considered to be members of the genus *Persicaria*. Consequently, some species that had originally been considered to belong to *Polygonum* were later assigned to *Persicaria*.

It should be noted that data for some of the functional attributes are missing for some of the collected species. For instance, many species do not have tap-roots, so rooting depth data (which are dependent on tap-root measurement) are missing for those species.

Henceforth, all the taxa included in the data analyses undertaken for this thesis will be referred to as 'ARCHFIBS families', 'ARCHFIBS genera' or 'ARCHFIBS species' as appropriate. This dataset will be referred to as the 'ARCHFIBS dataset'.

4.1.2 Fieldwork

The majority of fieldwork was carried out in central England and north-eastern Spain, areas chosen to represent the varying ecologies of north west Europe and the Mediterranean basin. Whenever possible, collections of an individual species were made in both areas. Functional attribute data are also included for plants that were collected from other areas of England and Spain, France, Germany, Greece and Jordan as part of other ARCHFIBS studies (Charles *et al.* 1997, 2002; Bogaard *et al.* 1998, 1999, 2001; Hoppé 1999; G. Jones *et al.* 2000).

Canopy dimensions were measured on plants growing *in situ*, and notes made of the plant's state of maturity and growth form. Herbarium specimens and samples of leaf and root material were bagged and labelled in the field. All samples were prepared for laboratory measurements as soon as possible after collection, either the same day or after a single night in cold storage.

4.1.3 Measurement and calculation of canopy size attributes

4.1.3.1 Maximum canopy height

Both canopy height (cm) and plant height (cm) were measured once for each collection of a species. Maximum plant heights were also abstracted from appropriate Floras (Zohary 1966, 1972; Tutin *et al.* 1968, 1972, 1976, 1980, 1993; Feinbrun-Dothan 1978, 1986; Clapham *et al.* 1987).

For plants with a 'leafy' growth form (free-standing, upright plants with little variation in leaf size through the canopy) or a 'basal' growth form (all leaves are confined to a basal rosette), the maximum canopy height of the species was calculated using the formula:

$$\frac{\text{mean measured canopy height}}{\text{mean measured plant height}} \times \text{max plant height given by Floras}$$

If, however, the largest field measurement of canopy height for a species exceeded this figure, then that field measurement was taken as the maximum canopy height of the species. This method of calculation was developed (G. Jones *et al.* 2000) in order give the best approximation of *potential* canopy height for the species.

For 'semi-basal' species (upright plants with leaves that become significantly smaller towards the top of the stem) smaller stem leaves (<75% as long as the largest basal leaf) were ignored for field measurements of canopy height. The maximum height calculation for these species was as for the leafy and basal species.

For climbing species, maximum canopy height was defined as the height of the stem tip above ground if the longest stem (measured in the field or taken from the floras) is held at an angle of 45° to the horizontal.

4.1.3.2 Maximum canopy diameter

The maximum canopy diameter (cm) of an individual plant was measured once for each collection. For perennial species that have horizontal root systems, the maximum canopy diameter of the 'clonal patch' (i.e. all the

genetically identical plants that arise from a single root system) was also measured. The extent of a clonal patch was estimated by pulling lengths of horizontal root out of the ground, and the distance between the outer canopy edges of the plants at the extremes of the root system was measured. For this dataset, each clonal patch had an essentially continuous canopy, so the second measurement was accepted as the true canopy diameter for patch-forming species. In all cases, the species value is the maximum diameter measured for that species.

4.1.3.3 Maximum canopy dimension

The mean of maximum canopy height and maximum canopy diameter was also calculated for each species, giving an overall maximum canopy dimension.

4.1.4 Preparation, measurement and calculation of leaf density and leaf size attributes

4.1.4.1 Laboratory preparation and measurements used in the calculation of more than one attribute

About 1g fresh weight of leaves from each collection was wrapped in damp paper towel and sealed inside a plastic bag. This sample was refrigerated overnight, allowing all the leaves to take up an equal amount of water and achieve an essentially uniform level of turgidity. After refrigeration, the turgid leaves were patted dry of surface moisture and weighed. The weighed material was sealed in paper envelopes and placed in an oven for two days at 80°C. The resulting dry samples were placed in a desiccator for half an hour before being reweighed. The measurements of fresh and dry leaf weights were used in the calculation of mean DMC and maximum leaf weight per node.

In addition, five large, complete leaves from each collection were pressed until they were completely flat and dry. Images of the leaves were captured using a video camera and ELViS II image capture card, and the areas of these images were calculated using the Aequitas Image Analysis™ program (Links 1993-1996). The five measured leaves were dried and weighed as described above. The leaf area measurements and dry weights of the same leaves were

used in the calculation of mean SLA, maximum leaf area per node and maximum leaf weight per node.

4.1.4.2 Mean specific leaf area (SLA)

The specific leaf area for each collection was calculated from the areas and weights of the pressed leaves as the ratio:

$$\frac{\text{mean leaf area } (mm^2)}{\text{mean leaf dry weight (mg)}}$$

The values for the different collections were averaged to give mean SLA for each species.

4.1.4.3 Mean leaf dry matter content (DMC)

For each collection, the percentage of mean dry matter content was calculated from the fresh and dry weights of the leaves that had been made uniformly turgid, using the formula:

$$\frac{\text{mean dry leaf weight}}{\text{mean fresh leaf weight}} \times 100$$

The values for the different collections were averaged to give mean DMC for each species.

4.1.4.4 Maximum leaf area per node

Maximum leaf area per node for each species was calculated as the area of the largest pressed leaf from the collections of that species, multiplied by the typical number of leaves per node.

4.1.4.5 Maximum leaf weight per node

The reciprocal of SLA (see Section 4.1.4.3) is the dry weight (mg) per mm^2 of leaf area. For each species, therefore, the maximum leaf weight per node was calculated by multiplying the species maximum leaf area per node by the reciprocal of the species mean SLA:

$$\text{Maximum leaf area per node } (mm^2) \times \frac{\text{mean leaf dry weight (mg)}}{\text{mean leaf area } (mm^2)}$$

4.1.4.6 *Maximum leaf width*

The width of the widest of the five pressed leaves for each collection was measured with a ruler on a more or less continuous expanse of leaf perpendicular to the midrib. In the case of compound leaves (e.g. *Trifolium* and *Vicia* spp.) and deeply dissected leaves (e.g. *Senecio* spp.), the greatest width of a more or less entire segment or leaflet was measured. In all cases, the maximum width (mm) measured amongst the collections was taken as the value for the species.

The measurements for the family Apiaceae (which is particularly prone to feathery, multiply dissected leaves) were discarded because it proved difficult to treat these species consistently.

4.1.4.7 Mean leaf thickness

For each collection, the interveinal thickness of five uniformly turgid leaves was measured (to the nearest 0.01 mm) using a dial thickness gauge. Mean leaf thickness was calculated for each collection, and these values were averaged to give the mean leaf thickness value for each species.

4.1.4.8 Ratio of leaf area to leaf thickness

The ratio of maximum leaf area per node to mean leaf thickness was calculated for each species.

4.1.5 Preparation, measurement and calculation of leaf stomatal and epidermal cell attributes

4.1.5.1 Laboratory preparation and measurement equipment

All the stomatal and epidermal cell attributes were measured from acetate leaf-impressions made using the method of Beerling and Chaloner (1992). The upper surface of a leaf (or a sample from larger leaves) was painted with acetone, a strip of acetate was laid over the painted surface and the whole was

pressed between two microscope mounting-slides for about a minute. This process partially dissolves the acetate onto the surface of the leaf, moulding it to the leaf's surface features. Once sufficiently dissolved, the acetate was pealed away from the leaf, laid flat on a mounting-slide and secured with clear tape. The process was repeated for the lower surface of the leaf. To average out the possible effects on stomatal attributes of variable levels of shade within the plant canopy, slides were made from three leaves per collection: one each from the top, middle and base of the canopy.

For each of the stomatal and cell attributes, images of the slides were captured and measured using the Aequitas Image Analysis program (Links 1993-1996), connected to a cytological binocular microscope via a ScopeMan MS500 video camera and ELViS II image capture card.

Epidermal cell dimensions do not vary significantly between upper and lower leaf surfaces (Charles *et al.* 1997), so all cell measurements were taken from a single surface for each leaf, usually the upper.

4.1.5.2 Mean stomatal size

When leaves are picked or a plant is uprooted, the stomata tend to close-up in order to minimise water loss. Consequently, it is rare to find fully open stomata on acetate impressions. Bogaard *et al* (1999) have, however, shown that the length of either of the two 'guard cells' surrounding a closed pore is strongly correlated with open pore size. This length was, therefore, used as measure of stomatal pore size.

Because the size of stomata does not vary significantly between the upper and lower leaf surfaces (Hodgson unpub.; Jalili *et al* unpub.) measurements were taken from a single surface impression for each leaf, usually the upper. Two length (μm) measurements were made per leaf, giving a total of six measurements per collection. Mean stomatal size was calculated for each collection, and these values were averaged to give the mean stomatal size value for each species.

4.1.5.3 *Mean stomatal density*

The field-of-view provided by the image capturing process (see Section 4.1.5.1) is always uniform, therefore stomatal density was simply measured by counting the number of stomata per field-of-view. The relative number of stomata on the two leaf surfaces is usually unequal, and varies with ecology and with taxonomy (Salisbury 1927; Wilkinson 1979; Peat and Fitter 1994b). For this reason, stomatal density was measured at 2 points on each upper and each lower leaf impression, giving a total of twelve measurements per collection. Mean stomatal density was calculated for each collection, and these values were averaged to give the mean stomatal density value for each species.

4.1.5.4 Stomatal distribution

The stomatal density values were also used to assess stomatal distribution. For each species, the mean stomatal densities of the upper and lower leaf surfaces were calculated from the measurements of the collections of that species. The figures for the two leaf surfaces were converted into percentages of the total stomatal density per species. Those species with 55% or less of stomata occurring on a single surface were classified as amphistomatous (having equal distribution of stomata on both surfaces). Species with greater than 55% of stomata occurring on a single surface were classified as non-amphistomatous (having unequal distribution of stomata).

4.1.5.5 Estimated epidermal cell endopolyploidy

The areas (μm^2) of two epidermal cells were measured for this attribute: one adjacent to a stomatal complex, and one at the furthest possible distance from all surrounding stomata (usually the largest cell). Two such pairs of measurements were made per slide, giving a total of twelve measurements per collection. Mean distant and adjacent cell sizes were calculated for each collection, and these values were averaged to give mean distant and adjacent cell size values for each species.

Epidermal cell endopolyploidy was evaluated for each species using the formula:

$$\frac{\text{mean area of cell furthest from surrounding stomata}}{\text{mean area of cell adjacent to a stomatal complex}} \times 100$$

Endopolyploidy is associated with values of 200% or greater, which indicate that distant cells are at least twice as large as cells adjacent to stomatal complexes.

4.1.5.6 Mean epidermal cell size

Cell size was defined as the area (μm^2) of the cell at the furthest distance from its surrounding stomata (as measured for calculating endopolyploidy). In cases where stomata were particularly dense, and all cells were adjacent to at least one stomatal guard cell, then the area of one of these stoma-adjacent cells was substituted. Two measurements were made per slide, giving a total of six measurements per collection. Mean cell size was calculated for each collection, and these values were averaged to give the mean cell size value for each species.

4.1.5.7 *Mean epidermal cell wall undulation*

The perimeter (μm) and maximum diameter (μm) of epidermal cells were measured for this attribute. Again, cells distant from stomata were preferred, but stoma-adjacent cells were substituted when necessary. Two such pairs of measurements were made per slide, giving a total of twelve measurements per collection.

The cell perimeter and diameter measurements for the collections of a species were averaged to give the species mean perimeter and diameter values. Epidermal cell wall undulation was calculated for each species as the ratio of mean cell perimeter to mean cell diameter.

4.1.6 Preparation, measurement and calculation of other attributes

4.1.6.1 Root diameter at 10cm depth

The direct measurement of rooting depth is both difficult and time consuming, and as such is inappropriate to the FIBS technique (which requires that all

attributes should be easy to measure). Fortunately, tap root diameter at a depth of 10 cm below the soil is positively correlated with rooting depth and has proved to be a reasonable surrogate for this measurement (Charles *et al.* 1997). Adventitious roots, stolons and rhizomes are not useful indicators of water conditions (Hodgson, pers. comm.), and have an essentially uniform diameter along their length, so this measurement is restricted to tap roots. Species with extensive lateral roots usually also have a tap root, but the difficulty of isolating this root resulted in such species being excluded from measurement.

For each collection, the longest tap root was cleaned by brushing, and the diameter (mm) of the root measured with callipers at a depth of 10 cm. The values for the various collections of a species were averaged to give the species mean root diameter. Complete tap roots that were shorter than 10 cm were taken to have a diameter of 0 mm.

4.1.6.2 *Seed shape, weight and longevity*

Seed[1] shape and weight were measured for field collections, and for reference material held at either the Department of Archaeology and Prehistory or the Unit of Comparative Plant Ecology (UCPE), University of Sheffield. Up to three seed collections per species were measured, depending on availability.

The length, breadth and thickness of five seeds from each collection were measured using a binocular microscope with an eyepiece graticule. The mean value of each of these measurements was calculated per collection, and these values were each divided by length, so that length was unity. Seed 'shape' per collection was finally calculated as the variance of these values. This process converts the measurements into a dimensionless value indicating the extent to which the seed differs from a sphere (Thompson *et al.* 1993; Bekker *et al.* 1998). For instance, a value of 0 indicates a perfectly spherical seed, whereas at the other extreme, 0.3 could indicate either a thin lenticular seed, or a long

[1] In this context 'seed' is used as shorthand for the normal form of dispersule for a given species, whether a seed or a fruit.

needle-like seed. Seed weight per collection was simply quantified as the mean weight of five seeds.

Following Bekker *et al* (1998), for each collection, seed weight and shape were combined into a single value using the following formula:

$$\log (\text{seed weight} \times \sqrt{\text{seed shape}})$$

The species values were averaged to give the mean value for each species. These values act as an index of the likelihood of seeds being incorporated into a seed bank, and thus of their longevity, with low values indicating greater longevity than high values.

To determine whether or not seed weight and seed shape vary independently of one another, both components were included in statistical analyses in addition to the fully calculated attribute, seed longevity.

4.1.6.3 Life History

Life history was abstracted from published Floras (Zohary 1966, 1972; Tutin *et al.* 1968, 1972, 1976, 1980, 1993; Feinbrun-Dothan 1978, 1986; Clapham *et al.* 1987). Species have been allocated to three life history categories:

1) Annual - completes its life cycle in a single growing season.

2) Biennial - monocarpic perennial, i.e. a perennial that fruits only once.

3) Perennial - polycarpic perennial (both obligate and facultative), i.e. a perennial that fruits more than once. This category encompasses both woody and herbaceous species.

4.1.6.4 *Vegetative spread*

Species were categorised as 'spreading' (stoloniferous and/or rhizomatous) or 'stationary' (other root types) based on field observations, collected root material and information extracted from Floras (Tutin *et al.* 1968, 1972, 1976, 1980, 1993; Clapham *et al.* 1987). Some tap-rooted species may regenerate from fragments of root (for instance *Taraxacum officionale*, dandelion, may regenerate from root that has been damaged by weeding or ploughing), and these species are also categorised as 'spreading'.

4.1.6.5 *Flowering start, length and period*

The month of flowering onset and the duration of the flowering period were abstracted from Floras (Zohary 1966, 1972; Feinbrun-Dothan 1978, 1986; Bolos and Vigo 1984; Clapham *et al.* 1987; Rothmaler 1995; Strid and Tan 1997). Flowering times are, however, affected by climatic variables, and so may not be consistent between the different regions from which a species has been collected. In order to overcome this problem, the months of flowering start and length were converted into general classes that are more easily applied between regions (Tables 4.2 and 4.3). The combined flowering start and length classes of each species were also used to define four classes of 'flowering period' (Table 4.4).

4.2 Methods of analysis

4.2.1 Data preparation

4.2.1.1 Classification

Because this thesis aims to identify the conservative expression of ecological attributes at higher taxonomic levels, it would be desirable to work with a fully resolved phylogenetic taxonomy that precisely reflects the evolutionary relationships between taxa. Unfortunately, such a taxonomy does not exist (see Section 2.1.1). Even if a 'true' phylogeny were available, the statistical methods used to analyse the data (see below) require that they are organised by a ranked hierarchy rather than by a true phylogeny, in which taxa are grouped into clades but not assigned to ranks that imply comparability between clades.

Two implicit assumptions are made when analysing data organised by a taxonomic hierarchy (Harvey and Mace 1982; G. Bell 1989; Martins and Garland 1991; Peat and Fitter 1994a): firstly, that all taxa at a given taxonomic level (for instance all genera) diverged from their common ancestor species at a similar time, and have therefore had comparable opportunity for independent adaptation; and secondly, that each taxon (for instance each genus or family) is monophyletic (i.e. it contains all the descendants of a single common ancestor and no other species). However, because taxonomic classification systems are

often not even *intended* to reflect phylogeny (Harvey and Pagel 1991 p. 51), these assumptions may not be valid. For instance, even such major groups as the mammalian orders Insectivora and Carnivora are no longer believed to be monophyletic, and the time since a group diverged from a common ancestor can vary to the extent that the insect genus *Dropsophila* is thought to be as old as the mammalian order Primates (Felsenstein 1985). These are extreme examples, but similar effects could be biasing the appearance of variation at any point in a taxonomic hierarchy.

To test the significance of taxonomic inaccuracies for analysing variation in plant taxonomic groups, Peat and Fitter (1994a) compared the results of analyses testing variation of plant functional attributes within taxonomic groups using data organised by the taxonomic classification in the *Flora of the British Isles* (Clapham *et al.* 1952) versus that of Stace's *New Flora* (1991), which is more informed by contemporary phylogenetic approaches to classification. The two taxonomic systems disagree over the generic classification of approximately 5% of species, and there are major differences between subclasses. The results of these tests showed that small taxonomic inaccuracies do not have a serious effect on the outcome of comparative analyses of plant attributes:

> "In none of the cases tested would the use of the alternative taxonomy have given rise to radically different conclusions... It would therefore appear that unless there are considerably different taxonomic trees available for a particular group, the decision of which taxonomy to use is not a vital one" (Peat and Fitter 1994a p. 103).

Other studies have compared the results of comparative analyses using data organised by (approximate) phylogenies versus taxonomies (Gittleman and Luh 1992; Kelly and Woodward 1996). Reassuringly, these tests also showed the same overall patterns of variation whichever method of data organisation was used, although there were differences in the details. In the absence of appropriate 'true' phylogenies, therefore, such results suggest that taxonomies can be used as substitutes for phylogeny as long as there is not good evidence that they are significantly inaccurate (Gittleman and Luh 1992; Peat and Fitter 1994a; Woodward and Kelly 1995; Kelly and Woodward 1996).

For the purposes of this thesis, the data have been organised using two different taxonomies. The first taxonomy will be referred to as the 'basic

taxonomy' and it follows Stace's *New Flora of the British Isles* (1997). This Flora was chosen because it attempts to use "the most up-to-date and accurate classification and nomenclature" (Stace 1997 p. ii), although it only departs from traditional phenetic classifications when there is firm evidence for doing so. As noted above (Peat and Fitter 1994a), such departures include changes in the generic classification of species. The *New Flora* also has the advantage of covering a large number of alien taxa, and so includes many of the species collected for this project from outside Britain. Species in the ARCHFIBS dataset that are not included in the *New Flora* have been added to the basic taxonomy provided that they belong to genera that the *New Flora* classifies according to normal taxonomic tradition. Where this was not the case, species were excluded from consideration in this thesis.

To test for possible inaccuracies in the basic taxonomy, the classification of genera and families was checked by comparison with published molecular phylogenies, which at least *intend* to reflect true phylogeny. Molecular phylogenies use genetic characters of extant species to reconstruct the evolutionary relationships between those species. A variety of techniques are available for determining the genetic characters of organisms, but the most common techniques analyse sequences of DNA or the order of genes in the genome (Judd *et al.* 2002 p. 109). When these techniques were first developed, it was hoped that molecular characters would be less prone to convergent and parallel evolution than morphological characters (Judd *et al.* 2002 p. 105). Although this proved not to be the case, molecular character states are generally less ambiguous than morphological character states and their interpretation is generally easier (Judd *et al.* 2002 p. 106). Consequently, molecular phylogenies are now widely used to reconstruct the evolutionary relationships among plant species, and broadly agreed upon molecular phylogenies for angiosperm families and orders exist (Angiosperm Phylogeny Group 1998; Soltis *et al.* 2000).

Where molecular phylogenies indicated that a genus or family in the basic taxonomy was inaccurately classified, and where changing the classification would affect the ARCHFIBS species, then these groups were reclassified in a

second taxonomy, called the 'revised taxonomy'. The results of this process are presented in Chapter 5.

4.2.1.2 Data transformation

The aims of this thesis will be addressed by calculating the extent to which plant functional attributes vary amongst the species within genera and families. Techniques for analysing variance require data to be normally distributed (Sokal and Rohlf 1995 p. 185; Dytham 1999 p. 192). In the case of biological data, this normal distribution should ideally be looked for at the very lowest level of classification for which there is more than one known value (N. Fieller pers. comm.). For the dataset used in this thesis, that level is usually the replicated measurements of the individual plants from which the species data are calculated. Unfortunately, there are not enough measurements at this level to allow a meaningful assessment of normal distribution. In such cases, normal distribution can instead be assessed by plotting the residuals from an analysis of variance (N. Fieller pers. comm.).

An analysis of variance (ANOVA) with genus as the factor was performed for each attribute for which the data type is continuous. The residuals from these analyses were plotted and visually compared to a computer-generated normal distribution for the dataset. None of the attribute data were normally distributed in their raw form, so all data were transformed using both logarithms to base 10 (Log_{10}) and square roots, and then re-tested. In every case the data were essentially normal when transformed to Log_{10}, so all statistical analyses have used the data transformed in this way. These tests were all performed using the statistics package MINITAB™ 13.1 (Minitab 2000).

4.2.2 Data analysis - Nested ANOVAs

4.2.2.1 Background

A nested ANOVA (Sokal and Rohlf 1995 pp. 273-320) describes how the total amount of variation among data for a particular trait is distributed among hierarchical levels. This distribution is illustrated in an equation from Harvey and Pagel (1991 p. 123):

$$\sigma^2_{tot} = \sigma^2_{s(g)} + \sigma^2_{g(f)} + \sigma^2_{f(o)} + \sigma^2_{o(c)}$$

The term σ^2_{tot} represents the total amount of variation among species for a given attribute. The total variation is then partitioned into a component representing the variation of species within their genera ($\sigma^2_{s(g)}$), the variation of genera within their families ($\sigma^2_{g(f)}$), families within orders ($\sigma^2_{f(o)}$), and finally orders within the class ($\sigma^2_{o(c)}$). The variation at each level is calculated from the mean of the values from the level immediately below.

These components of variation can be converted into percentages of total variation by dividing the right side of the equation by σ^2_{tot} and multiplying by 100 (Harvey and Pagel 1991 p.123):

$$[(\sigma^2_{s(g)} + \sigma^2_{g(f)} + \sigma^2_{f(o)} + \sigma^2_{o(c)})/ \sigma^2_{tot}] \times 100$$

In comparative biology (Clutton-Brock and Harvey 1978; Harvey and Mace 1982; Harvey and Clutton-Brock 1985; Bell 1989), nested ANOVAs have been used to identify the effects of phylogenetic relationships on cross-taxa comparisons. Cross-taxa similarities in any biological trait could be due to common but independent adaptation, or to the retention of ancestral traits within particular phylogenetic groups. Such 'phylogenetic conservatism' (see Section 2.2.4) could be the result of a number of processes (Harvey and Pagel 1991 pp. 38-48), which may not necessarily 'constrain' adaptation, but which do result in the canalisation of attributes within phylogenetic groups (Miles and Dunham 1993).

If, for a given attribute, all the species within a genus are similar due to phylogenetic conservatism, then the species data would be considered statistically biased (Harvey and Mace 1982). Rather than each species representing independent points of adaptation, one single (ancestral) point of adaptation will be represented as many times as there are species in the genus. In a cross-taxa comparative analysis this would give undue significance to taxa that are similar due to phylogenetic conservatism.

The taxonomic level at which data points *can* however be considered to be independently adapted, is indicated in a nested ANOVA by the relative proportion of variation at the different levels. If there is little variation among

species-within-genera, but a large amount of variation between genera-within-families, then this suggests that the species within any of the genera are likely to be similar to one another because of their shared ancestry rather than because of independent adaptation. The large amount of variation at the higher level, however, does suggest independent adaptation. If this information was applied to a cross-taxa analysis, then the phylogenetic effect could be circumvented by using the mean value of the species within a genus to provide a single, independent data point for the genus.

Comparative biologists, therefore, generally use nested ANOVAs as a means of *avoiding* using data from taxa that are similar due to phylogenetic conservatism (Clutton-Brock and Harvey 1978; Harvey and Mace 1982; Harvey and Clutton-Brock 1985; Bell 1989). In this thesis, however, phylogenetically conservative taxonomic groups are of interest precisely because the species with them are not independently adapted. Here, nested ANOVAs will be used to suggest which functional attributes are most and least likely to be phylogenetically conservative within plant genera and families.

4.2.2.2 Taxonomic levels

Typically, nested ANOVAs reveal that most of the variation in a given attribute occurs among orders-within-classes, and among families-within-orders (Harvey and Pagel 1988; 1991 p.124). For a taxonomic level to be suitable for analysis by nested ANOVA, however, each taxon at that level must be represented by more than one sub-taxa at the next lowest level (Sokal and Sneath 1963 p. 272; Dytham 1999 p. 144). Because of this, in the ARCHFIBS dataset used for this thesis the levels of order and class were not suitable for analysis. The order level was excluded because most orders in the dataset are represented by only a single family. In a nested ANOVA this would result in the apparent variation between orders actually being largely composed of the variation between families, but shifted up a level. Representation of the two angiosperm classes is extremely uneven in the dataset, the monocotyledons being represented by only one family (Poaceae), so any apparent intra-class variation in a nested ANOVA would in fact consist of variation between a class and a family.

The low hierarchical level of replicate (or individual plants within a species) was excluded from the analyses because the methods for calculating the attribute data are purposely designed to approximate the species' *potential* rather than an individual's performance under particular circumstances. Including the replicate data would, therefore, add another axis of variation - that of individual performance.

This taxonomic restriction is not a problem for the purposes of this thesis, however, because it still allows the partitioning of variation between the three taxonomic levels to which archaeobotanical remains are commonly identified: species, genus and family. All the ARCHFIBS families belong to the division *Angiospermae*, so the highest-level comparison of families-within-dataset is an approximation of families-within-division. Each family in the dataset is represented by more than one genus, and all single-species genera were removed from the dataset used for the nested analyses. Each taxon was also checked for missing data attribute by attribute. If, for instance, a genus was represented overall by three species, but a canopy height measurement was only available for one of these species, then that genus was removed from the canopy height analyses but retained in the other analyses. From now on this dataset (used only for the nested ANOVAs) will be referred to as the 'reduced dataset'.

4.2.2.3 Calculation and use

Nested ANOVA is not suitable for analysing nominal (or categorical) scale data (Dytham 1999 p.85), so attributes that were measured on a nominal scale (i.e. stomatal distribution, life history, vegetative spread, flowering start, flowering length and flowering period) are excluded from these analyses. All ANOVAs were calculated using the 'Stat menu' in MINITAB 13.1 (Minitab 2000). Because the sample sizes for most analyses were unequal (i.e. all the taxa at a given level did not contain the same number of sub-taxa), MINITAB did not automatically calculate significance tests for the nested ANOVAs. It is possible to perform approximate significance tests for nested ANOVAs performed on data-sets with unequal sample sizes, but, because these tests can be very inexact (Sokal and Rohlf 1995 p. 292), this was not done.

The analyses were run on the reduced dataset, with the variance of each attribute being partitioned between the taxonomic levels of species-within-genera, genera-within-families and families-within-dataset. Because true phylogeny is estimated in this project by two different taxonomies, these analyses were run separately using data organised by both the 'basic taxonomy' and the 'revised taxonomy', and the results of these separate analyses will be compared.

4.2.3 Data analysis - Coefficient of Variation

4.2.3.1 Background

If all the taxa at a given level had genuinely diverged from their common ancestor species at a similar time, and had therefore had comparable opportunity for independent adaptation (Harvey and Mace 1982; Bell 1989; Martins and Garland 1991), there would be an approximately equal amount of variation within each genus in a family, each family in an order, and so on. Because taxonomy is just an estimation of true phylogeny, however, this is unlikely to be true, and in fact a high amount of variance at a particular taxonomic level may be the result of differences in variation between the groups at that level (Woodward and Kelly 1995). Consequently, it is also necessary to assess the variance *within* particular taxonomic groups.

Perhaps the most familiar measures of variability in a sample are standard deviation and variance (standard deviation squared). When populations differ appreciably in their means, however, the direct comparison of their standard deviations or variances is inappropriate, since larger organisms usually vary more than smaller ones (Sokal and Rohlf 1995 p.58). In biometrics this situation is often illustrated by comparing elephants with mice:

> "Elephants have ears that are perhaps 100 times larger than those of mice. If elephant ears were no more variable, relative to their size, than mouse ears, relative to their size, the standard deviation of elephant ear lengths would be 100 times as great as the standard deviation of mouse ear lengths (and the variance of the former would be 100^2 = 10,000 times the variance of the latter.)" (Zar 1999 p. 40).

The same problem could occur when comparing the standard deviation or variance of attributes within the different genera and families in the ARCHFIBS

dataset. For instance, the standard deviation or variance of canopy heights in a relatively tall genus such as *Prunus* will almost certainly be much greater than in a relatively short genus such as *Cerastium*. Indeed the standard deviation of *Prunus* heights is likely to be greater than the height of a *Cerastium* species. This problem can, however, be overcome by calculating the coefficient of variation, which is the standard deviation divided by the mean, and thus expresses sample variability *relative* to the mean of the sample (Zar 1999 p. 40). The coefficient of variation is commonly used to compare the variability of a single attribute within different populations (Sokal and Rohlf 1995 p.58), and that is how it will be used in this thesis.

4.2.3.2 Calculation and use

The coefficient of variation can be calculated only for ratio-scale data (Zar 1999 p. 40) so, as for the nested ANOVAs, those attributes that were measured on a nominal scale were excluded from these analyses. (Attributes that were measured on a nominal scale will be considered in section 4.2.4).

The coefficient of variation (CV) is independent of the unit of measurement, and is expressed as a percentage (Sokal and Rohlf 1995 p.58) :

$$CV = \frac{\text{standard deviation} \times 100}{\text{mean}}$$

This simple calculation is, however, a biased estimator of the population coefficient of variation (Sokal and Rohlf 1995 p.58). When the sample size is small, the population variation tends to be underestimated. The following calculation of CV*, in which *n* is the number of species in the genera or family for which CV* is calculated, was used partially to correct for this bias (Sokal and Rohlf 1995 p.58):

$$CV^* = (1 + 1/4n) \times CV$$

For all the attributes measured on a ratio-scale, CV* was calculated from the full dataset for each ARCHFIBS genus and family in the basic taxonomy. The coefficient of variation of each revised group in the revised taxonomy was also

calculated, and the results for the basic and revised taxonomies will be compared.

4.2.4 Data analysis - Index of diversity

4.2.4.1 Background

Calculations of variation are unsuitable for data measured on a nominal scale because such scales do not allow the calculation of a mean or median to serve as a reference for the dispersion of data (Zar 1999 p. 40). Instead, the variability within genera and families for nominal-scale attributes was analysed in terms of diversity, that is, the distribution of observations among categories.

For instance, flowering plants may be sorted into three life history categories: perennial, biennial and annual. If, out of 60 species in a genus, 20 were found to be perennial, 20 biennial and 20 annual, then that genus could be said to have great diversity in the life histories of its component species. If, however, 58 species were perennial, 1 was biennial and 1 annual, then the genus could be said to have very low diversity in the life histories of its component species. In other words, observations distributed evenly among categories display high diversity, whereas observations that are primarily concentrated on a single or very few categories display low diversity (Zar 1999 p. 40).

The method used to calculate diversity for this thesis was the Shannon-Weaver index (or Shannon-Wiener index) (Shannon 1948). For this method, diversity can be considered to be synonymous with uncertainty (Zar 1999 p. 41). If 58 out of 60 species in a genus were found to be perennial, then one could be relatively certain of correctly predicting the life history of a newly discovered species of the genus. If, however, the 60 species were evenly distributed between the life history categories, then one would be uncertain of making a correct prediction.

4.2.4.2 Calculation and use

There are two equations by which this index of diversity (H') can be calculated, and the simplest of these was used (Zar 1999 p. 41):

$$H' = \frac{n \log_{10} n - \sum_{i=1}^{k} fi \log 10\ fi}{n}$$

(where n is the number of species in the genus of family for which ID is calculated, k is the number of categories of attribute states, fi is the number of observations in category i).

The magnitude of H' is affected by the distribution of the data, and also by the number of categories (Zar 1999 p. 41). The maximum possible diversity for a set of data consisting of k categories is log k. Consequently, diversity (H') can be converted to a percentage (ID) that expresses the observed diversity as a proportion of the maximum possible diversity[2]:

$$ID = \frac{H'}{\log k}$$

For all the attributes measured on a ratio-scale, ID was calculated from the full dataset for each ARCHFIBS genus and family in the basic taxonomy. The ID of each revised group in the revised taxonomy was also calculated, and the results for the basic and revised taxonomies will be compared.

4.2.5 Data analysis – Correspondence Analysis

The ordination technique 'correspondence analysis' was used to simplify the CV* and ID results in order to determine *which* functional attributes are phylogenetically conservative (or independently adapted) for *which* taxonomic groups. In this case, correspondence analysis arranges ARCHFIBS genera and families along axes on the basis of their variability with respect to different functional attributes. These analyses were performed using the program CANOCO™ for Windows (ter Braak and Smilauer 1997-1999) and the results were plotted using CANODRAW for Windows™ (Smilauer 1992). All plots were symmetrically scaled.

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[2] Zar (1999) calls this quantity J', but for ease of understanding it will be referred to as ID (for Index of Diversity) throughout this thesis.

Chapter 5 - Molecular phylogenetic evidence for the phylogenetic status of ARCHFIBS taxa

5.1 Background

As explained in the previous chapter, to test for possible inaccuracies in the basic taxonomy, the classification of genera and families was checked by comparison with published molecular phylogenies. Where molecular phylogenies indicated that a genus or family in the basic taxonomy was inaccurately classified, and where changing the classification would affect the ARCHFIBS species, then these groups were reclassified in a second taxonomy, called the 'revised taxonomy'. This process serves two purposes. Firstly, by reviewing molecular phylogenetic studies of the ARCHFIBS genera and families it is possible to gauge the extent to which the basic taxonomy differs from phylogeny. Secondly, where it is possible to classify species differently in the basic and revised taxonomies, nested ANOVA, CV* and ID will be calculated for both the basic and revised group. Comparison of the results for the two groups will suggest how significant a problem taxonomic inaccuracies are for the methods of calculating variation in functional attributes.

The molecular phylogenetic analyses were used to determine whether or not the ARCHFIBS genera and families are monophyletic, and thus true reflections of evolutionary relationships. By a strict definition, a monophyletic group must contain all the descendants of a single common ancestor, which must itself be a member of the group (Stace 1989 p. 29; Harvey and Pagel 1991 p. 52). For instance, in Figure 5.1, group A is monophyletic because it contains all the descendants of species *y*, and that species is itself a member of the group. Taxonomic groups that do not fulfil these criteria are either *polyphyletic* or *paraphyletic.* The members of both these types of taxonomic group are also descended from a single common ancestor in the sense that *all* organisms are probably descended from the same ultimate ancestor (Stace 1989 p. 29; Sivarajan and Robson 1991 p. 34). A polyphyletic group is different to a

monophyletic group, however, in that its single common ancestor could not be classified as a member of the group (Hennig 1966; Stace 1989 p. 30). For instance, in Figure 5.1, group B is polyphyletic because, although all its members have a common ancestor in species *z*, that species is not a member of group B. The members of group B are, therefore, most recently descended from two different species, *x* and *y*. Finally, a paraphyletic group is different to a monophyletic group in that it does not include *all* the descendants of a single common ancestor (Hennig 1966; Stace 1989 p. 30). So group C (Figure 5.1) is paraphyletic because, although its members have a common ancestor in species *z*, one of its descendants, species *t*, is excluded from the group. Because the ancestor species of each group of extant species is unknown, in practice it is difficult to distinguish between polyphyletic and paraphyletic groups. In the following review of molecular phylogenetic studies, therefore, any ARCHFIBS genus or family that the evidence suggests is not monophyletic will simply be referred to as 'non-monophyletic'.

Because molecular phylogenetic techniques are still in their infancy the representation of ARCHFIBS species in molecular phylogenetic studies is currently extremely patchy. The molecular phylogenetic relationships of some ARCHFIBS genera and families (e.g. *Rumex* and Polygonaceae) have yet to be studied in any detail, whereas some other genera and families (e.g. *Ranunculus* and Ranunculaceae) have been the subject of considerable research (e.g. Hoot 1995; Jensen *et al.* 1995; Johansson 1995, 1998; Johansson and Jansen 1993; Ro *et al.* 1997).

There is, however, molecular evidence that some families and genera in the 'basic taxonomy' used in this thesis are non-monophyletic. As a result, the ARCHFIBS species have also been organised according to a second taxonomy, to be referred to as the 'revised taxonomy'. This second taxonomy is also based on the *New Flora of the British Isles* (Stace 1997), but with the genera and families that are thought to be non-monophyletic revised according to the relevant molecular phylogenies. Table 5.1 shows the ARCHFIBS species arranged according to the 'revised taxonomy'. Because the rank names applied to taxa in phenetic taxonomies (species, genus, family etc) have particular meanings (Stace 1989 p. 8), it is not appropriate to apply these

names to the revised groups in the 'revised taxonomy'. Instead, the revised groups have all been given taxonomically neutral names that end with the word 'group'.

In some cases the differences between groups in the basic taxonomy and molecular phylogenies are very slight. For instance, molecular analysis suggests that the genus *Torilis* non-monophyletic (Figure 5.2), but that it can be made monophyletic simply by extending its definition to include the genus *Chaetosciadium*, which contains only one species (Lee and Downie 1999, 2000). In other cases, however, molecular analyses suggest that groups in the basic taxonomy are a very poor reflection of phylogenetic relationships. For instance, the genus *Potentilla* seems to be considerably non-monophyletic (Figure 5.3) (Eriksson *et al.* 1998): the smallest monophyletic group that includes all the *Potentilla* species also includes species that are traditionally assigned to at least ten other genera.

Where there is evidence that ARCHFIBS genera or families in the basic taxonomy are non-monophyletic, it would be desirable to reassign their constituent species to relatively small monophyletic groups that have similar status to traditional genera and families. For instance, in Figure 5.3, *Potentilla* species are included with other taxa in three primary groups labelled A, B, and C, each of which could be treated as a separate genus (Eriksson *et al.* 1998). However, in the current state of research, plant genera and families are usually represented in phylogenetic studies by only a small fraction of their constituent species. As a result, few studies provide enough detail to assign all the ARCHFIBS species in a genus or family to relatively small monophyletic groups. For instance, there is only one molecular phylogenetic analysis devoted to *Potentilla* and its immediate relatives (Eriksson *et al.* 1998), and of the 8 ARCHFIBS *Potentilla* species, only 4 are included in this analysis. Of the genus-like monophyletic groups in Figure 5.3, only group C contains more than one ARCHFIBS *Potentilla* species. Thus, reassigning the ARCHFIBS *Potentilla* species to such small monophyletic groups would reduce the number of species that could contribute to calculations of variation and diversity in this group to two.

An alternative strategy for dealing with a taxonomic group that is non-monophyletic is to replace it in the revised taxonomy with the smallest monophyletic group that includes all the species of the original group. For instance, in Figure 5.3 the large monophyletic group labelled X includes all the *Potentilla* species that were considered in the analysis (Eriksson *et al.* 1998). Although only 4 of the 8 ARCHFIBS genera are included in this group, it is not unreasonable to assume that all the species traditionally assigned to *Potentilla* would fall within such a large group, which is more akin to a tribe than a genus. Likewise, although the other genera that are indicated as belonging within group X are represented by fewer species, it is not unreasonable to assume that all their constituent species would also fall within such a large group. Consequently, where molecular phylogenetic evidence suggests that a genus or family in the basic taxonomy is non-monophyletic, the approach adopted in this thesis has been to replace it in the revised taxonomy with the smallest monophyletic group that includes all the species of the original group.

The ARCHFIBS dataset contains only a sample of the genera and species from 15 families, so there may be limited practical difference between a group in the basic taxonomy and the replacement monophyletic group to which its species are assigned in the revised taxonomy. To take *Potentilla* as an example again, Figure 5.3 shows that the monophyletic group that includes all the *Potentilla* species considered also includes species from at least 10 other genera (Eriksson *et al.* 1998). Of these genera, however, only *Aphanes* is also included in the ARCHFIBS dataset, so the monophyletic 'Potentilla group' to which *Potentilla* belongs in the revised taxonomy consists of only the ARCHFIBS *Potentilla* and *Aphanes* species. In other cases, the ARCHFIBS dataset is sufficiently restricted that redefining a traditional taxonomic group to make it monophyletic would add no extra ARCHFIBS taxa to the group. For instance, Figure 5.2 shows that the monophyletic group that includes all the *Torilis* species considered in one phylogenetic analysis also includes the genus *Chaetosciadium* (Lee and Downie 1999, 2000). *Chaetosciadium* is not included in the ARCHFIBS dataset, however, so *Torilis* is represented identically in the basic and revised taxonomies.

In many cases, however, the available phylogenetic evidence does not disprove the monophyly of ARCHFIBS families and genera in the basic taxonomy. In some cases, this may simply be a consequence of a lack of detailed research. Nonetheless, the monophyly of some ARCHFIBS taxa is suggested by a number of detailed phylogenetic analyses based on a variety of genes, and is therefore likely to be genuine. Whatever the quality of the evidence, however, if there is no proof that a taxonomic group is not monophyletic, then it is represented identically in the basic and revised taxonomies.

In summary, for a taxonomic group to be represented identically in the basic and revised taxonomies, this means either that (a) no molecular phylogenetic information was available for that group; or (b) molecular phylogenetic information was available and suggested (however tentatively) that the group is genuinely monophyletic; or (c) the group seems not to be monophyletic, but the smallest monophyletic group that includes all the group's species does not include any other ARCHFIBS species. For a taxonomic group to be replaced by a phylogenetically defined group in the 'revised taxonomy', this means that (a) molecular phylogenetic information was available for that group; (b) that information suggested that the traditional taxonomic group is not monophyletic, and (c) the smallest monophyletic group that includes all the taxonomic group's species does include other ARCHFIBS taxa.

5.2 Molecular phylogenetic evidence for ARCHFIBS families and genera

It should be noted that, in many of the studies referred to below, the families are represented by only one or a few genera, and the genera are represented by only one or a few species. Genera for which no molecular phylogenetic evidence was found (or which are represented in the ARCHFIBS dataset by only one species) are not discussed.

5.2.1 Apiaceae

Although the family Apiaceae as a whole seems to be non-monophyletic, the two subfamilies to which all the ARCHFIBS Apiaceae species belong

(Apioideae and Saniculoideae) occur together in a single monophyletic group (Plunkett *et al.* 1996). The genus *Torilis* is non-monophyletic, although it can be made monophyletic simply by extending its definition to include the genus *Chaetosciadium* (see above & Lee and Downie 1999, 2000). *Chaetosciadium* is not an ARCHFIBS genus, however, so the genus *Torilis* remains unchanged in the revised taxonomy. *Bupleurum* seems to be monophyletic (Downie 1998).

Thus, whilst there is evidence that the family Apiaceae and at least one of its genera are non-monophyletic, there are insufficient Apiaceae species in the ARCHFIBS dataset for any changes in the classification of this family to affect the basic taxonomy. The Apiaceae are, therefore, classified identically in the basic and revised taxonomies (Tables 4.1 and 5.1).

5.2.2 Asteraceae

The family Asteraceae seems to be monophyletic (D. Jansen *et al.* 1990; Chase *et al.* 1993; Kim and Jansen 1995; Bayer and Starr 1998; Eldenäs *et al.* 1999; Olmstead *et al.* 2000; Soltis *et al.* 2000). *Centaurea,* however, seems to be non-monophyletic (Susanna *et al.* 1995; Garcia-Jacas *et al.* 2001), and a monophyletic group that includes all the *Centaurea* species would also have to include species currently assigned to a number of other genera, one of which is the ARCHFIBS genus *Carthamus.* In the revised taxonomy, therefore, these two genera are brought together as 'Centaurea group'. *Sonchus* also seems to be non-monophyletic (Kim *et al.* 1999), and a monophyletic group that includes all the *Sonchus* species would also have to include taxa currently ascribed to a number of other genera. None of these are ARCHFIBS genera, however, so *Sonchus* remains unchanged in the revised taxonomy. *Lactuca* seems to be monophyletic (Kim *et al.* 1999).

Of the Asteraceae, therefore, only *Centaurea* and *Carthamus* are classified differently in the basic and revised taxonomies (Tables 4.1 and 5.1).

5.2.3 Boraginaceae

The family Boraginaceae seems (very tentatively) to be non-monophyletic (D. Chase *et al.* 1993; Soltis *et al.* 2000), and a monophyletic group that includes all the Boraginaceae species would also have to include species

currently assigned to the family Hydrophyllaceae. Hydrophyllaceae is not an ARCHFIBS family, however, so Boraginaceae remains unchanged in the revised taxonomy. The phylogenetic relationships of Boraginaceae are as yet poorly understood, and this group has been particularly targeted for future research (D. Soltis *et al.* 2000).

The Boraginaceae are, therefore, classified identically in the basic and revised taxonomies (Tables 4.1 and 5.1).

5.2.4 Brassicaceae

The family Brassicaceae seems to be monophyletic, although it is probably nested within the non-monophyletic family Capparaceae (D. Chase *et al.* 1993; Rodman *et al.* 1993; Rodman *et al.* 1998; Soltis *et al.* 2000). The genus *Brassica* is non-monophyletic (Pradhan *et al.* 1992; Warwick and Black 1994), however, and a monophyletic group that includes all the *Brassica* species would also have to include species currently ascribed to a number of other genera, including the ARCHFIBS genera *Sinapis, Erucastrum, Diplotaxis* and *Raphanus.* In the revised taxonomy, therefore these genera are brought together as 'Brassica group'. The genus *Neslia* also seems to be non-monophyletic (Zunk *et al.* 1999), and a monophyletic group that included all the *Neslia* species would also have to include the ARCHFIBS genus *Camelina.* In the 'revised taxonomy' therefore, these genera are brought together as 'Neslia group'.

In each case where there is evidence that a genus of Brassicaceae is non-monophyletic, changes in the classification of these genera do affect the basic taxonomy. *Brassica, Sinapis, Erucastrum, Diplotaxis, Raphanus, Neslia* and *Camelina* are classified differently in the basic and revised taxonomies (Tables 4.1 and 5.1), and all other genera in this family are unchanged in the revised taxonomy.

5.2.5 Caryophyllaceae

The family Caryophyllaceae seems to be monophyletic (Rettig *et al.* 1992; Downie and Palmer 1994; Downie *et al.* 1997). The genus *Silene* is non-monophyletic (Oxelman *et al.* 1997), however, and a monophyletic group that

includes all the *Silene* species would also have to include species from a number of different genera. None of these are ARCHFIBS genera, however, so *Silene* remains unchanged in the revised taxonomy. Phylogenetic studies of this family have concentrated on higher-level relationships so the phylogenetic status of other ARCHFIBS Caryophyllaceae genera is as yet unclear. A more complete phylogeny of the intra-family relationships of the Caryophyllaceae is, however, in preparation (M. Nepokroeff pers. comm.).

The Caryophyllaceae are, therefore, classified identically in the basic and revised taxonomies (Tables 4.1 and 5.1).

5.2.6 Chenopodiaceae

Some studies (based on very few species) have suggested that Amaranthaceae and Chenopodiaceae are monophyletic sister-groups (groups that have their most recent ancestor in common) (Rettig *et al.* 1992; Downie and Palmer 1994). Other studies (including the most extensive phylogenetic analysis published for this group) suggest that both families are non-monophyletic (Chase *et al.* 1993; Downie *et al.* 1997). By this scheme, a monophyletic group that includes all the Chenopodiaceae species would also have to include the genus *Amaranthus* (Downie *et al.* 1997). One *Amaranthus* species is included in the broader ARCHFIBS database so for the revised taxonomy these taxa are brought together as 'Chenopodiaceae group'. Phylogenetic studies of this family have concentrated on higher-level relationships, so the phylogenetic status of the ARCHFIBS genera is as yet unclear. A more complete intra-family phylogeny of the Chenopodiaceae is in preparation, however, and the research-group working on this considers Amaranthus to be part of the Chenopodiaceae (D. Pratt pers. comm.).

Thus, the family Chenopodiaceae is classified differently in the basic and revised taxonomies (Tables 4.1 and 5.1), but the Chenopodiaceae genera are unchanged in the revised taxonomy.

5.2.7 Fabaceae

The family Fabaceae seems to be monophyletic (D. Chase *et al.* 1993; Doyle *et al.* 1997; Soltis *et al.* 2000), as do the genera *Lathyrus* (Amussen and Liston 1998), *Medicago* (Bena *et al.* 1998) and *Trifolium* (Watson *et al.* 2000).

The Fabaceae are, therefore, classified identically in the basic and revised taxonomies (Tables 4.1 and 5.1).

5.2.8 Lamiaceae

The family Lamiaceae seems to be monophyletic (D. Wagstaff and Olmstead 1997; Wagstaff *et al.* 1998; Soltis *et al.* 2000), as does the genus *Stachys* (Wink and Kauffman 1995). *Lamium*, however, seems to be non-monophyletic (Wink and Kauffman 1995), and a monophyletic group that includes all the *Lamium* species would also have to include species from the genus *Marrubium*. *Marrubium* is not an ARCHFIBS genus, however, so *Lamium* remains unchanged in the revised taxonomy.

The Lamiaceae are, therefore, classified identically in the basic and revised taxonomies (Tables 4.1 and 5.1).

5.2.9 Papaveraceae

Some phylogenetic morphological (Kadereit *et al.* 1994) and molecular (Hoot *et al.* 1997) studies suggest that Papaveraceae and Fumariaceae are monophyletic sister families. Other phylogenetic morphological (Loconte *et al.* 1995) and molecular (Chase *et al.* 1993) studies, however, suggest that Papaveraceae is non-monophyletic, and a monophyletic group that includes all the Papaveraceae species would also have to include the family Fumariaceae. The phylogenetic status of Papaveraceae is, therefore ambiguous. In case Papaveraceae truly is non-monophyletic, and as *Fumaria* species are represented in the broader ARCHFIBS database, in the revised taxonomy these taxa are brought together as Papaveraceae group. In addition, the genus *Papaver* seems to be non-monophyletic (Kadereit and Sytsma 1992; Kadereit *et al.* 1997), and a monophyletic group that includes all the *Papaver* species would also have to include taxa currently ascribed to a number of

other genera, one of which is the ARCHFIBS genus *Roemeria.* In the 'revised taxonomy', therefore, these genera are brought together as 'Papaver group'.

Thus, the family Papaveraceae and the genera *Papaver* and *Roemeria* are classified differently in the basic and revised taxonomies (Tables 4.1 and 5.1), but all other genera in this family are unchanged in the revised taxonomy.

5.2.10 Poaceae

The family Poaceae seems to be monophyletic (Chase *et al.* 1993; Clark *et al.* 1995; Hilu *et al.* 1999), as, tentatively, do the genera *Poa* (Soreng 1990; Catalán *et al.* 1997), *Avena* (Catalán *et al.* 1997) and *Hordeum* (Hsiao *et al.* 1995). The genus *Festuca*, however, is non-monophyletic, and a monophyletic group that includes all the *Festuca* species would also have to include the ARCHFIBS genus *Lolium* (Stammers *et al.* 1995; Catalán *et al.* 1997). In the revised taxonomy, therefore, these genera are brought together as 'Festuca group'.

Of the Poaceae, therefore, only *Festuca* and *Lolium* are classified differently in the basic and revised taxonomies (Tables 4.1 and 5.1).

5.2.11 Polygonaceae

It is possible that the family Polygonaceae is monophyletic, and a monophyletic group that includes all the Polygonaceae species would have to include the genus *Plumbago,* but this is far from certain (Yasui and Ohnishi 1996). As *Plumbago* is not an ARCHFIBS genus, however, Polygonaceae remains unchanged in the revised taxonomy. The genus *Persicaria* seems (very tentatively) to be monophyletic (Yasui and Ohnishi 1996). This family is as yet very poorly represented in the molecular phylogenetic literature.

The Polygonaceae are, therefore, classified identically in the basic and revised taxonomies (Tables 4.1 and 5.1).

5.2.12 Ranunculaceae

The family Ranunculaceae seems to be monophyletic (D. Hoot 1995; Soltis *et al.* 2000), as do the genera *Ranunculus* (Johansson and Jansen 1993;

Jensen *et al.* 1995; Johansson 1998), *Adonis* (Jensen *et al.* 1995; Johansson 1995) and *Thalictrum* (Jensen *et al.* 1995; Ro *et al.* 1997).

The Ranunculaceae are, therefore, classified identically in the basic and revised taxonomies (Tables 4.1 and 5.1).

5.2.13 Rosaceae

The family Rosaceae seems to be monophyletic (D. Chase *et al.* 1993; Morgan *et al.* 1994; Soltis *et al.* 2000), as does the genus *Rubus* (Alice and Campbell 1999). The genus *Potentilla*, however, is non-monophyletic (see above and Eriksson *et al.* 1998), and a monophyletic group that includes all the *Potentilla* species would also have to include taxa currently ascribed to a number of other genera, one of which is the ARCHFIBS genus *Aphanes.* In the revised taxonomy, therefore, these genera are brought together as 'Potentilla group'. *Prunus* may also be non-monophyletic, and a monophyletic group that includes all the *Prunus* species would also have to include the genus *Maddenia* (Lee and Wen 2001). *Maddenia* is not an ARCHFIBS genus, however, so *Prunus* remains unchanged in the revised taxonomy.

Of the Rosaceae, therefore, only *Potentilla* and *Aphanes* are classified differently in the basic and revised taxonomies (Tables 4.1 and 5.1).

5.2.14 Rubiaceae

The family Rubiaceae, the subfamily (Rubioideae) and the tribe (*Rubieae*), to which most of the ARCHFIBS Rubiaceae species belong, all seem to be monophyletic (D. Manen *et al.* 1994; Natali *et al.* 1995; Natali *et al.* 1996; Anderrson and Rova 1999; Soltis *et al.* 2000). Phylogenetic studies confirm that the genus *Theligonum* (which has been considered to belong to a variety of different families) is in fact a member of the Rubiaceae family (Natali *et al.* 1995; Anderrson and Rova 1999).

Of the genera within the tribe *Rubieae, Rubia* seems to be a monophyletic sister group to the rest of the tribe (Manen *et al.* 1994; Natali *et al.* 1995, 1996). The genera *Galium, Asperula, Cruciata* and *Sherardia*, however, require considerable modification from their traditional taxonomic definitions (Manen *et al.* 1994; Natali *et al.* 1995, 1996). Broadly speaking, Galium is non-

monophyletic, and a monophyletic group that includes all the *Galium* species would also have to include species currently ascribed to a number of other genera, including the ARCHFIBS genera *Asperula, Cruciata* and *Sherardia.* In the revised taxonomy, therefore, these taxa are brought together as 'Galium group'.

Thus, the genera *Galium, Asperula, Cruciata,* and *Sherardia* are classified differently in the basic and revised taxonomies (Tables 4.1 and 5.1), but Rubiaceae and *Rubia* are unchanged in the revised taxonomy.

5.2.15 Scrophulariaceae

There is little doubt that the Scrophulariaceae are non-monophyletic (D. Olmstead and Reeves 1995; Nickrent *et al.* 1998; Soltis *et al.* 2000). The genera that are usually considered members of the Scrophulariaceae form at least two distinct monophyletic groups (Olmstead and Reeves 1995), and as many as three or four groups in a recent analysis (D. Soltis *et al.* 2000). One of these monophyletic groups includes the ARCHFIBS genera *Verbascum* and *Scrophularia*, so in the 'revised taxonomy' they are brought together as 'Scrophulariaceae A group'. A second group is represented in the ARCHFIBS dataset by only a single genus, *Veronica.* Because each monophyletic group above the species level in the revised taxonomy must contain more than one sub-group, *Veronica* was excluded from the revised taxonomy. The other Scrophulariaceae genera in the ARCHFIBS dataset (*Linaria, Kickxia, Odontities, Misopotes* and *Chaeonorhinum*) were not included in the available molecular phylogenies, so are excluded from the revised taxonomy.

Thus, the family Scrophulariaceae is classified differently in the two taxonomies (Tables 4.1 and 5.1), and the genera *Veronica, Linaria, Kickxia, Odontities, Misopotes* and *Chaeonorhinum* are absent from the revised taxonomy. The other genera from this family are classified identically in the two taxonomies.

5.2.16 Summary

Although molecular phylogenies are not necessarily exact reflections of evolutionary relationships (see Section 2.1.1.2), and ARCHFIBS genera and

families are often poorly represented in these phylogenetic studies, this body of evidence does suggest that there are some considerable taxonomic inaccuracies in the basic taxonomy, and so in the Floras on which it is based. The majority of families (nine out of fifteen) appear to be monophyletic, but, of the thirteen families for which evidence regarding ARCHFIBS genera was available, nine include at least one non-monophyletic ARCHFIBS genus. The extent of any taxonomic inaccuracy varies considerably between families. For instance, both the Ranunculaceae (Johansson and Jansen 1993; Hoot 1995; Jensen *et al.* 1995; Johansson 1995; Ro *et al.* 1997; Johansson 1998; D. Soltis *et al.* 2000) and Rubiaceae (D. Manen *et al.* 1994; Natali *et al.* 1995; Natali *et al.* 1996; Anderrson and Rova 1999; Soltis *et al.* 2000) are relatively well represented in molecular phylogenetic studies, and yet the ARCHFIBS Ranunculaceae genera all seem to be monophyletic, whereas most of the ARCHFIBS Rubiaceae genera seem to be non-monophyletic.

The extent to which these taxonomic inaccuracies affect calculations of the variation in functional attributes at higher taxonomic levels will be addressed in the next chapter.

Chapter 6 – Analysis of the variation in functional attributes at higher taxonomic levels

The results of three different types of analyses are presented in this chapter, each of which examines variation in functional attributes at higher taxonomic levels. The nested ANOVA analyses how the total amount of variation is distributed among taxonomic levels for attributes measured on a ratio scale; the coefficient of variation analyses the variation within individual higher taxonomic groups for attributes measured on a ratio scale; and the index of diversity analyses the distribution of data among categories within individual higher taxonomic groups for attributes measured on a nominal scale. All analyses have been carried out on data organised by both the basic and revised taxonomies. In each case interpretation will concentrate on results of analyses using the basic taxonomy and comparison will be made with results for the revised taxonomy.

The number of species within different groups at the same taxonomic level can vary greatly and, for the majority of the functional attributes considered, most of the ARCHFIBS higher taxonomic groups are represented by only a sample of their component species. As an indication of this, Tables 6.1 and 6.2 show the number of species collected for this project for each ARCHFIBS genus and family compared with the number of species listed in the *Flora Europaea* (Tutin *et al.* 1968, 1972, 1976, 1980, 1993) for the same taxonomic groups. In the majority of cases the genera are represented in the ARCHFIBS dataset by less than 50% of their European species and, in all cases, the families are represented by 20% or less of their European species. In some cases, therefore, the following results are estimates of the variability of genera and families based on small samples of their species populations.

6.1 Partitioning variance between different taxonomic levels – results of nested ANOVAs (ratio-scale attributes)

The nested ANOVA results for each of the ratio-scale functional attributes are presented in Tables 6.3 to 6.21. In each of these tables, the total variation of an individual attribute is broken down to show what percentage of the variation is accounted for at the different levels of 'species within genera', 'genera within families' and 'families within dataset'. For the sake of simplicity, these different taxonomic levels are henceforth referred to as the within-genera, within-families and within-dataset levels.

6.1.1 Phylogenetic conservatism and independent adaptation in functional attributes

The nested ANOVA results (Tables 6.3 to 6.21) provide data by which part of the first objective of this thesis can be met:

1. To determine what useful ecological inferences can and cannot be drawn from ancient plant remains identified to higher taxonomic groups (but not to species), and to target higher taxonomic groups from which few useful ecological inferences can be drawn for research into more precise taxonomic identification of their fossilised remains.

The nested ANOVAs suggest which functional attributes (and so, using the ARCHFIBS method, which ecological inferences) are most and least likely to be phylogenetically conservative within plant genera and families. The most conservative attributes have the greatest potential for allowing ecological inferences to be drawn from plant remains identified only to those higher taxonomic groups. Conversely, the least conservative attributes (i.e. those that have undergone independent adaptation within those groups) are those that have the greatest potential for allowing very precise ecological inferences to be drawn from plant remains identified to species.

Examination of the nested ANOVA results suggested that some attributes behave similarly in the partitioning of variance between the different taxonomic levels. This apparent patterning in the results was confirmed by plotting the nested ANOVA results as ternary graphs (also known as triplots). Figure 6.1 is

a ternary graph based on the nested ANOVA results obtained from data arranged by the basic taxonomy. Each ratio-scale attribute is plotted according to the relative percentage of variance in the ARCHFIBS taxa that is accounted for at each of the taxonomic levels of within-genera, within-families and within-dataset. Six groups in which attributes behave similarly in the partitioning of variance between the different taxonomic levels can be identified in this graph. Two attributes, leaf thickness and root diameter, are rather ambiguous in their group membership, so have been designated 'ungrouped'. Table 6.22 shows the nested ANOVA results obtained from data arranged by the basic taxonomy divided into the groups suggested by Figure 6.1.

In order to interpret these groups, it is necessary to understand the evolutionary significance of differing proportions of variance at different taxonomic levels. If the proportion of the overall variance in an attribute accounted for at a particular taxonomic level is low, then this indicates that many taxa at that level are relatively unvarying in that attribute. The unvarying expression of an attribute in all the immediate descendents of a single ancestral taxon results from phylogenetic conservatism. Thus, if a low proportion of variance in an attribute is accounted for at a particular taxonomic level, this suggests that, in general, the taxa at that level are phylogenetically conservative for that attribute.

If, however, a high proportion of the overall variance in an attribute is accounted for at a particular taxonomic level, then this may indicate that taxa at that level are highly variable in that attribute. The highly variable expression of an attribute in all the immediate descendants of a single ancestral taxon results from independent adaptation. Thus, if a high proportion of variance in an attribute is accounted for at a particular taxonomic level, this suggests that, in general, the taxa at that level have undergone independent adaptation of that attribute.

There are, however, two important caveats to this explanation. Firstly, a high level of variance accounted for at a particular taxonomic level could instead be the result of considerable differences in variance between the groups that comprise that level (Peat and Fitter 1994a; Woodward and Kelly 1995). In other words, a high level of variance at a particular taxonomic level indicates *either*

high variance in most taxa at that level, *or* considerable differences in variance between taxa at that level. When used alone, nested ANOVAs are insufficient to suggest which of these interpretations is correct. Either possibility, however, suggests that the taxa within a level are not *generally* phylogenetically conservative.

Secondly, in addition to considering how the total amount of variation is distributed between taxonomic levels it is also necessary to take into account how generally variable the different attributes are. For example, two different attributes, X and Y, each have 70% or their total variation accounted for at the within-dataset level, 20% at the within-families level and only 10% at the within-genera level. If attribute X is generally very variable, then the within-genera and within-families levels have low variance *relative* to the very high variance at the within-dataset level, but the actual amount of variance represented at the within-genera and within-families levels may be considerable. If, in contrast, attribute Y is generally quite unvarying, then the actual amount of variance represented at the within-genera and within-families levels is truly very low, but the actual amount of variance represented at the within-dataset level may also be quite low. The within-dataset level only has high variance *relative* to the very low variance at the within-genera and within-families levels. The total variance of an attribute across all taxonomic levels can be included in the nested ANOVA results, but the variance of different attributes cannot be compared directly because variance is affected by differences in scale (Dytham 1999 p.49) and different attributes are measured on different scales.

Coefficients of variation and indices of diversity can be used both to determine the nature of high levels of variation in particular instances and to compare the total variation of different attributes, and these will be dealt with in Section 6.2. Firstly, however, the different groups shown in Figure 6.1 and Table 6.22 will be analysed solely in terms of the patterns of phylogenetic constraint and independent adaptation that are suggested by the nested ANOVAs alone.

Group 1 (seed shape and epidermal cell wall undulation):

The percentage of total variance accounted for at the within-genera and within-families levels is low, but the percentage accounted for at the within-dataset level is very high. This pattern of variation may indicate that independent adaptation of these attributes occurred when orders diverged into families, but when families diverged into genera and genera diverged into species taxa were relatively phylogenetically conservative with regard to these attributes. Alternatively, the high level of variation at the within-dataset level could be due to considerable *differences* in variance between the different families.

Attributes in Group 1, therefore, are those for which a relatively high proportion of both ARCHFIBS genera and families are likely to have been phylogenetically conservative.

Group 2 (seed longevity):

The percentage of total variance accounted for at the within-genera and within-dataset levels is low, but the percentage accounted for at the within-families level is quite high. This pattern of variation may indicate that taxa were phylogenetically conservative with regard to seed longevity when orders diverged into families, but that considerable independent adaptation of this attribute occurred when families diverged into genera. When genera diverged into species, however, taxa may have been phylogenetically conservative for seed longevity once more. Alternatively, the high level of variation at the within-families level could be due to considerable *differences* in variance between the different genera.

A relatively high proportion of ARCHFIBS genera, therefore, are likely to be phylogenetically conservative with respect to seed longevity. A high proportion of ARCHFIBS families *may* be independently adapted for seed longevity, but this is less clear.

Group 3 (stomatal size, epidermal cell size, leaf width, stomatal density):

The total amount of variance for these attributes is divided more-or-less equally between the different taxonomic levels. Peat and Fitter (1994a) suggest that this pattern of variation may indicate that independent adaptation of these

attributes occurred at all the taxonomic levels considered, that is, when orders diverged into families, families diverged into genera, and genera diverged into species. It would seem, however, that this pattern could equally indicate that taxa were phylogenetically conservative with respect to these attributes at each of the different taxonomic levels, or that taxa show no strong trend towards either phylogenetic conservatism or independent adaptation for these attributes at any of the taxonomic levels. Alternatively, it may be that there are considerable *differences* in variance between taxa at each of the three taxonomic levels.

Although the percentage of total variance accounted for at the genus and family levels is quite low for the attributes in Group 3, it is not necessarily the case that taxa at those levels are phylogenetically conservative. Indeed, it may even be the case that a high proportion of the ARCHFIBS genera and families are independently adapted for these attributes.

Group 4 (endopolyploidy, DMC):

The percentage of total variance accounted for at the within-families level is low, but the percentage accounted for at the within-genera and within-dataset levels is quite high. Peat and Fitter (1994a) suggest that this pattern of variation indicates that independent adaptation of these attributes occurred when orders diverged into families and more recently when genera diverged into species. When families diverged into genera, however, taxa may have been relatively phylogenetically conservative with respect to these attributes. Alternatively, the high level of variation at the within-genera and within-dataset levels could be due to considerable *differences* in variance between the taxa at these levels.

A relatively high proportion of ARCHFIBS families, therefore, are likely to be phylogenetically conservative with respect to attributes in Group 4. A high proportion of ARCHFIBS genera *may* be independently adapted for these attributes, but this is less clear.

Group 5 (leaf weight per node, canopy height, leaf area per node, seed weight, leaf area:leaf thickness):

The percentage of total variance accounted for at the within-dataset level is very low, but the percentage accounted for at the within-genera and within-

families levels is quite high. This pattern of variation indicates that taxa were phylogenetically conservative with respect to these attributes when orders diverged into families, but that considerable independent adaptation of these attributes may have occurred both when families diverged into genera and when genera diverged into species. Alternatively, the high level of variation at the within-genera and within-families levels could be due to considerable *differences* in variance between the taxa at these levels.

A high proportion of ARCHFIBS genera and families, therefore, *may* be independently adapted for these attributes, but this is unsure.

Group 6 (canopy dimension, canopy diameter, SLA):

The percentage of total variance accounted for at the within-genera level is very high, the percentage accounted for at the within-families level is low, and that accounted for at the within dataset level is very low. This pattern of variation indicates that taxa were phylogenetically conservative with regard to these attributes when orders diverged into families, that a little more independent adaptation of these attributes may have occurred when families diverged into genera, and considerable independent adaptation may have occurred when genera diverged into species. Alternatively, the high level of variation at the within-genera level could be due to considerable *differences* in variance between the species at that level.

A fairly high proportion of ARCHFIBS families, therefore, are likely to be phylogenetically conservative with respect to attributes in Group 6. A very high proportion of ARCHFIBS genera *may* be independently adapted for these attributes, but this is unsure.

Ungrouped (leaf thickness, root diameter):

These two attributes are intermediate between groups 3 and 6. For both these attributes, the percentage of total variance accounted for at the dataset and family levels is quite low (and roughly equal), but the percentage accounted for at the genus level is relatively high. This pattern of variation indicates that these attributes were phylogenetically fairly conservative when ancestral taxa diverged into families and when families diverged into genera, but that a relatively greater amount of independent adaptation may have occurred when

genera diverged into species. Alternatively, the higher level of variation at the within-genera level could be due to considerable *differences* in variance between the species at that level.

A high proportion of ARCHFIBS families, therefore, are likely to be phylogenetically conservative with respect to these attributes. A fairly high proportion of ARCHFIBS genera *may* be independently adapted for these attributes, but this is unsure.

Summary

Those attributes for which a high proportion of both genera *and* families are phylogenetically conservative have considerable potential for allowing ecological inferences to be drawn from plant remains identified only to genus or family. The nested ANOVAs suggest, therefore, that the attributes in Group 1 (seed shape and epidermal cell wall undulation) have the greatest potential in this respect. Attributes for which a high proportion of genera, but not families, are phylogenetically conservative have considerable potential for allowing ecological inferences to be drawn from plant remains identified only to genus, though not for remains identified only to family. The nested ANOVAs suggest that the Group 2 attribute (seed longevity) has potential in this respect.

Those attributes for which a high proportion of both genera and families, or genera alone, have undergone independent adaptation have considerable potential for allowing very precise ecological inferences to be drawn from plant remains identified to species. The nested ANOVAs suggest that the attributes in Group 4 (endopolyploidy and DMC), Group 5 (leaf weight, canopy height, leaf area, seed weight and leaf area:thickness), Group 6 (canopy dimension, canopy diameter and SLA) and to a lesser extent the ungrouped attributes (leaf thickness, root diameter) have the greatest potential in this respect. As explained above, however, nested ANOVAs do not distinguish between overall high levels of variation at a particular taxonomic level and considerable *differences* in variance between the different taxa at a particular level.

6.1.2 Nested ANOVAs and the revised taxonomy

Each taxon included in a nested ANOVA analysis must be represented by more than one of its descendent taxa at the next lowest taxonomic level (Sokal and Rohlf 1995 p.272). Consequently, all genera that are represented in the full ARCHFIBS dataset by only a single species are absent from the reduced dataset on which the nested ANOVAs are based. Of the species that remain, the basic and revised taxonomies disagree over the generic classification of approximately 13% of the species. In addition, one family (Papaveraceae) is represented in the basic taxonomy by only one multi-species genus so is it absent from the nested ANOVA analyses that use data arranged by the basic taxonomy. In the revised taxonomy, however, Papaveraceae is represented by two multi-species genera so the family is present in the nested ANOVA analyses that use data arranged by the revised taxonomy. Consequently, for each attribute, the nested ANOVA results based on data arranged by the revised taxonomy include data from one more family than the results based on the data arranged by the basic taxonomy.

Notwithstanding these differences, the nested ANOVA results for the basic and revised taxonomies are remarkably similar for most of the functional attributes analysed by this method. Figure 6.2 is a ternary graph based on the nested ANOVA results obtained from data arranged by the revised taxonomy. As for Figure 6.1, each ratio-scale attribute is plotted according to the relative percentage of variance in the ARCHFIBS taxa that is accounted for at each of the taxonomic levels of within-genera, within-families and within-dataset. For this graph, each attribute carries the same group symbol as in Figure 6.1, and by comparing the positions of the group symbols in the two graphs it is possible to see if the taxonomic differences in the two datasets result in differences in the grouping of attributes.

The only notable difference is that seed weight groups with seed longevity (Group 2) in the analysis using the revised taxonomy whereas using the basic taxonomy it was part of Group 3. Groups 5 and 6 are also less clearly distinguished using the revised taxonomy than they were using the basic taxonomy. Table 6.23 shows the nested ANOVA results obtained from data

arranged by the revised taxonomy divided into new groups as suggested by Figure 6.2.

Overall the parity between the results of nested ANOVAs for plant attributes using data organised by the two different taxonomies, one more informed by phylogeny than the other, reflects that found by Peat and Fitter (1994a). They concluded that nested ANOVAs are little affected by the differences between taxonomies and phylogenies, and these results seem to support that conclusion. The ARCHFIBS taxa are not well represented in published molecular phylogenies, however, so the revised taxonomy is only a very partial revision of the basic taxonomy. Those detailed molecular phylogenetic analyses that are available tend to suggest quite substantial revisions to traditional taxonomies so it seems probable that the fully worked-out phylogeny of the ARCHFIBS taxa would differ more from the basic taxonomy than does the revised taxonomy. It is, therefore, possible that nested ANOVAs would be more severely affected by the differences between taxonomies and complete phylogenies than these results suggest.

6.2 Detailed breakdown of variation within taxonomic groups – results of coefficients of variation (ratio-scale attributes) and indices of diversity (nominal-scale attributes)

The nested ANOVA results showed how the total variation of an individual attribute is partitioned between different taxonomic levels. In order to answer the objectives of this thesis, it is also necessary to consider how much variability there is in the functional attributes within *particular* taxonomic groups. The majority of ARCHFIBS functional attributes are measured on a ratio scale, and the level of variability in these attributes within taxonomic groups was calculated by the coefficient of variation (Sokal and Rohlf 1995 pp.57-59; Zar 1999 p.40). A number of ARCHFIBS functional attributes are measured on a nominal scale, however, and calculations of variation (in its strict statistical sense) are unsuitable for nominal-scale data (Zar 1999 p.40). Consequently, the level of variability in these attributes within taxonomic groups was calculated as an index of diversity (Zar 1999 pp.40-44). Because the coefficient of variation and

index of diversity are methods of asking essentially the same question of different types of data, the results of these analyses will be considered together.

The coefficient of variation (CV*) results for each of the ratio-scale functional attributes are presented in Tables 6.24 to 6.42. For each of these tables, the CV* of each higher taxonomic group has been calculated independently (as a percentage) and shows how much each individual genus and family varies with respect to the different attributes. The taxa in the tables are always arranged in ascending order of CV*s.

The index of diversity results for each of the nominal-scale functional attributes are presented in Tables 6.43 to 6.48. For each of these tables, the diversity of each higher taxonomic group has been calculated independently and shows how observations for each genus and family are distributed between categories. In all cases diversity has been converted to a quantity (ID) that expresses the observed diversity as a proportion of the maximum possible diversity (Zar 1999), on a scale from 0 to 1. The taxa in the tables are always arranged in ascending order of their IDs.

6.2.1 Predictive value

The CV* and ID results can both be used to indicate how reliable a taxonomic group as a whole is as a predictor of the individual species within the group with respect to each functional attribute. To take the attribute 'canopy height' as an example of how this works for coefficients of variation, if a higher taxonomic group has a low CV* for canopy height, then the mean canopy height of all the species in that group is likely to be similar to the canopy height of an individual species belonging to that group. If, on the other hand, a higher taxonomic group has a high CV* for canopy height, then the mean canopy height of all the species in that group may be very dissimilar to the canopy height of an individual species belonging to that group.

The significance of this for archaeobotanical and palaeopalynological applications is that it allows some functional attribute values to be predicted for some ancient plant remains identified only to higher taxonomic groups. Thus, if a higher taxonomic group has a low CV* for canopy height, then the canopy height of ancient plant remains identified to that group, but not to species, could

be predicted reasonably accurately from the mean canopy height of all the measured species in that group. Henceforth, if a higher taxonomic group is considered to have a low enough CV* with respect to a particular attribute to allow such predictions to be made, it is referred to as having 'predictive value' for that attribute.

Indices of diversity are used somewhat differently in gauging the predictive value of higher taxonomic groups. To take the attribute 'vegetative spread' as an example, each ARCHFIBS species is classified as either 'spreading' or 'stationary'. If a higher taxonomic group has an ID of 0 for this attribute, then all the sampled species in that group belong to the same vegetative spread class. In such circumstances, and if the group's diversity was calculated from its full population, then the spread class of an individual species belonging to that group could be predicted with total confidence. In other words: that particular taxonomic group has definite predictive value for vegetative spread. If the group's diversity was calculated from a sample of its population, however, then the spread class of an individual species belonging to that group could be predicted with reasonable, but not total, confidence. In other words: it is likely that the group has predictive value, but not definite. At the other extreme, if a higher taxonomic group has an ID of 1 for this attribute, then the sampled species in that group are evenly divided between the two vegetative spread classes. In such circumstances it is impossible to predict the spread class of an individual species belonging to the group, so it can be considered to have no predictive value.

Thus, the tables of results for CV* (Tables 6.24 to 6.42) and ID (Tables 6.43 to 6.48) provide data by which the first objective of this thesis can be met:

1. To determine what useful ecological inferences can and cannot be drawn from ancient plant remains identified to higher taxonomic groups (but not to species), and to target higher taxonomic groups from which few useful ecological inferences can be drawn for research into more precise taxonomic identification of their fossilised remains.

If a higher taxonomic group has low predictive value for a large number of functional attributes, then little useful ecological data can be drawn from ancient

plant remains identified to that group, but not to species. There is, therefore, significant ecological information to be gained from more precise taxonomic identification of the fossilised remains of such groups. If, however, a higher taxonomic group has high predictive value for a large number of functional attributes, then considerable useful ecological data can be drawn from plant remains identified to that group. There is, therefore, relatively little to be gained from more precise taxonomic identification of these groups.

The nested ANOVAs suggested which functional attributes (and so, using the ARCHFIBS method, which ecological inferences) are most and least likely to be phylogenetically conservative within plant genera and families. The CV* and ID results supplement the nested ANOVAs by indicating in which *particular* taxonomic groups each attribute is more or less conservatively expressed.

Unfortunately, there is no straightforward means of deciding when a higher taxonomic group has sufficiently low CV* to have predictive value for a particular attribute. As a general rule, however, the higher taxonomic groups that are located towards the top of each of the tables of CV* results for different attributes (Tables 6.24 to 6.42) are most likely to have predictive value for the relevant attributes, whilst the groups that are located towards the bottom of each table are least likely to have predictive value.

It is comparatively easy to decide whether or not some higher taxonomic groups have sufficiently low ID to have predictive value for a particular attribute. This is because the diversity indices 0 and 1 both have relatively unambiguous meanings: if a group has an ID of 0 then it is very likely to have predictive value, but if a group has an ID of 1 then if is very unlikely to have predictive value. For each of the nominal-scale functional attributes considered in this thesis, a relatively large number of the ARCHFIBS higher taxonomic groups had an ID of 0 (Tables 6.43 to 6.48). Consequently, the ID results are of practical use even if only the taxa with a diversity index of 0 are considered to have predictive value. Nonetheless, a higher taxonomic group that has an ID greater than 0 for a particular attribute may also be sufficiently uniform to have reasonable predictive value for that attribute. As for CV*, the higher taxonomic groups that are located towards the top of each of the tables of ID results for different attributes (Tables 6.43 to 6.48) are most likely to have predictive value for the

relevant attributes, whilst the groups that are located towards the bottom of each table are least likely to have predictive value.

CV* and ID are both measures of how variable a genus or family is with regard to a particular attribute. Phylogenetic conservatism results in an attribute being essentially unvarying within a taxonomic group, so groups with low CV* or ID for a particular attribute are phylogenetically conservative with respect to that attribute. Predictive value, therefore, is a consequence of phylogenetic conservativeness. Independent adaptation results in an attribute being highly variable within a taxonomic group, so groups with high CV* or ID for a particular attribute are independently adapted with respect to that attribute. Lack of predictive value, therefore, is a consequence of independent adaptation. If the species in a genus or family are independently adapted with respect to a particular attribute, then those species are likely to be quite precise indicators of the ecological conditions to which that attribute is related.

6.2.2 Temporal stability

In addition to higher taxonomic groups having predictive value, if an attribute varies little (i.e. has a low CV* or ID) within a particular higher taxonomic group, then it is probable that the species within that group have undergone little recent evolutionary change with respect to that attribute. If this is the case, then it is reasonable to assume that contemporary measurements of that attribute in that particular taxonomic group are relevant to the past. Conversely, if an attribute varies considerably (i.e. has a high CV* or ID) within a particular higher taxonomic group, then this suggests that the species within that group have undergone considerable recent evolutionary change with respect to that attribute. If this is the case, then contemporary measurements of that attribute in that particular taxonomic group may not be relevant to the past.

The significance of this for archaeobotanical and palaeopalynological applications is that it provides a means of identifying which *contemporary* measurements of functional attributes can reliably be applied to *ancient* plant remains. Thus, in a higher taxonomic group with a low CV* for canopy height, contemporary canopy height measurements for the species within that group can be applied with some confidence to ancient remains of the same species.

Similarly, if a higher taxonomic group has a low ID for vegetative spread, then contemporary vegetative spread measurements for the species within that group can be applied with some confidence to ancient remains of the same species. Henceforth, if a higher taxonomic group is considered to have a low enough CV* or ID for a particular attribute that measurements of that attribute are relevant to the past, then it is referred to as being 'temporally stable' with respect to that attribute.

Thus, the tables of results for CV* (Tables 6.24 to 6.42) and ID (Tables 6.43 to 6.48) provide data by which the second objective of this thesis can be met:

2. To determine which present-day ecological preferences of plant species are reliable indicators of the ecological preferences of the same species in the past.

As for predictive value, it is impossible to be sure when a higher taxonomic group has a sufficiently low CV* or ID to be considered temporally stable with respect to a particular attribute. As a general rule for the CV* and ID results, however, the species belonging to the higher taxonomic groups that are located towards the top of each of the tables of results for different attributes (Tables 6.24 to 6.48) are most likely to have temporal stability for the relevant attributes, whilst the species belonging to the groups that are located towards the bottom of each table are least likely to have temporal stability.

6.2.3 Overall variability of individual genera and families

The tables of results for CV* (Tables 6.24 to 6.42) and ID (Tables 6.43 to 6.48) show which ARCHFIBS genera and families have high or low predictive value and temporal stability for particular functional attributes. It is also possible to identify those higher taxonomic groups which, according to their CV*s and IDs, have relatively high or low predictive value and temporal stability for a wide variety of functional attributes.

If a higher taxonomic group has (a) high predictive value and (b) high temporal stability for a wide variety of functional attributes, then considerable ecological inferences can be drawn from ancient plant remains identified to that group (but not to species). If, however, a higher taxonomic group has (a) low

predictive value and (b) low temporal stability for a wide range of functional attributes, then few if any ecological inferences can be drawn from ancient plant remains identified to that group.

6.2.3.1 Comparison of rank order variability between higher taxonomic groups

The overall predictive value and temporal stability of individual higher taxonomic groups can be assessed by calculating the mean variability of each group for a set of functional attributes. For ARCHFIBS functional attributes measured on a ratio-scale, the variability of higher taxonomic groups is calculated by the coefficient of variation (CV*). For other ARCHFIBS functional attributes, measured on a nominal-scale, the variability of higher taxonomic groups is calculated by an index of diversity (ID). These two methods of calculating variability produce results on different scales, so it is not possible to average raw CV* results for a taxonomic group with raw ID results for the same group. If the ratio-scale and nominal-scale attributes are to be considered together, therefore, it is necessary to convert the raw results to a standard form (Fieller pers. comm.). This was achieved by ranking the CV* and ID results for various functional attributes and calculating the mean variability *rank* for each ARCHFIBS genus and family.

It was not appropriate to include all the functional attributes in the calculations of mean variability ranks for ARCHFIBS genera and families. This is because some of the attributes for which CV* and ID have been calculated are not mutually independent. For instance, dry leaf weight (the weight of one gram of dry leaf material) is used in the calculation of DMC, SLA and leaf weight per node. In such circumstances that single measurement influences the CV* and/or ID ranks of the genera and families for each of the attributes to which it contributes. If the ranks for each of these attributes were included in the calculation of a taxonomic group's mean rank, that measurement would, therefore, have an exaggerated influence on the result. Consequently, the number of attributes included in the calculation of mean rank was reduced so that each FIBS measurement contributes to only one attribute. When choosing

between attributes, preference was given to those that are considered to be most ecologically significant and ecologically stable.

In some cases a single attribute is calculated from two different attributes, and all three of these attributes are essentially measures of the same ecological factor. For instance, canopy dimension is simply the mean of canopy height and canopy diameter, both of which are approximations of maximum plant size. In such cases, only the compound attribute was included in the calculation of mean ranks.

Stomatal density and stomatal size are inversely related approximations of a plant's capacity to restrict transpirational water loss. Although these two attributes are calculated from different measurements, because they are closely related approximations of the same factor, only stomatal size was included in the calculation of mean ranks.

Finally, for two attributes, root diameter and leaf width, data are missing for an unusually large number of taxa. Large numbers of missing data would also affect the calculation of average ranks, so these attributes were also excluded. Table 6.49 lists the attributes that were selected and rejected for the calculation of mean variability ranks.

For each of the selected ratio-scale functional attributes, the ARCHFIBS genera and families (following the basic taxonomy) were arranged in ascending order of their CV*s and then ranked on the basis of this order. The same basic procedure was followed for the selected nominal-scale functional attributes except that, for these attributes, a number of different taxa typically share the same ID so a simple ranking would be inappropriate for such taxa. In such cases, the tied rank of all the taxa sharing the same ID was calculated, and each of those taxa was given that tied rank. The mean variability rank of each ARCHFIBS genus and family for all the selected attributes was calculated from the resulting set of ranks. Table 6.50 shows the CV* or ID rank of each of the ARCHFIBS genera and families for each of the eleven chosen attributes, and the mean rank of each genus and family.

Table 6.51 shows the mean variability ranks for all the ARCHFIBS genera and families, arranged in ascending order of rank. Perhaps unsurprisingly, all of

the ARCHFIBS families have high mean variability ranks and occur in the bottom half of Table 6.51. This suggests that all of the ARCHFIBS families are too ecologically heterogeneous to have much overall predictive value (and so could usefully be targeted for research into criteria for more precise taxonomic identification at least to the genus level), and that they are not temporally stable. Particular families may, however, have predictive value and temporal stability for particular attributes.

Of the ARCHFIBS genera, all those that are represented by 10 or more species have high mean variability and occur in the bottom half of Table 6.51. Approximately two thirds of the taxa that are represented by 5 or more species also have high mean variability and occur in the bottom half of Table 6.51. This suggests that large genera are generally likely to be too ecologically heterogeneous to have much *overall* predictive value (and so could usefully be targeted for research into criteria for more precise taxonomic identification).

6.2.3.2 Coefficient of variation/index of diversity and the two taxonomies

The majority of taxa are classified identically in the two taxonomies, and therefore have the same CV*s and IDs for both taxonomies. The CV*s for the 'basic' taxonomic groups that have been replaced by phylogenetically defined groups in the 'revised taxonomy', however, are always (and the IDs often) different to the CV*s (and IDs) for the groups that replace them.

Table 6.52 shows the *mean* difference in CV* between each of the relevant basic taxa and the revised groups for all the attributes for which data are available, and the *mean* number of rank order places separating them. It was not always possible to measure each functional attribute for each ARCHFIBS species. Consequently, for this table and Table 6.53, the number of ARCHFIBS species quoted for each basic and revised group is the mean of the number of species from those groups measured for all the functional attributes. A general pattern can be seen: if both a basic taxonomic group and the relevant group in the revised taxonomy contain a relatively large number of species, then there is relatively little difference between the mean placement (or CV*) of the basic and revised groups. If, however, both the basic and revised groups, or only the basic

group, contains few species, then there is a relatively large difference between the mean placement (or CV*) of the basic and revised groups.

Table 6.53 shows the *mean* difference in ID between each of the relevant pairs of basic and revised taxonomic groups for all the attributes for which data are available. Because a number of different taxa tend to share the same ID for a functional attribute, it was not possible to arrange these data in order of the number of rank order places separating the basic and revised groups (as in Table 6.52). Instead, this table is arranged in ascending order of the size of the difference in ID between the basic and revised groups. Although the order of the data is slightly different to that in Table 6.52, the same general pattern is evident.

These results suggest that, if a relatively large non-monophyletic traditional taxonomic group has much the same species composition as a true monophyletic group, then the CV* or ID for a given attribute of the traditional group is likely to be a good estimate of the variability of that attribute for the monophyletic group. In other circumstances, however, the CV* or ID of a non-monophyletic traditional taxonomic group for a particular attribute may be a poor estimate of the variability of that attribute for the most similar true monophyletic group.

Ideally, the use of coefficients of variation and indices of diversity to assess the predictive value and temporal stability of higher taxonomic groups should always be applied to true monophyletic groups. In the current state of phylogenetic and archaeobotanical research, however, this is not always possible, and traditional taxonomic groups are of necessity substituted for true monophyletic groups. If the available phylogenetic evidence suggests a difference between traditional taxonomic groups and true monophyletic groups, however, then it would appear preferable to use CV* and ID results based on data arranged according to the true monophyletic groups.

6.2.4 Overall variability of individual functional attributes

The nested ANOVAs showed how the total variance of individual attributes was distributed between three taxonomic levels. There were, however, two factors that limited the interpretative potential of the nested ANOVAs. Firstly, in

addition to considering how the total amount of variation is distributed between taxonomic levels it is also necessary to take into account how generally variable the different attributes are. If an attribute exhibits generally little variation, then the actual amount of variation accounted for at any taxonomic level will be low, even if the proportion of the total variation accounted for at a given level is high. Because variance is affected by differences in scale, and different attributes are measured on different scales, it was not possible to use nested ANOVAs to compare the general variability of different attributes.

Coefficients of variation can be used to overcome this problem. The mean CV* of the ARCHFIBS genera and families for a ratio-scale functional attribute is a good indication of how *generally* variable that attribute is for those taxonomic groups. Furthermore, because this statistic is not affected by differences of scale, it allows the general variability of different attributes to be compared. For instance, if the ARCHFIBS genera and families have low mean CV* for an attribute, then that attribute varies little in those groups. If the ARCHFIBS genera and families have high mean CV* for a different attribute, however, then that attribute varies relatively greatly in those groups.

Nested ANOVAs are inappropriate for use with nominal-scale data so they could not be applied to the six FIBS functional attributes that were measured on a nominal scale. The mean ID of the ARCHFIBS genera and families for a nominal-scale functional attribute can, however, be used in the same way as the mean CV* of the ARCHFIBS genera and families for a ratio-scale attribute. Table 6.54 shows the mean CV* of the ARCHFIBS genera and families for each of the ratio-scale functional attributes, and Table 6.55 shows the mean ID of the ARCHFIBS genera and families for each of the nominal-scale functional attributes.

The second factor that limits the interpretative potential of the nested ANOVAs is that there are two possible explanations for a high level of variance being accounted for at a particular taxonomic level. This circumstance could either be the result of high variance in most taxa at that level or the result of considerable differences in variance between taxonomic groups at that level. Because the nested ANOVAs give no details of the variance of individual

taxonomic groups, they are insufficient to suggest which of these interpretations is correct.

Histograms of CV* can be used to overcome this problem. Histograms provide a useful means of graphically describing the CV* data for individual attributes: they illustrate any trends in the data and show similarities and differences between functional attributes. The difference between an attribute for which most genera are highly variable and an attribute for which there are considerable differences in variability between genera is, therefore, made clear by histograms of the CV*s of the ARCHFIBS genera for those attributes. By plotting histograms of ID, it is also possible to identify trends in the variance of individual taxonomic groups for the nominal-scale attributes.

Figure 6.3 shows histograms of CV* of the ARCHFIBS genera for each of the ratio-scale functional attributes, and Figure 6.4 shows histograms of CV* of the ARCHFIBS families for the same attributes. Figure 6.5 shows histograms of ID of the ARCHFIBS genera for each of the nominal-scale functional attributes, and Figure 6.6 shows histograms of ID of the ARCHFIBS families for the same attributes.

Because only the CV* results for the ratio-scale attributes are relevant to the nested ANOVAs, the variability of the ratio-scale and nominal-scale attributes will be considered separately. Conclusions based on the CV* results will be applied to the interpretation of the nested ANOVAs.

6.2.4.1 Ratio-scale attributes

For all ratio-scale attributes, the mean CV* of the families is greater than that of the genera. The attributes can, however, be divided into rough groups (A-D) on the basis of varying mean CV* of the genera and families (see Table 6.54, Figs. 6.3 and 6.4).

Group A (endopolyploidy, seed shape, cell wall undulation, DMC, leaf width and stomatal density):

Mean CV*s are relatively low (<15) for both the ARCHFIBS genera and families. The difference between the two means for genera and families is

always small. These attributes, therefore, are particularly unvarying within the ARCHFIBS genera and families.

The histograms for the ARCHFIBS genera show that the majority have a low CV* for these attributes. There is little difference in CV* between the ARCHFIBS genera. The majority of ARCHFIBS families also have a low CV* for these attributes (although this is less pronounced for leaf width than for the other attributes). There is very little difference in CV* between the ARCHFIBS families, indeed the range of CV*s is even less than for the ARCHFIBS genera.

Group B (leaf thickness, leaf area:thickness, canopy dimension, SLA, canopy height, leaf area per node, stomatal size epidermal cell size and canopy diameter):

Mean CV*s for both ARCHFIBS genera and families are moderate (between 10 and 22). The difference between the two means for genera and families is always small. These attributes, therefore, are moderately variable within the ARCHFIBS genera and families.

The histograms for the ARCHFIBS genera show that, whilst many have a low CV* for these attributes, a considerable number have a more moderate CV*. For both canopy height and canopy diameter, a single outlying genus has a very high CV*. For these attributes, therefore, there are quite large differences in CV* between some ARCHFIBS genera.

The histograms for the ARCHFIBS families show that, although a few families have quite a low CV* for these attributes, the majority have a more moderate CV*. No families have a very low CV* for these attributes. For leaf thickness and SLA, there is little difference in CV* between the ARCHFIBS families. For the other attributes, there are quite large differences in CV* between some ARCHFIBS families, although this is less pronounced than for the genera.

Group C (seed longevity, seed weight and leaf weight per node):

Mean CV* for the ARCHFIBS genera is moderate (between 10 and 25) but that for the families is high (>25). In all cases, the difference between these two means is great. These attributes, therefore, are moderately variable within the ARCHFIBS genera, but highly variable within the ARCHFIBS families.

For seed longevity and seed weight, the histograms for the ARCHFIBS genera show that some have a low CV*, but a smaller number have a moderate CV* and a few have a particularly high CV*. For leaf weight, similar numbers of genera have low, moderate and high CV*s, and a few have a very high CV*. For all these attributes there are large differences in CV* between many of the genera.

The histograms for the ARCHFIBS families show that the majority have a moderate CV*, but some have a high CV* and a few have a very high CV*. There is a slightly smaller range of CV*s for the ARCHFIBS families compared to the genera, but nonetheless there are quite large differences in CV* between some of the families.

Group D (root diameter):

Mean CV*s for both the ARCHFIBS genera and families are high (>25) and the difference between the two means is small. This attribute, therefore, is highly variable within the ARCHFIBS genera and families.

The histogram for the ARCHFIBS genera shows that a few have a low CV* for this attribute, but similar amounts have a moderate or a high CV*, and a few have a very high CV*. There are large differences in CV* between many of the genera. The histogram for the ARCHFIBS families shows that a few have a low CV* for this attribute, but more have a moderate or a high CV*. There are large differences in CV* between many of the families.

*6.2.4.2 CV*s of ratio-scale attributes combined with nested ANOVA results*

Table 6.56 summarises the nested ANOVA results of section 6.1.1 and the CV* results of section 6.2.3.1 for the ratio-scale functional attributes. The final column of this table shows ten groups of attributes that are similar in both sets of results, and those ten groups are the basis of the following discussion. For each of these attribute groups, the combined ANOVA/CV* results will be used to indicate general tendencies towards phylogenetic conservativeness or independent adaptation within the ARCHFIBS genera and families. Where the

nested ANOVA results are ambiguous, the CV* results will be used to indicate which possible interpretation of the ANOVA results is correct.

Group I (cell wall undulation, seed shape):

For these attributes, the nested ANOVA and CV* results are in clear agreement: the nested ANOVAs show little variation in these attributes at either the genus or family levels, and most genera and families have a low CV*. This overall pattern of low variation confirms that the ARCHFIBS genera and families tend to be phylogenetically conservative for these attributes.

Group II (seed longevity):

For this attribute, the CV* results refine interpretation of the nested ANOVAs. Whereas the nested ANOVA results suggest that the ARCHFIBS genera are all phylogenetically conservative for seed longevity, only some of the genera have a low CV* for this attribute. Only those genera are truly phylogenetically conservative. Most other genera have a moderate CV*, so are neither phylogenetically conservative nor highly independently adapted for this attribute.

The CV* and nested ANOVA results both indicate that the families are more variable for seed longevity than the genera. However, most families have a moderate CV* rather than a high CV*, so the ARCHFIBS families are also generally neither phylogenetically conservative nor highly independently adapted for this attribute.

Group III (leaf width, stomatal density):

The nested ANOVAs for these attributes suggest a variety of possible interpretations and the CV* results indicate which of these is correct. The majority of the ARCHFIBS genera and families have a low CV* for these attributes, so the equal (and low) percentage of variation at the genus and family levels in the nested ANOVAs is a result of low variation within and between both genera and families. This pattern of generally low variation indicates that the ARCHFIBS genera and families tend to be phylogenetically conservative for these attributes.

Group IV (stomatal size, epidermal cell size):

The nested ANOVA results for these attributes are essentially similar to those for Group III, but in this case the CV* results suggest a different interpretation. Whilst some genera and a few families have a low CV* for these attributes, the majority of both genera and families have a moderate CV*. The essentially equal (and low) percentage of variation at the genus and family levels in the nested ANOVAs is, therefore, a result of the variation within genera and families being similar but moderate. There are also quite considerable *differences* in CV* both between genera and between families, and this contributes to the equal division of variation between those taxonomic levels in the nested ANOVAs.

This pattern of generally moderate variation suggests that neither the ARCHFIBS genera nor families show an overall trend towards phylogenetic conservatism or independent adaptation.

Group V (endopolyploidy, DMC):

For these attributes, the nested ANOVA and CV* results for the families are in agreement: the nested ANOVAs show little variation accounted for at the family level, and most families have a low CV*. This low variation indicates that the ARCHFIBS families tend to be phylogenetically conservative for these attributes.

For the genera, however, the CV* results refine interpretation of the ambiguous nested ANOVA results. Although a relatively large amount of variance is accounted for at the genus level compared to the family level in the nested ANOVAs, most genera *and* families have a low CV* for these attributes. Low mean CV*s at both taxonomic levels demonstrate that these are particularly unvarying attributes overall, so there is in fact very little *absolute* variance accounted for at either the genus or family level in the nested ANOVAs. The *relatively* high proportion of variance accounted for at the genus level compared to the family level in the nested ANOVAs is, therefore, likely to be a result of the slightly greater difference in CV* between the groups at the genus level. The ARCHFIBS genera, therefore, tend also to be phylogenetically conservative for these attributes.

Group VI (leaf area:thickness, canopy height, leaf area per node):

Some genera and a few families have a low or high CV* for these attributes, but the majority of genera and families have a moderate CV*. The essentially equal (and moderate) percentage of variation at the genus and family levels in the nested ANOVAs is, therefore, largely a result of the variation within genera and families being similar and moderate. There are also quite considerable *differences* in CV* between both genera and families, and this contributes to the equal division of variation between those levels in the nested ANOVAs.

This pattern of generally moderate variation suggests that neither the ARCHFIBS genera nor the families show an overall trend towards phylogenetic conservatism or independent adaptation. This group of attributes is, therefore, very similar to Group IV. The two groups differ in that the variation is spread evenly between all three levels (genus, family and dataset) in the nested ANOVAs for Group IV, whereas for Group VI the variation is spread evenly between only the genera and families.

Group VII (seed weight, leaf weight):

The nested ANOVAs for these attributes are essentially similar to those for Group VI, but in this case the CV*s suggest a slightly different interpretation. For these attributes, there is no overall trend towards low, moderate, or high CV*s for either the genera or families. There are, however, particularly large *differences* in CV* between genera and between families. Consequently, it seems that the amount of variation accounted for at the genus and family levels in the nested ANOVAs is essentially equal (and moderate) for these attributes because of the *differences* in variation between taxa at both levels, not because all taxa have similar variation.

Although the genera or families are neither *usually* phylogenetically conservative nor independently adapted for these attributes, it should be noted that a relatively high proportion of ARCHFIBS genera and particularly families do have a high CV* for these attributes and so have undergone considerable independent adaptation.

Group VIII (canopy dimension, SLA, canopy diameter):

For these attributes, the nested ANOVAs suggest that genera are variable and families largely unvarying. Both genera and families tend towards moderate or low CV*s, so the high percentage of variance accounted for at the genus level is not the result of high variation within genera. It seems, therefore, that the amount of variation accounted for at the genus level in the nested ANOVAs is higher than at the family level because of the greater *differences* in variation between genera than between families.

The pattern of generally moderate variation suggests that neither the ARCHFIBS genera nor the families show an overall trend towards phylogenetic conservatism or independent adaptation, although the genera are more often conservative than the families.

Group IX (leaf thickness):

The nested ANOVAs suggest that genera are moderately variable and families largely unvarying. Some genera have a low CV* for leaf thickness, but some genera and all families have a moderate CV*, so the higher percentage of variance accounted for at the genus level is not the result of high variation within genera. There are, however, moderate *differences* in CV* between genera and very little between families. Therefore, the amount of variation accounted for at the genus level in the nested ANOVAs is higher than that at the family level family because of the greater *differences* in variation between genera.

The pattern of generally moderate variation suggests that neither the ARCHFIBS genera nor the families show an overall trend towards phylogenetic conservatism or independent adaptation, although the genera are more often conservative than the families.

Group X (root diameter):

The nested ANOVAs suggest that genera are moderately variable and families largely unvarying. Both the genera and the families have similar amounts of low, moderate and high CV*s, however, so the higher percentage of variance accounted for at the genus level is not the result of generally high variation within genera. There are, however, extreme *differences* in CV*

between genera and slightly less between families. The amount of variation accounted for at the genus level in the nested ANOVAs is, therefore, higher than that at the family level because of the greater *differences* in variation between genera.

The wide range of variability for root diameter means that a small proportion of ARCHFIBS genera and families show signs of considerable independent adaptation of this attribute, and a similar proportion show signs of considerable phylogenetic conservatism, but the majority show no strong trend in either direction.

Summary

When considering the nested ANOVAs alone it was suggested that there are only two ratio-scale attributes for which a high proportion of ARCHFIBS genera and families are phylogenetically conservative: seed shape and epidermal cell wall undulation. When the CV* results are considered alongside the nested ANOVAs this list can be extended to include: leaf width, stomatal density, endopolyploidy, DMC and leaf thickness. Together these are the ratio-scale attributes that have the greatest potential for allowing ecological inferences to be drawn from plant remains identified only higher taxonomic groups and for projecting these inferences into the past. The nested ANOVA results suggested that a high proportion of ARCHFIBS genera, but not families, are phylogenetically conservative for seed longevity, and the CV* results confirm this. Seed longevity, therefore, also has considerable potential in this respect, although only for plant remains identified to genus.

The nested ANOVA results alone suggested that a high proportion of ARCHFIBS genera and families are considerably independently adapted for five attributes: leaf weight, canopy height, leaf area, seed weight and leaf area:thickness. In contrast, the CV* results suggest that there are no ratio-scale attributes for which a high proportion of ARCHFIBS genera and families are considerably independently adapted. When the CV* results are considered alongside the nested ANOVAs, those ratio-scale attributes for which the ARCHFIBS higher taxonomic groups show the strongest trend towards considerable independent adaptation are: leaf weight, root diameter and seed

weight. The attributes may provide the most precise indication of ecological conditions for plant remains identified to species.

For the remainder of the ratio-scale attributes, the ARCHFIBS genera and families are neither phylogenetically conservative overall nor considerably independently adapted overall. It is therefore necessary to look at the specific functional attributes of particular genera and families to determine which show independent adaptation and which are phylogenetically conservative (see Section 6.2.4).

6.2.4.3 Nominal-scale attributes

The nominal-scale attributes were divided into two groups (Y and Z) based on the mean ID of the ARCHFIBS genera and families for each attribute (Table 6.56). Mean IDs and histograms of ID (Figs. 6.5 and 6.6) will be discussed for each of these groups. For all nominal-scale attributes (as for ratio-scale attributes), the mean ID of the families is greater than that of the genera.

Group Y (flowering start, stomatal distribution and vegetative spread):

For these three attributes, the mean IDs of the ARCHFIBS genera are relatively low (<0.3) and the mean IDs of the ARCHFIBS families are moderate (0.4 – 0.6). The difference between the two means for genera and families is always moderate.

The histograms for the ARCHFIBS genera show that the majority have a very low ID for these attributes, but a few have medium or high ID. This pattern of generally low variation indicates that the ARCHFIBS genera tend to be phylogenetically conservative for these attributes.

The histograms for the ARCHFIBS families suggest a somewhat different pattern of adaptation for each attribute. For flowering start, some families have a low or high ID, but most have a moderate ID, so the families do not exhibit a strong trend towards either phylogenetic conservatism or independent adaptation. For stomatal distribution, a relatively high proportion of families have a low ID and so are phylogenetically conservative. Most families have a moderate or high ID for this attribute, however, so this is not a particularly strong trend. For vegetative spread, quite a high proportion of the ARCHFIBS

families have a high ID and so are considerably independently adapted. Some families have a low or moderate ID for this attribute, however, so again this is not a particularly strong trend.

Group Z (life history, flowering period, and flowering length):

The mean ID of the ARCHFIBS genera is moderate (between 0.4 and 0.5). The mean ID of the ARCHFIBS families is considerably higher (between 0.6 and 0.8). For these three attributes, therefore, the mean IDs of both the genera and families are higher than those of the group Y attributes.

Compared to group Y, the histograms for the group Z attributes show a more even spread of genera from low to high ID, with a slight emphasis on low and moderate IDs. The ARCHFIBS genera, therefore, do not show an overall trend towards either phylogenetic conservatism or independent adaptation for these attributes.

For life history and flowering period, there is also a more even spread of families from low to high ID compared to Group Y, although there is an emphasis on moderate and high IDs and there are no families with very low IDs. The ARCHFIBS families tend towards independent adaptation for these attributes, therefore, but the trend is not particularly strong. For flowering length, all families have a high ID, so are considerably independently adapted.

Summary

Amongst the nominal-scale variables stomatal distribution has the highest proportion of genera and families which are phylogenetically conservative and therefore has the greatest potential for allowing ecological inferences to be drawn from plant remains identified only to higher taxonomic groups, and for projecting these inferences into the past. Flowering start and vegetative spread, for which a high proportion of genera, but not families, are phylogenetically conservative, also have considerable potential in this respect. None of the nominal-scale attributes have a high proportion of both genera and families or genera alone that are independently adapted.

As for CV*, more useful information can be gained from considering specific functional attributes in relation to particular taxonomic groups (see below).

6.2.5 Variability of taxonomic groups and attributes combined

So far the analyses have considered a) how variable individual taxonomic groups are with respect to functional attributes in general, and b) how variable particular functional attributes are for taxonomic groups as a whole. In this section, the variation of specific functional attributes in relation to individual taxonomic groups will be considered to determine more precisely *which* functional attributes are phylogenetically conservative (or independently adapted) for *which* taxonomic groups.

This was done using the ordination technique 'correspondence analysis'. It would be inappropriate to perform correspondence analysis on data composed of a mixture of different types of measurement, for instance CV* and ID. So that the variability of taxonomic groups with respect to both ratio-scale and nominal-scale attributes could be analysed together, the CV* and ID ranks for each taxonomic group, previously used to assess the overall variability of individual taxonomic groups (Table 6.50), was also used here. As before, the total set of FIBS attributes was reduced to a subset in which no attributes shared data measurements, or were inversely related approximations of the same environmental factors. Only those attributes for which data were available for the great majority of ARCHFIBS species were included. Taxonomic groups that were missing data for one or more of the remaining attributes were excluded from these analyses (13 out of 66 genera, but no families). Genera and families were analysed separately.

For both correspondence analyses (genera and families), the first two correspondence axes are plotted against one another. If a taxon is located away from the centre of the plot and in the same direction as one or more functional attributes, then that taxon will have a high CV* or ID rank for most or all of those attributes. That taxon has therefore undergone considerable independent adaptation for most or all of those attributes. Conversely, if the same taxon is located in the opposite area of the plot to one or more functional attributes, then that taxon will have a low CV* or ID rank for most or all of those attributes. That taxon is therefore phylogenetically conservative for most or all of those attributes. The further from the centre of the plot a taxon and functional

attribute are located, the more phylogenetically conservative or independently adapted the taxon is for that attribute.

The relationship between functional attributes and taxa located near the centre of the plot is more complicated. Taxa located near the centre of the plot may have high CV* or ID ranks for the attributes also located near the centre. Alternatively, taxa located near the centre of the plot may be essentially 'neutral', that is, they do not have particularly high or low CV* or ID ranks for any functional attributes. Finally, taxa near the centre of the plot may have approximately equally high or low CV* or ID ranks for attributes that are located away from the centre of the plot, but in opposite directions to one another.

Some of the taxa located near the centre of the plot may be explored further by plotting the third and fourth axes from the same correspondence analysis. These axes account for less of the variation in functional attributes between taxa than do axes 1 and 2. However, the relationship between functional attributes and taxa that are located towards the centre of the plot of the first two axes is, in some cases, clearer from the plot of the third and fourth axes.

Some genera and one family are located near the centre of the plots of both axes 1 and 2 and of axes 3 and 4. Examination of the functional attribute ranks for these taxa (Tables 6.50) shows that they tend to have particularly high or low CV* or ID ranks for attributes located near the centre of the plots for both sets of axes, and/or for attributes located away from the centre of the plots, but in opposite directions to one another. It is not the case that these genera and families are neutral for the functional attributes.

Attributes which tend to be variable (or unvarying) in the same taxa tend to be located in the same direction from the origin. Figures 6.7-6.8 show plots of the correspondence analysis for the ARCHFIBS genera, Figures 6.9-6.10 for the ARCHFIBS families.

In Figure 6.7, where axis 1 is plotted against axis 2, both cell size and stomatal density tend to be variable for genera located in the bottom left quadrant of the plot; and stomatal distribution, leaf area:thickness and DMC for genera located in the bottom right quadrant of the plot. The upper two quadrants of the plot are each dominated by a single attribute: life history tends

to be variable in genera where stomatal density and cell size tend to be unvarying, while cell wall undulation tends to be variable in genera where stomatal distribution, leaf area:thickness and DMC show little variation. Genera distinguished on the third and fourth correspondence axes tend to be distinguished by different combinations of attributes (Fig. 6.8). The functional attributes for which each genus is most independently adapted (highly variable) or phylogenetically conservative (relatively unvarying) are listed in Table 6.57.

The relationship of functional attributes on the first two axes for the correspondence analysis of families broadly reflects that for the genera. In particular, as for genera, cell wall undulation tends to be variable in families in which leaf area:thickness and DMC are not and vice versa; life history is variable in families where stomatal density is not; and cell size is variable where stomatal distribution is not (Figure 6.9). The similarity between the functional attributes in distinguishing genera and families of the third and fourth axes is less strong, though families, like genera, which are highly variable for canopy dimension and seed longevity have low variability for DMC, cell wall undulation and stomatal density (Figure 6.10). The functional attributes for which each family is most independently adapted or phylogenetically conservative are listed in Table 6.58.

Similarities in the overall relationship of functional attributes to families and genera reflect specific instances in which the same attributes have high (or low) variation for genera and the families to which they belong. All such instances discussed below are evident only from the plots of axes 1 and 2 (Figs. 6.7 and 6.9).

Chenopodiaceae shows the strongest correspondence in the variability of functional attributes between a family and its genera. Stomatal distribution, DMC and leaf area:thickness are all variable for Chenopodiaceae, whereas cell wall undulation and epidermal cell size are unvarying. All the same attributes are variable for both the Chenopodiaceae genera represented (*Chenopodium* and *Atriplex*), and cell wall undulation and, to a lesser extent, epidermal cell size are unvarying. For both Poaceae and Polygonaceae, leaf area:thickness, stomatal density and, to a lesser extent, DMC are variable, whereas cell wall undulation and life history are unvarying. A similar pattern of variation in

functional attributes is evident for most of the Poaceae genera represented (*Avena, Lolium, Bromus, Poa, Anisantha, Bromopsis, Festuca,* and *Setaria*), but not for *Holcus* or *Phalaris*. Of the Polygonaceae genera, a very similar pattern of variation is evident for *Rumex*, but not for *Polygonum* or *Persicaria*.

In other instances, the correspondence in the variability of functional attributes between a family and its genera is considerably weaker. Stomatal distribution is unvarying for Rosaceae and for the genera *Prunus* and *Rubus*, but otherwise attributes vary differently for the family and its genera. Some of the same attributes are variable or unvarying for Ranunculaceae and the genus *Thalictrum*, but not for *Ranunculus* or *Adonis*. Stomatal distribution and life history are both unvarying for Rubiaceae and *Rubia*, but different attributes are variable for the family and its genera. (Stomatal distribution is also completely unvarying for *Galium*, another genus in the same family, but this is not evident from Figure 6.7 because *Galium* is located towards the centre of the plot). Life history is variable and stomatal density is unvarying for Boraginaceae and the genera *Anchusa* and *Myosotis*, however, other attributes vary differently for these three taxa. There is no similarity in the variation of functional attributes between Fabaceae and any of its genera. However, the same attributes are variable and unvarying for the genera *Lathyrus* and *Vicia*, which both belong to the Fabaceae tribe *Vicieae.*

No clear correspondence in the variability of functional attributes between a family and its genera can be distinguished for Apiaceae, Asteraceae, Brassicaceae, Caryophyllaceae, Lamiaceae, Papaveraceae or Scrophulariaceae. This suggests that an evolutionary line that is phylogenetically conservative for particular attributes at one point in time is likely to undergo independent adaptation of that attribute at a later stage of evolution, and vice versa. Those cases in which families and some of their genera are phylogenetically conservative or independently adapted for the same attributes are an exception to this general rule.

Chapter 7 – Application of functional attribute data for higher taxonomic groups to present-day surveys of arable weed floras

In the previous chapter, it was noted that there is no simple means of deciding when a taxonomic group has sufficiently low CV*/ID to have predictive value for a particular attribute. The goal of this chapter is to determine whether or not this can de decided from the results of applying functional attribute values calculated for higher taxonomic groups to ecological studies based on the functional attributes of species. Two simple methods for calculating the functional attribute values of higher taxonomic groups will be described, and the resulting values will be incorporated into studies of the functional attributes of agricultural weed species.

Although these methods are intended for application to unspeciated plant material in assemblages of ancient plant remains, their potential will be investigated with reference to known plant species occurring as weeds in modern crop fields. Modern crop weeds were chosen as the source of ecological evidence because there are readily available modern crop weed studies in which the relationship of species functional attributes to agricultural regimes is known. Consequently, the relationship between higher taxonomic group functional attributes and particular agricultural regimes can be tested in circumstances where the relationship between species functional attributes and agricultural regimes has already been established. For any assemblage of ancient plant remains, the agricultural practices applied to the crops (and the ecological conditions in which the weeds grew) are unknown.

As described in Chapter 3, a number of modern weed studies (Charles *et al.* 1997; Bogaard *et al.* 1999, 2001; G. Jones *et al.* 2000) have used the same functional attributes measured for this thesis to determine the ecological characteristics of the weed communities that distinguish a variety of agricultural regimes. In this chapter, functional attribute values for higher taxonomic groups

will be substituted for the species functional attribute values in correspondence analysis plots from these studies. This will indicate whether functional distinctions between the plants typical of different agricultural regimes are evident when only the functional attributes of higher taxonomic groups are known. Where this is not the case, it will be determined how low a CV*/ID higher taxonomic groups must have for the functional distinctions to be apparent.

7.1 Methods

7.1.1 Methods for determining functional attribute values for higher taxonomic groups

Because of the different nature of the data, different methods were used to determine the functional attribute values of higher taxonomic groups for ratio-scale and nominal-scale attributes.

7.1.1.1 Ratio-scale attributes

For each ratio-scale attribute, the value for an ARCHFIBS genus (or family) was calculated as the mean of the values for that attribute for all the ARCHFIBS species belonging to the genus (or family).

7.1.1.2 Nominal-scale attributes

Because species have no *numeric* value for nominal-scale attributes, it is not possible to calculate mean genus or family values for these attributes. Instead, if over half the ARCHFIBS species in a higher taxonomic group belong to a particular category of a nominal-scale attribute, then that category is taken as the functional attribute value for the group. Henceforth, such categories will be referred to as 'dominant' categories. In some cases, the ARCHFIBS species in a higher taxonomic group are distributed amongst the categories of a nominal-scale functional attribute such that no category is dominant (in other words, no single category accounts for the majority of species in the group). If a higher taxonomic group does not have a dominant category for a particular attribute, then no functional attribute value can be calculated for the group, and it is considered functionally neutral.

7.1.2 Methods for applying functional attribute values for higher taxonomic groups to correspondence analyses from ARCHFIBS studies

Four published weed studies used correspondence analysis to investigate the effect of different agricultural regimes on the composition of crop weed floras: irrigation and dry farming in Borja, Spain (G. Jones *et al.* 1995); crop rotation regime in Irbid, Jordan (Palmer 1998); garden- and field-scale cultivation in Evvia, Greece (G. Jones *et al.* 1999); autumn and spring crop sowing in Germany (Hüppe and Hofmeister 1990; Bogaard *et al.* 2001). For each of these studies, the correspondence analyses demonstrated that there are differences in weed flora between fields (or, in the case of Germany, phytosociological associations) under different agricultural regimes. Subsequent studies (Charles *et al.* 1997; Bogaard *et al.* 1999, 2001; G. Jones *et al.* 2000) used functional attribute data for the species recorded to interpret the correspondence analysis plots of the species distinguishing different regimes. These studies show how the functional attribute measurements of *species* pattern in relation to various agricultural regimes. To test the potential for using functional attribute values calculated for higher taxonomic groups, attribute values of *genera* and *families* have been used in place of measured species functional attributes in correspondence analysis plots distinguishing the various agricultural regimes.

Many of the species included in the weed surveys (Hüppe and Hofmeister 1990; G. Jones *et al.* 1995, 1999; Palmer 1998) belong to the genera and families considered in this thesis. As a first step in the evaluation of functional attribute values for higher taxonomic groups the original correspondence analysis plots of species showing functional attributes (Charles *et al.* 1997; Bogaard *et al.* 1999, 2001; G. Jones *et al.* 2000) were replotted using only those species belonging to ARCHFIBS genera. This is because it is important for the evaluation that the same patterning in relation to agricultural regime is still evident in the plots which show only species that belong to ARCHFIBS genera (henceforth referred to as plots of decreased species) as in the original plots showing all the species recorded. Any correspondence analysis plot for which this was not the case was excluded from further investigation and the plots are not shown here. Clear patterning of species in relation to agricultural

regime was not evident in the plots of decreased species for *any* of the functional attributes used in the original Irbid study (Bogaard *et al.* 1999), so the Irbid study was totally excluded from further investigation.

Figure 7.1 shows the correspondence analysis plots of fields/weed associations for the Borja (G. Jones *et al.* 1995; Charles *et al.* 1997), Evvia (G. Jones *et al.* 1999, 2000) and Germany (Bogaard *et al.* 2001) weed surveys. The fields (or, in the Germany study, phytosociological associations) are classified according to the agricultural regimes considered in each study. These plots were compared with the plots of species for the same studies (Figs. 7.2 to 7.23) to identify patterning in the functional attribute data which related to agricultural regime.

For ratio-scale attributes, where clear patterning in relation to agricultural regime was evident in the plots of decreased species, each species was reclassified according to the functional attribute value of its genus. For nominal scale attributes, however, functional attribute values cannot necessarily be calculated for all genera because some of them are functionally neutral for these attributes. Species from these genera cannot be reclassified, and so they retain their original classification in the plots of decreased species. The reclassification process is best explained by an example:

Figure 7.2a is the original plot of all species classified according to canopy height from the Borja irrigation study (Charles *et al.* 1997). Figure 7.2b is the plot of decreased species for the same study and attribute. The species in the taller canopy class (≥ 60 cm) are mostly located in the area to the left of the plot that is associated with irrigated fields (cf. Figure 7.1a). In Figure 7.2c each species has been reclassified according to the canopy height value of its genus. For example, the data-point indicated by an arrow in Figure 7.2b represents the species *Atriplex rosea* which, when measured at Borja, had a canopy height of 45 cm, placing it in the '< 60cm' class. In Figure 7.2c, where the attribute value for this species has been replaced by the value for the genus *Atriplex*, which is 142 cm, it is classified as '≥ 60 cm'.

In this example, the pattern in functional attributes relating to agricultural regime is obscured when all species are reclassified according to the mean canopy heights of their genera. This is because many or all of the species

represented belong to genera that are not sufficiently unvarying to have predictive value for canopy height in this study. In cases where the pattern was preserved when all species values were replaced by genus values, all the genera have predictive value for the attribute in question, so the correspondence analyses were not further investigated using genus values.

For the rest, to determine how unvarying a genus needs to be in order to have predictive value in these studies, the number of species reclassified according to the functional attribute values of their genera was progressively reduced. First, those species that belong to the genus with the highest CV*/ID for the attribute were replaced by their original classification, based on the *species* value of the attribute, whilst all other species remained classified according to the attribute value of their *genus.* This process was repeated for the species from each genus, in descending order of genus CV*/ID, until a similar patterning in relation to agricultural regime was evident in the 'partially reclassified' plots as in the original plots of decreased species (based entirely on *species* values). For example, in Figure 7.2d, the pattern of canopy height relating to irrigation level is very similar to that in the original plot of decreased species (Figure 7.2b), even though a third of the species (those from the least varying genera) are reclassified according to the canopy height values of their genera.

The point at which the original plot and the plot with some species reclassified according to their genus value were considered to be similar was decided subjectively. Rather than requiring the two plots to be identical, it was required that the same conclusions about the pattern of functional attributes in relation to fields could be drawn from both the original plot and the partially reclassified plot.

Essentially the same method was used to reclassify species in terms of the functional attribute values of families but this process was carried out only for correspondence analysis plots that had already shown pattering with genus functional attribute values. Only those species belonging to an ARCHFIBS *family* were used in the correspondence analysis plots of species showing functional attributes, these species were reclassified according to the functional attributes values of their families, and so on.

In cases where the pattern in ratio-scale functional attributes relating to agricultural regime is obscured when all species are reclassified, the highest CV* value at which a species can be reclassified according to its genus/family values without considerably altering the pattern in functional attributes will be referred to as the 'cut-off CV* for predictive value'. In some cases, however, the pattern is preserved when every species is reclassified according to the CV* value of its genus, so all the ARCHFIBS genera represented in the weed study have predictive value. Consequently, it is possible that a genus with a higher CV* than any of those represented in the weed study would also have predictive value. In such cases, the CV* value of the most variable ARCHFIBS genus represented in the weed study will be referred to as the '*minimum* cut-off CV* for predictive value'.

For nominal-scale attributes, only species belonging to genera and families that have a dominant functional attribute category can be reclassified, and these genera and families have low ID compared to those that do not have a dominant attribute category. If all species belonging to genera/families with a dominant attribute category are reclassified and the pattern in functional attributes is preserved, then the ID 'cut-off' is artificial – it is not possible to determine if genera and families with higher ID would also have predictive value. In such cases, the ID value of the most variable ARCHFIBS genus/family that has a dominant functional attribute category will be referred to as the '*minimum* cut-off ID for predictive value'.

Tables 7.1 to 7.11 show whether the ARCHFIBS genera and families have a tendency towards low, moderate or high CV*/ID values for each of the functional attributes in question, or whether they are evenly distributed among the calculated values. The cut-off CV*s/IDs for predictive value of the genera and families are indicated in each of these tables.

7.2 Application of the methods to correspondence analysis plots of species classified according to functional attributes

In the decreased plots of species based on the correspondence analyses of the modern weed studies, eight of the FIBS functional attributes showed

patterning in relation to agricultural regime. Each of these eight functional attributes is considered separately here. If an attribute showed patterning in relation to agricultural regime in more than one study, then these methods were followed for each relevant study.

Tables 7.12 and 7.13 summarise the results of these comparisons for each functional attribute for which the pattern was preserved in the decreased plot of species from at least one of the three weed studies. Table 7.12 summarises the results for the plots reclassified by genus values and Table 7.13 for the plots reclassified by family values.

7.2.1 Canopy height

Canopy height exhibits patterning in relation to husbandry regime in the Borja (Charles *et al.* 1997), Evvia (G. Jones *et al.* 2000) and Germany (Bogaard *et al.* 2001) weed studies.

7.2.1.1 Borja irrigation study

The correspondence analysis plot of species classified according to canopy height from the Borja irrigation study (Charles *et al.* 1997) is presented in Figure 7.2a. The species with the tallest canopies (≥ 60 cm) are mostly located towards the negative (left) end of axis one (and, to a lesser extent, towards the positive end of axis one and negative end of axis two – bottom right). These are the areas of the plot where irrigated fields are located in Figure 7.1a (especially fully irrigated fields to the left). Species with shorter canopies (<60 cm) are more widespread in their occurrence.

Removal of species that do not belong to ARCHFIBS genera does not alter this pattern (Figure 7.2b) but reclassification of the remaining species according to the canopy height value of their genus obscures the pattern (Figure 7.2c) – species with tall canopies appear in all areas of the plot including that associated with dry farming (top right). The original pattern in canopy height becomes clear again when only the thirteen species belonging to the nine least variable genera (CV* ≤8.47) are reclassified by their genus values, the rest retaining their species value (Figure 7.2d). A CV* cut-off of 8.47 is low for canopy height (Table 7.1).

The case is similar for families (Figures 7.3) except that the original pattern in the data remains somewhat obscured even when only the six species belonging to the least variable family for canopy height (CV* 11.35, Chenopodiaceae) are reclassified according to the value of that family (Figure 7.3d). There is, therefore, no family CV* cut-off for canopy height.

In the Borja study, the genera have an essentially even distribution of CV* for canopy height, and the families all have moderate or high CV* (Table 7.1).

7.2.1.2 Evvia cultivation intensity study

The correspondence analysis plot of species classified according to canopy height from the Evvia cultivation intensity study (G. Jones *et al.* 2000) is presented in Figure 7.4a. The classes of canopy height by which species pattern in relation to agricultural regime for the Evvia cultivation intensity study differ to those for the Borja irrigation study. The species with the tallest canopies (≥85 cm) are mostly located towards the negative (left) end of axis one (and, to a lesser extent, towards the negative (bottom) end of axis two). These are the areas of the plot where fields with high fertility and low disturbance are located in Figure 7.1b. Species with shorter canopies (<85 cm) are more widespread in their occurrence.

Removal of species that do not belong to ARCHFIBS genera does not alter this pattern (Figure 7.4b), and neither does the reclassification of the remaining species according to the canopy height value of their genera (Figure 7.4c). The *minimum* cut-off CV* for these genera is 28.45, which is a high CV* for canopy height (Table 7.2).

Removal of species that do not belong to ARCHFIBS families does not alter the pattern in canopy height (Figures 7.5a and b) but reclassification of the remaining species according to the canopy height value of their family obscures the pattern (Figure 7.5c) – very few tall canopied species are present, and one is located towards the far right of the plot in the area particularly associated with low fertility. The original pattern in canopy height becomes clear again when only 39 species belonging to the six least variable families (CV* ≤15.49) are reclassified according to their family values, the rest retaining their species

values (Figure 7.5d). A CV* cut-off of 15.49 is moderate for canopy height (Table 7.2).

In the Evvia study, the genera have an essentially even distribution of CV* for canopy height, and the families all have moderate or high CV* (Table 7.2).

7.2.1.3 Germany sowing time study

The correspondence analysis plot of species classified according to canopy height from the Germany sowing time study (Bogaard *et al.* 2001) is presented in Figure 7.6a. The classes of canopy height by which species pattern in relation to canopy height for the Germany sowing time study differ to those for the Borja irrigation and Evvia cultivation intensity studies. The species with the tallest canopies (>65 cm) are mostly located towards the negative (bottom) end of axis two, where associations characteristic of spring sowing are located in Figure 7.1c. The species with the shortest canopies (<25 cm) are mostly located towards the positive (top) end of the same axis, where associations characteristic of autumn sowing are located in Figure 7.1c. The species with intermediate canopy heights (25-65 cm) are more widespread in their occurrence.

Removal of species that do not belong to ARCHFIBS genera does not alter this pattern (Figure 7.6b) and neither does the reclassification of the remaining species according to the canopy height value of their genera (Figure 7.6c). The *minimum* cut-off CV* for these genera is 28.45, which is a high CV* for canopy height (Table 7.3).

Removal of species that do not belong to ARCHFIBS families does not alter the pattern in canopy height (Figures 7.7a and b) but reclassification of the remaining species according to the canopy height value of their family obscures the pattern (Figure 7.7c) – species with tall canopies (>65 cm) are located throughout the diagram and there are no species with short canopies (<25 cm). The original pattern in canopy height becomes clear again when only the twelve species belonging to the four least variable families (CV* ≤13.03) are reclassified according to their family values, the rest retaining their species values (Figure 7.5d). A CV* cut-off of 13.03 is moderate for canopy height (Table 7.3).

In the Germany study, the genera tend to have quite low CV* for canopy height, and the families all have moderate or high CV* (Table 7.3).

7.2.2 Canopy diameter

Canopy diameter exhibits patterning in relation to husbandry regime in only the Evvia weed study (G. Jones *et al.* 2000).

Figure 7.8a is the correspondence analysis plot of species classified according to canopy diameter from the Evvia cultivation intensity study (G. Jones *et al.* 2000). The species with the broadest canopies (≥100 cm) are mostly located towards the negative (left) end of axis one, the area of the plot where fields with high fertility and low disturbance are located in Figure 7.1b. Species with narrower canopies (<100 cm) are more widespread in their occurrence.

Removal of species that do not belong to ARCHFIBS genera does not alter this pattern (Figure 7.8b) but reclassification of the remaining species according to the canopy diameter value of their genus obscures the pattern (Figure 7.8c) – a greater number of species with broad canopies are located towards the top and right of the plot. The original pattern in canopy diameter becomes clear again when only the fourteen species belonging to the ten least variable genera (CV* ≤13.00) are reclassified according to their genus values, the rest retaining their species values (Figure 7.8d). A CV* cut-off of 13.00 is low for canopy diameter (Table 7.4).

The case is similar for families (Figures 7.9), and the original pattern in canopy diameter becomes clear again when only the ten species belonging to the three least variable families (CV* ≤17.25) are replaced by their family values, the rest retaining their species values (Figure 7.9d). A CV* cut-off of 17.25 is moderate for canopy diameter (Table 7.4).

In the Evvia study, the genera have an essentially even distribution of CV* for canopy diameter, and the families tend to have moderate or high CV*, although one family has relatively low CV* (Table 7.4).

7.2.3 Leaf area per node

Leaf area per node exhibits patterning in relation to husbandry regime in both the Evvia (Jones *et al.* 2000) and Germany (Bogaard *et al.* 2001) weed studies.

7.2.3.1 Evvia cultivation intensity study

Figure 7.10a is the correspondence analysis plot of species classified according to leaf area per node from the Evvia cultivation intensity study (Jones *et al.* 2000). The species with the largest leaf areas (>3700 mm^2) are all located towards the negative (left) end of axis one; and the species with the smallest leaf areas (<200 mm^2) are all located towards the positive (right) end of the same axis. Thus the larger leaved species occur in the area of the plot where fields with high fertility are located in Figure 7.1b, and the smaller leaved species occur where fields with low fertility are located. The species with intermediate leaf areas (200-3700 mm^2) are more widespread in their occurrence.

Removal of species that do not belong to ARCHFIBS genera does not alter this pattern (Figure 7.10b) and neither does the reclassification of the remaining species according to the leaf area per node value of their genus (Figure 7.4c). The *minimum* cut-off CV* for these genera is 25.36, which is a high CV* for leaf area per node (Table 7.5).

Removal of species that do not belong to ARCHFIBS families does not alter the pattern in leaf area per node (Figure 7.11a and b) but reclassification of the remaining species according to the canopy height value of their family obscures the pattern (Figure 7.11c) – species with large leaf areas are located throughout the plot and there are no species with small leaf areas. The original pattern in canopy height becomes clear again when only the 43 species belonging to the eight least variable families (CV* ≤18.41) are reclassified by their family values, the rest retaining their species values (Figure 7.11d). A CV* cut-off of 18.41 moderate to high for leaf area per node (Table 7.5).

In the Evvia study, the genera have an essentially even distribution of CV* for leaf area per node, and the families all have moderate or high CV* (Table 7.5).

7.2.3.2 Germany sowing time study

The correspondence analysis plot of species classified according to leaf area per node from the Germany sowing time study (Bogaard *et al.* 2001) is presented in Figure 7.12a. With one exception, the species with the largest leaf areas (>1300 mm^2) are located towards the negative (bottom) end of axis 2. The species with the smallest leaf areas (<150 mm^2) are located towards the positive (top) end of the same axis. Thus the larger leaved species occur in the area of the plot where associations characteristic of spring sowing are located in Figure 7.1c, and the smaller leaved species occur where associations characteristic of autumn sowing are located. Species with intermediate leaf areas (150-1300 mm^2) are more widespread in their occurrence.

Removal of species that do not belong to ARCHFIBS genera does not alter this pattern (Figure 7.12b) but reclassification of the remaining species according to the leaf area per node value of their genus obscures the pattern (Figure 7.12c) - additional species with large leaf areas occur towards the top of the plot. The original pattern in leaf area per node becomes clear again when only the 25 species belonging to the 18 least variable genera (CV* ≤12.58) are reclassified according to their genus values, the rest retaining their species value (Figure 7.12d). A CV* cut-off of 12.58 is moderate for leaf area per node (Table 7.6).

The case is similar for families (Figures 7.13a-d), and the original pattern in leaf area becomes clear again when only the five species belonging to the least variable family for leaf area per node (Lamiaceae, CV* 12.07) are reclassified according to their family value, the rest retaining their species values (Figure 7.13d). A CV* cut-off of 12.07 is also moderate for leaf area per node (Table 7.6).

In the Germany study, the genera tend to have quite low CV* for leaf area per node, and the families all have moderate or high CV* (Table 7.6).

7.2.4 Leaf weight per node

Leaf weight per node exhibits patterning in relation to husbandry regime in only the Evvia weed study (Jones *et al.* 2000).

Figure 7.14a is the correspondence analysis plot of species classified according to leaf weight per node from the Evvia cultivation intensity study (Jones *et al.* 2000). The species with the largest leaf weights (> 125 mg) are all located towards the (left) negative end of axis one; and the species with the smallest leaf weights (<5 mg) are located towards the (right) positive end of the same axis. Thus the species with larger leaf weights occur in the area of the plot where fields with high fertility are located in Figure 7.1b, and the species with smaller leaf weights occur where fields with low fertility are located. Species with intermediate leaf weights (5-125 mg) are more widespread in their occurrence.

Removal of species that do not belong to ARCHFIBS genera does not alter this pattern (Figure 7.14b) but reclassification of the remaining species according to the leaf weight per node value of their genus obscures the pattern (Figure 7.14c) - species with large leaf weights are no longer only located towards the left of the plot. The original pattern in leaf weight becomes clear again when only the eleven species belonging to the eight least variable genera (CV* ≤15.37) are reclassified according to their genus values, the rest retaining their species value (Figure 7.14d). A CV* cut-off of 15.37 is low for leaf weight per node (Table 7.7).

The case is similar for families (Figures 7.15a-d), and the original pattern in leaf area only becomes clear again when only the single species belonging to the least variable family for leaf weight per node (Papaveraceae, CV* 16.10) is replaced by its family value, the rest retaining their species values (Figure 7.15d). A CV* cut-off of 16.10 is moderate for leaf weight per node (Table 7.7).

In the Evvia study, the genera have an essentially even distribution of CV* for leaf weight per node, and the families tend to have moderate or high CV*, although one family has relatively low CV* (Table 7.7).

7.2.5 Leaf area per node:leaf thickness

Leaf area per node:leaf thickness exhibits patterning in relation to husbandry regime in the Germany (Bogaard *et al.* 2001) weed study.

The correspondence analysis plot of species classified according to leaf area from the Germany sowing time study (Bogaard *et al.* 2001) is presented in Figure 7.16a. The species with the highest values (>9000 mm) are mostly located towards the negative (bottom) end of axis two; and the species with the lowest values (<1000 mm) are all located towards the positive (top) end of the same axis. Thus the species with higher values occur in the area of the plot where associations characteristic of spring sowing are located in Figure 7.1c, and the species with lower values occur where associations characteristic of autumn sowing are located. Species with intermediate values (1000-9000 mm) are more widespread in their occurrence.

Removal of species that do not belong to ARCHFIBS genera does not alter this pattern (Figure 7.16b) but reclassification of the remaining species according to the leaf area:thickness value of their genus obscures the pattern (Figure 7.16c) - additional species with large leaf area:thickness values are located towards the top of the plot. The original pattern in leaf area:thickness becomes clear again when only the 31 species belonging to the 20 least variable genera (CV* ≤12.68) are reclassified according to their genus values, the rest retaining their species values (Figure 7.16d). A CV* cut-off of 12.68 is moderate for leaf area:thickness (Table 7.8).

The case is similar for families (Figures 7.17a-d), and the original pattern in leaf area:thickness becomes clear again when only the nine species belonging to the three least variable families (CV* ≤10.47) are reclassified according to their family values, the rest retaining their species values (Figure 7.17d). A CV* cut-off of 10.47 is also moderate for leaf area:thickness (Table 7.8).

In the Germany study, the genera tend to have quite low CV* for leaf area: thickness, and the families tend to have moderate or high CV*, although one family has low CV* (Table 7.8).

7.2.6 SLA

SLA exhibits patterning in relation to husbandry regime in both the Borja (Charles *et al.* 1997) and Germany (Bogaard *et al.* 2001) weed studies.

7.2.6.1 Borja irrigation study

The correspondence analysis plot of species classified according to SLA from the Borja irrigation study (Charles *et al.* 1997) is presented in Figure 7.18a. The species with the highest SLA values (>20 mm^2) are mostly located towards the negative (left) end of axis one; the species with the lowest values (<5 mm^2) are mostly located towards the positive (top and right) ends of both axes. Thus the species with higher values occur in the area of the plot where fully irrigated fields are located in Figure 7.1a, and the species with lower values occur where dry farmed fields and those with low levels of irrigation are located. Species with intermediate values (5-20 mm^2) are more widespread in their occurrence.

Removal of species that do not belong to ARCHFIBS genera does not alter this pattern (Figure 7.18b) but reclassification of the remaining species according to the canopy height value of their genus obscures the pattern - there are no species with very low SLA, and species with high SLA are more widespread than before (7.18c). The original pattern in SLA becomes clear again when only the 17 species belonging to the thirteen least variable genera (CV* ≤9.98) are replaced by their genus values, the rest retaining their species values (Figure 7.18d). A CV* cut-off of 9.98 is moderate for SLA (Table 7.9).

The case is similar for families (Figures 7.19), and the original pattern in leaf area:thickness becomes clear again when only the fifteen species belonging to the two least variable families (CV* ≤12.45) are replaced by their family values, the rest retaining their species values (Figure 7.19d). A CV* cut-off of 12.45 is also moderate for SLA (Table 7.9).

In the Borja study, the genera have an essentially even distribution of CV* for SLA, and the families all have moderate or high CV* (Table 7.9).

7.2.6.2 Germany sowing time study

The correspondence analysis plot of species classified according to SLA from the Germany sowing time study (Bogaard *et al.* 2001) is presented in Figure 7.20a. The species with the highest SLA values (≥28 mm^2) are mostly located towards the negative (bottom) end of axis two. This is the area of the plot where spring-sown fields are located in Figure 7.1c. Species with low SLA values (<28 mm^2) are more widespread in their occurrence.

Removal of species that do not belong to ARCHFIBS genera does not alter this pattern (Figure 7.20b) and neither does the reclassification of the remaining species according to the SLA value of their genera (Figure 7.20c). The *minimum* cut-off CV* for these genera is 23.86, which is a high CV* for SLA (Table 7.10)

Removal of species that do not belong to ARCHFIBS families does not alter the pattern in leaf area per node (Figure 7.21a and b) but reclassification of the remaining species according to the canopy height value of their family obscures the pattern (Figure 7.21c) – all species have low SLA. The original pattern in SLA becomes clear again when only the 32 species belonging to the eight least variable families (CV* ≤13.55) are reclassified according to their family values, the rest retaining their species values (Figure 7.21d). A CV* cut-off of 13.55 is moderate for SLA (Table 7.10).

In the Germany study, the genera tend to have quite low CV* for SLA, and the families all have moderate or high CV* (Table 7.10).

7.2.7 Flowering period

The timing and length of the flowering period exhibits patterning in relation to husbandry regime in both the Germany (Bogaard *et al.* 2001) and Evvia (G. Jones *et al.* 2000) weed studies. The pattern in the Evvia study is obscured when non-ARCHFIBS species are removed from the plot, however, so this attribute has been explored only for the Germany study. Flowering period is the only nominal-scale functional attribute that showed sufficiently good patterning in relation to husbandry regime in the modern weed studies to allow this method to be followed.

The correspondence analysis plot of species classified according to flowering period from the Germany sowing time study (Bogaard *et al.* 2001) is presented in Figure 7.22a. Short-flowering species with early to intermediate onset of flowering are located towards the positive (top) end of axis 2. This is the area of the plot where associations characteristic of autumn sowing are located in Figure 7.1c. Both late-onset and long-flowering species tend to be located towards the (bottom) negative end of axis two. This is the area of the plot where associations characteristic of spring sowing are located in Figure 7.1c. Species

with an intermediate onset of flowering and a flowering period of medium duration are more widespread in their occurrence.

All the genera and families that have an ID of <0.50 for this attribute have a dominant flowering period category (i.e. over half the species in the genus or family belong to a single flowering period category). In these cases, the dominant category is taken as the functional attribute value for the group. In addition, the species of each genus and family that have an ID of 0.50 are evenly split between two flowering period categories: 'intermediate', which is functionally neutral, and one other functionally significant category. For these genera and families, the functionally significant category was considered dominant.

Removal of species that do not belong to ARCHFIBS genera does not alter the pattern in flowering period (Figure 7.22b). The reclassification of the 29 species belonging to the 20 genera for which flowering period value can be calculated (those with ID ≤0.50) does not alter the pattern (Figure 7.22d).

Likewise, removal of species that do not belong to ARCHFIBS families does not alter the pattern (Figure 7.23b), and neither does the reclassification of the eight species belonging to the three families for which flowering period value can be calculated (ID ≤0.50) (Figure 7.23d). The *minimum* cut-off ID for these genera and families is, therefore, 0.50, which is a moderate ID for flowering period.

In the Germany study, the genera tend to have quite low ID for flowering period, and the families all have moderate or high CV* (Table 7.10).

7.3 Discussion and conclusions

For each weed study, the species recorded are more likely to be members of one of the ARCHFIBS families than they are to be members of the particular ARCHFIBS genera selected for each family. Consequently, considerably more species are eliminated from the original plots of species to create the decreased plots for genera than to create the decreased plots for families. Because of this difference, no direct comparison of the results for genera and families can be made. The CV*/ID cut-offs for predictive value are, however, generally higher

for genera than for families, and few families have CV*/ID values below the family cut-offs. Thus, as predicted in Chapter 6, genera are overall more likely to have predictive value for a particular functional attribute than are families.

The goal of this chapter, however, is to determine whether the replacement of functional attribute values for species by their genus or family values in the modern weed studies can be used to define an approximate CV*/ID cut-off for predictive value for each of the functional attributes. In each case where the same attribute was indicative of agricultural regime in more than one modern weed study, the cut-off CV*s (or minimum cut-off CV*s) differed between the studies (Tables 7.12 and 7.13). As the studies differ both in the agricultural regimes represented and in the species composition of the weed flora, the functional attribute values which distinguish contrasting regimes also differ. These differences probably account for the variation in cut-off CV*s for the same attribute in different studies. This demonstrates that the CV*/ID cut-off for predictive value is strongly dependent on the particular circumstances of a study, both the species included and the relationship of the functional attribute to the particular ecological conditions brought about by the different agricultural regimes.

The information summarised in Tables 7.12 and 7.13 was closely examined to see if any factor or combination of factors present in the weed studies clearly determines the cut-off CV*/ID levels in different weed studies. Few families proved to have predictive value for functional attributes, and no association between family CV*/ID cut-off values and factors present in the weed studies was evident (Table 7.13). Although no clear overall pattern could be discerned from the summary table for genera (Table 7.12), two factors have a *tendency* to be associated with relatively high cut-off CV*s/IDs for genera. Where the ARCHFIBS genera represented in a weed study have a tendency towards low to moderate values of CV*/ID, the cut-off CV*/ID for predictive value is either moderately high, or it is only possible to define a *minimum* cut-off and this minimum is high. In other words, if most genera are relatively unvarying for a functional attribute, then, unsurprisingly, many species can be reclassified according to the functional attribute value of their genera without changing attribute class. There are, however, exceptions to this association: for both leaf

area per node and leaf area:thickness in the Germany weed study, genera tend towards low to moderate values of CV*, but the genus cut-off CV* for predictive value is moderate.

Thus, whilst there is a general association between relatively unvarying genera and quite high cut-off CV*s, this association is weak and confounded by other factors.

The second factor that has some association with the level of cut-off CV*/ID for genera is the functional attribute values that distinguish different agricultural regimes. For the original correspondence analysis plots of species classified according to functional attributes from the modern weed studies (Figs 7.2 to 7.23, plot a) (Charles *et al.* 1997; G. Jones *et al.* 2000; Bogaard *et al.* 2001), it is usually the case that only species with extreme attribute values have a functional relationship to agricultural regime. All other species (those in broad classes with a widespread distribution in the correspondence analysis plots) are functionally neutral. In cases where the majority of species are assigned to one broad, functionally neutral class for an attribute, there is a tendency either for the genus cut-off CV* for predictive value to be quite high, or for there to be a *minimum* cut-off CV* that is high (Table 7.12). This is because, if a species' attribute value falls within a broad attribute class, then the mean attribute value of its genus can be considerably lower or higher than the species value and yet not cause the species to change attribute class when it is reclassified by the genus value. There are exceptions to this association however: for both canopy diameter and leaf weight per node in the Evvia weed study, the majority of species belong to a single broad class but the cut-off CV* for predictive value is low (Table 7.12).

It seems, therefore, that the cut-off CV*/ID for genera is most likely to be relatively high in circumstances in which many genera have low CV*/ID and the majority of species belong to a broad functionally neutral class of attribute. In such cases, a species' attribute value is relatively unlikely to differ greatly from the mean attribute value of its genus, and, in addition, considerable difference in these values could be tolerated without causing the species to change attribute class when reclassified by its genus value. Once again, however, this is not a firm rule. In the Germany sowing time study (Bogaard *et al.* 2001), genera have

a tendency towards low to moderate CV* values for leaf area per node, and the majority of species belong to a single broad functional attribute class, but the CV* cut-off for genera in this study is moderately low (Table 7.12). In the Evvia cultivation intensity study (G. Jones *et al.* 2000), the genera have an even distribution of CV* values, but the majority of species belong to a single very broad functional attribute class, and the *minimum* CV*/ID cut-off is twice as high as the cut-off for the Germany study (Table 7.12).

It should be noted that the ability to predict the attribute values of functionally neutral species is of little (if any) practical value for the ecological interpretation of ancient plant remains. It is, therefore, unfortunate that broad classes of functional attributes are, at least in the weed studies considered here (Charles *et al.* 1997; G. Jones *et al.* 2000; Bogaard *et al.* 2001), always associated with functionally neutral species.

In each of the cases considered in this chapter functional attribute values for genera could be substituted for some species' functional attributes without altering the way in which the dataset as a whole would be interpreted. In five cases, it was possible to replace all the species' values with the functional attribute values for their genera but, for the most part, only the species from the least variable genera could be replaced. In most cases, functional attribute values for families could be substituted for a relatively small number of species' functional attributes.

It was, however, difficult to use the results of the reclassification of species by genera and family functional attributes to define CV*/ID cut-off for predictive value for particular functional attributes. It seems, rather, that in each of the contexts considered in the weed studies (Charles *et al.* 1997; G. Jones *et al.* 2000; Bogaard *et al.* 2001), a complex interaction of different factors affects the predictive value of plant genera and families.

Nevertheless, for the weed studies considered here, mean attribute values for genera with a CV* below ten or an ID ≤0.50 were generally acceptable substitutes for species attribute values. For most attributes, at least some genera with a CV* greater than ten are also acceptable substitutes for species attribute values. It is also encouraging that, for the ratio-scale attributes included in this thesis, about a quarter to a half of the ARCHFIBS genera have CV*

below ten and, for the nominal-scale attributes, about a quarter to three-quarters have ID ≤0.50.

This indicates that functional attribute values for genera can, in some circumstances, be used to provide functional attribute values for unspeciated material in assemblages of ancient plant remains: values of CV* <10 or ID ≤0.50 for genus values could be recommended as 'safe' for application of generic functional attribute data.

Chapter 8 – Summary of the results and discussion of their archaeological implications

8.1 Summary of results

In the course of this thesis, data measured for plant species have been used to estimate how variable particular genera and families are for a selection of plant functional attributes. Altogether, the analyses used data for 25 functional attributes from a total of 15 families, 172 genera, and 413 species.

The variation in functional attributes was analysed using three statistical techniques. For attributes measured on a ratio scale, Nested ANOVA was used to analyse how the total amount of variation is distributed among taxonomic levels and the coefficient of variation (CV*) was used to analyse the variation within particular genera and families. For attributes measured on a nominal scale, the Shannon-Weaver index of diversity (ID) was used to analyse the distribution of data among categories within particular genera and families, which serves the same purpose as CV*.

The results of these analyses were used to address the two primary aims of this thesis:

1. To determine what useful ecological inferences can and cannot be drawn from ancient plant remains identified to higher taxonomic groups (but not to species), and to target higher taxonomic groups from which few useful ecological inferences can be drawn for research into more precise taxonomic identification of their fossilised remains.
2. To determine which present-day ecological preferences of plant species are reliable indicators of the ecological preferences of the same species in the past.

In Chapter 6, the nested ANOVA, CV* and ID results were used to identify the functional attributes for which the ARCHFIBS genera and/or families tend to be either phylogenetically conservative or independently adapted. The CV* and ID results were used to indicate which particular ARCHFIBS genera and families

are most and least likely to have 'predictive value' and 'temporal stability' for each attribute.

The results of these analyses suggested that ARCHFIBS genera and families tend to be phylogenetically conservative for seed shape, epidermal cell wall undulation, leaf width, stomatal density, endopolyploidy, DMC, leaf thickness and stomatal distribution. These, therefore, are the attributes that have the greatest potential for allowing useful ecological data to be drawn from plant remains identified only to higher taxonomic groups and for projecting these inferences into the past. ARCHFIBS genera (but not families) also tend to be phylogenetically conservative for seed longevity, flowering start and vegetative spread, so these attributes also have considerable potential in this respect, although only for plant remains identified to genus. Perhaps surprisingly, there are no attributes for which ARCHFIBS genera and families are strongly independently adapted, but ARCHFIBS genera and families show some trend towards independent adaptation for leaf weight, root diameter, and seed weight. These attributes may, therefore, provide the most precise indication of ecological conditions for plant remains which can be identified to species.

ARCHFIBS genera and families with the lowest CV* or ID for a particular attribute are most likely to have predictive value and temporal stability for that attribute. Those genera and families with highest CV* or ID are least likely to have predictive value and temporal stability, but the species in those groups are likely to be good ecological indicators. The ARCHFIBS genera and families that have low or high CV* or ID vary from functional attribute to functional attribute. Overall, however, ARCHFIBS genera represented by relatively few species tend to have low CV* and ID for a number of different functional attributes. ARCHFIBS families are relatively unlikely to have predictive value or temporal stability compared to genera.

Correspondence analysis was used to simplify the CV* and ID data and so to show *which* functional attributes are phylogenetically conservative or independently adapted for *which* genera and families, and the results are summarised in Tables 6.57 and 6.58. These results also indicate that there are similarities in the relationship of functional attributes to genera and to families: certain attributes tend to be variable in both genera and families in which other

attributes tend to be quite unvarying. In some instances, attributes have high (or low) variation both for particular genera and the families to which they belong. In most cases, however, there is no clear correspondence in the variability of functional attributes between a family and its genera.

In chapter 7, an attempt was made to determine an approximate CV*/ID cut-off for predictive value for each of the functional attributes. The functional attribute values of ARCHFIBS genera and families were substituted for the functional attribute values of species in studies of the *modern* weed floras that characterise different agricultural regimes. Each of the modern weed studies had established the relationship between species functional attributes and a particular agricultural regime.

The results demonstrated that the predictive value of a genus or family for a particular attribute in a particular context is dependent on a complex interaction of factors. These include, but are not restricted to, the species composition of the plant community studied and the relationship of the functional attribute to the ecological conditions brought about by the agricultural regime in question. Consequently, it proved difficult to define CV*/ID cut-off for predictive value for particular functional attributes. For all the ratio-scale attributes evaluated, however, genera with CV* <10 seem likely to have predictive value in a given context. For each of these attributes, about a quarter to a half of the ARCHFIBS genera have CV* <10. For the nominal-scale attributes, genera with ID ≤0.50 seem likely to have predictive value in a given context. For each of these attributes, about a quarter to three-quarters of the ARCHFIBS genera have ID ≤0.50. Families, in contrast, rarely had low enough CV* or ID to have predictive value for an attribute.

8.2 Archaeological implications

8.2.1 Ancient plant remains to which the results can be applied

The ARCHFIBS project of which this thesis is a part (Charles *et al.* 1997, 2002; Bogaard *et al.* 1998, 1999, 2001; Hodgson *et al.* 1999; Hoppé 1999; G. Jones *et al.* 2000) aims to use the functional attributes of crop weeds recorded in archaeobotanical assemblages to determine the agricultural regimes under

which those crops were grown. A considerable dataset of crop weed functional attributes already exists, and studies have established the relationship between species functional attributes and a number of different agricultural regimes (Charles *et al.* 1997; Bogaard *et al.* 1999, 2001; G. Jones *et al.* 2000). Consequently, the results of this thesis can most readily be applied to the ecological interpretation of charred crop-weed assemblages. It will be possible to predict quite accurately the functional attribute values of some ancient crop weeds identified only to genus, and also to recognise those species for which modern functional attribute measurements are likely to be reliable indicators of their past functional attributes.

It should be noted, however, that the methods proposed in this thesis could also be applied to different sorts of ancient plant remains, both non-crop weed macrofossils and pollen, and to the interpretation of different types of ecological conditions. Indeed, it could be argued that these methods would be of particular utility to the ecological interpretation of fossil pollen. As explained in Chapter 1, few plant species have morphologically unique pollen, and it is quite common for entire genera and families to share the same pollen morphology (Bennett 1994). Consequently, fossil pollen assemblages tend to be dominated by material that can be identified only to 'types' above the species level, and a single pollen type may include some species that are good indicators of particular ecological conditions and others that have broad ecological amplitude (Behre 1981; Hicks 1988; Gaillard *et al.* 1992; Hicks 1992).

As a result, the ecological interpretation of fossil pollen assemblages tends to rely heavily on subjective decisions as to which species are most likely to be represented by pollen types in particular circumstances (Bennett 1994). Because pollen types often coincide with genera (Bennett 1994), it should be possible to predict the functional attribute values of many pollen types quite accurately and thus to reduce the subjectivity involved in interpreting such material. The methods described here could, therefore, be used to improve the reliability of reconstructions of ancient vegetation and of the interaction between people and their environment. As yet, however, no attempt has been made to collect functional attribute data particularly intended for application to ancient plant remains other than arable crop weeds.

8.2.2 Predictive value and temporal stability

This thesis has demonstrated that genus functional attribute values can often be used to predict the functional attribute values of ancient plant remains identified to genus, but not to species. The attribute values of these genera can be applied to the ecological interpretation of assemblages of ancient plant remains.

Some higher taxonomic groups have low predictive value for a wide range of functional attributes, and little useful ecological data can be drawn from ancient plant remains identified only to these groups. There is, therefore, significant information to be gained from more precise taxonomic identification of the fossilised remains of species in such groups. All of the ARCHFIBS families, and most of the large ARCHFIBS genera, proved to be too ecologically heterogeneous to have much overall predictive value. These families and genera could, therefore, usefully be targeted for research into criteria for more precise taxonomic identification.

This thesis has also presented a simple method for determining which present-day functional attributes of particular species are likely to be reliable indicators of the functional attributes of the same species in the past. Species from genera and families that have predictive value for a range of functional attributes are also likely to have been temporally stable for those attributes. The species that are the most precise ecological indicators, however, are those that belong to genera and families that *do not* have predictive value for many functional attributes. Consequently, there is a 'trade-off' between a species' precision as an ecological indicator and its reliability as an indicator of past conditions (J. Krebs pers. comm.) This means that the species that are of the most practical use as indicators of past ecological conditions are those from genera and families in which there is moderate variability for functional attributes. Species from these groups should be moderately precise indicators of modern ecological conditions and moderately reliable indicators of those same conditions in the past.

This trade-off between precision and reliability is a particular problem for approaches to the ecological interpretation of ancient plant remains that rely on indicator species. Compared to methods based on broad groups of species,

indicator species methods have the advantage that they use species with very precise ecological requirements, although such species are few, but the disadvantage of relying heavily on the assumption that the ecological preferences of those species have not changed over time (see Chapter 3 and G. Jones 1992; van der Veen 1992 p. 109; Hodgson et al. 1999). If species that are precise ecological indicators are relatively likely to have changed their ecological preferences over time, then this assumption cannot be justified. Consequently, interpretations of ancient plant remains that are based on modern ecological indicator species should be viewed with particular caution.

8.2.3 Problems and future research

8.2.3.1 Sample sizes

The results presented in this thesis indicate the potential of the proposed methods for predicting functional attribute values for unspeciated ancient plant remains. Because the sample sizes are often small, however, the variability of functional attributes for most of the ARCHFIBS genera and families should be considered preliminary estimates. Although the genera and families in this thesis are often represented by few of their species, it is worth noting that those species are predominantly crop weeds, either those common in the archaeobotanical record or those found in modern studies of arable contexts. Consequently, the species used in this thesis are likely to be quite representative of the variability in arable weed species of the different genera and families.

This thesis is part of an ongoing research project, and it is the intention of this project to measure the functional attributes considered here for the c.350 most common weed species represented in archaeobotanical assemblages from north-west Europe and south-west Asia. As functional attribute data for additional species from the ARCHFIBS genera and families are added to the dataset it will be a simple matter to update the calculations of attribute variability for these genera and families and to recalculate mean functional attribute values for these groups. This proposed research will also allow variability in functional attributes and mean functional attribute values to be calculated for additional genera and families. If species are collected in sufficient numbers

from different regions within the research area, it may also be possible to use these data to consider regional differences in the functional attributes of particular species.

8.2.3.2 Taxonomic inaccuracies

The fact that taxonomies do not necessarily reflect phylogeny is currently a serious limiting factor for the proposed methods of assessing predictive value and temporal stability in plant genera and families. This, however, is also a problem that will be significantly reduced in the near future. Molecular phylogenetics has only become a major field of research in the last fifteen years or so, but a very considerable amount of research has taken place in that time, and this has greatly facilitated our understanding of plant phylogeny (Harvey and Pagel 1991 p. 65; Soltis and Soltis 1998; Judd et al. 2002 p. 105-106). The phylogenetic relationships between angiosperm orders and families are already well understood (APG 1998; D. Soltis et al. 2000), and the relationships between taxa at lower levels are the focus of a huge amount of current research. Given that contemporary techniques for molecular phylogenetic analysis are neither time consuming nor expensive (D. Soltis et al. 2000 p. 428), it is reasonable to expect that the quantity of published phylogenetic research relevant to the genera and families commonly represented in assemblages of ancient plant remains will increase considerably in the near future. Most of the ARCHFIBS families that are as yet particularly poorly represented in published molecular phylogenies have either been targeted for future research (Boraginaceae – D. Soltis et al 2000), or are the subjects of research that is currently in preparation (Caryophyllaceae - M. Nepokroeff pers. comm.; Chenopodiaceae - D. Pratt pers. comm.).

Just as it will be simple to update calculations of attribute variability and mean functional attribute values as data for new species become available, so it will be simple to update the calculations to reflect improved knowledge of the phylogenetic relationships between species.

Bibliography

Ackerly, D. D. and Donoghue, M. J. 1995 Phylogeny and ecology reconsidered. *Journal of Ecology,* 83: 730-732

Alice, L. A. and Campbell, C. S. 1999 Phylogeny of Rubus (Rosaceae) based on nuclear ribosomal DNA internal transcribed spacer region sequences. *American Journal of Botany,* 86: 81-97

Amussen, C. B. and Liston, A. 1998 Chloroplast DNA characters, phylogeny, and classification of Lathyrus (Fabaceae). *American Journal of Botany,* 85: 387-401

Angiosperm Phylogeny Group 1998 An ordinal classification for the families of flowering plants. *Annals of the Missouri Botanical Garden,* 85: 531-553

Anderrson, L. and Rova, J. H. E. 1999 The rps16 intron and the phylogeny of Rubioideae (Rubiaceae). *Plant Systematics and Evolution,* 214: 161-186

Anderson, S. and Ertag-Yaras, F. 1998 Fuel fodder and faeces: an ethnographic and botanical study of dung fuel use in Central Anatolia. *Environmental Archaeology,* 1: 99-109

Andrieu-Ponel, V., Ponel, P., Jull, A. J. T., de Beaulieu, J.-L., Bruneton, H. and Leveau, P. 2000 Towards the reconstruction of the Holocene vegetation history of Lower Provence: two new pollen profiles from Marais des Baux. *Vegetation History and Archaeobotany,* 9: 71-84

Bassett, I. J. and Terasmäe, J. 1962 Ragweeds, Ambrosia species, in Canada and their history in postglacial time. *Canadian Journal of Botany,* 40: 141-150

Bayer, R. J. and Starr, J. R. 1998 Tribal phylogeny of the Asteraceae based on two non-coding chloroplast sequences, the trnL and trnL/trnF intergenic spacer. *Annals of the Missouri Botanical Garden,* 85: 242-256

Beerling, D. J. and Chaloner, W. G. 1992 Stomatal density as an indicator of atmospheric CO_2 concentration. *The Holocene,* 2: 71-78

Behre, K.-E. 1976 *Die Pflanzenreste aus der frühgeschichtlichen Wurt Elisenhog. Studien zur Küstenarchäologie Schleswig-Holsteins A 2 Bern.* Frankfurt, Herbert Lang

Behre, K.-E. 1981 The interpretation of anthropogenic indicators in pollen diagrams. *Pollen et Spores,* 23: 225-245

Behre, K.-E. 1985 Die ursprüngliche Vegetation in den deutschen Marschgebieten und deren Veränderung durch prähistorische Besiedlung und Meeresspiegelbewegungen. *Verhandlungen der Gesellschaft für Ökologie,* 13: 85-96

Behre, K.-E. and Jacomet, S. 1991 The ecological interpretation of archaeobotanical data. In van Zeist, W., Wasylikova, K. and Behre, K.-E. (eds) *Progress in Old World palaeoethnobotany.* Rotterdam, Balkema: 81-108

Bekker, R. M., Bakker, J. P., Grandin, U., Kalamees, R., Milberg, P., Poschlod, P., Thompson, K. and Willems, J. H. 1998 Seed size, shape and vertical distribution in the soil: indicators of seed longevity. *Functional Ecology,* 12: 834-842

Bell, G. 1989 A comparative method. *The American Naturalist,* 133: 553-571

Bena, G., Prosperi, J. M., Lejeune, B. and Olivieri, I. 1998 Evolution of annual species of the genus Medicago: a molecular phylogenetic approach. *Molecular Phylogenetics and Evolution,* 9: 552-559

Bennett, K. D. 1994 *Annotated catalogue of pollen and pteridophyte spore types of the British Isles.* Cambridge, University of Cambridge: Department of Plant Sciences

Berglund, B. E., Emanuelsson, U., Persson, E. and Persson, T. 1986 Pollen/vegetation relationships in grazed and mowed plant communities of South Sweden. In Behre, K.-E. (ed.) *Anthropogenic indicators in pollen diagrams.* Rotterdam, Balkema: 37-52

Birks, H. J. B. 1970 Past and present vegetation of the Isle of Skye. *New Phytologist,* 69: 807-20

Birks, H. J. B. 1981 The use of pollen analysis in the reconstruction of past climates: a review. In Wigley, T. M. L., Ingram, M. J. and Farmer, G. (eds) *Climate and history.* Cambridge, Cambridge University Press: 11-138

Birks, H. J. B. 1994 The importance of pollen and diatom taxonomic precision in quantitative palaeoenvironmental reconstructions. *Review of Palaeobotany and Palynology,* 83: 107-117

Birks, H. J. B. and Birks, H. H. 1980 *Quaternary Palaeoecology.* London, Arnold

Boardman, S. and Jones, G. 1990 Experiments on the effects of charring on cereal plant components. *Journal of Archaeological Science,* 17: 1-11

Bogaard, A., Hodgson, J. G., Wilson, P. J. and Band, S. R. 1998 An index of weed size for assessing the soil productivity of ancient crop fields. *Vegetation History and Archaeobotany,* 7: 17-22

Bogaard, A., Palmer, C., Jones, G., Charles, M. and Hodgson, J. G. 1999 A FIBS approach to the use of weed ecology for the archaeobotanical recognition of crop rotation regimes. *Journal of Archaeological Science,* 26: 1211-1224

Bogaard, A., Jones, G., Charles, M. and Hodgson, J. G. 2001 On the archaeobotanical inference of crop sowing time using the FIBS method. *Journal of Archaeological Science,* 28: 1171-1183

Bolos, O. and Vigo, J. 1984 *Flora dels paisos Catalans.* Barcelona, Barcino

Boutin, C. and Keddy, P. A. 1993 A functional classification of wetland plants. *Journal of vegetation science,* 4: 591-600

Braun-Blanquet, J. 1928 *Pflanzensoziologie. Grundzüge der Vegetationskunde.* Berlin, Biologische Studienbücher

Braun-Blanquet, J. 1936 *Prodrome des groupements végétaux, classe de rudereto-secalinetales.* Montpellier, Sigma

Braun-Blanquet, J., Roussine, N. and Negre, R. 1952 *Les groupements végétaux de la France Méditerranéene.* Montpellier, CNRS

Broström, A., Gaillard, M.-J., Ihse, M. and Odgaard, B. 1998 Pollen-landscape relationships in modern analogues of ancient cultural landscapes in southern Sweden - a first step towards quantification of vegetation openness in the past. *Vegetation History and Archaeobotany,* 7: 189-201

Butler, A. 1988 The SEM and seed identification, with particular reference to the Vicieae. In Olsen, L. (ed.) *Scanning electron microscopy in archaeology. BAR International Series, 452.* Oxford, BAR: 215-224

Butler, A. 1991 The Vicieae: problems of identification. In Renfrew, J. M. (ed.) *New light on early farming - recent developments in palaeoethnobotany.* Edinburgh, Edinburgh University Press: 61-73

Butler, A. 1996 Trifolieae and related seeds from archaeological contexts: problems in identification. *Vegetation History and Archaeobotany,* 5: 157-167

Buurman, J. 1979 Cereals in circles - crop processing activities in Bronze Age Bovenkarpsel (the Netherlands). *Archaeo-Physika,* 8: 21-37

Buurman, J. 1987 A Middle Bronze Age corn-stack at Twisk, province of North Holland. *Rijksdieust Oudheidkundig Bodemanderzoek,* 37: 7-36

Cantino, P. D. and de Queiroz, K. 2000 PhyloCode: a phylogenetic code for botanical nomenclature. *www.ohiou.edu/phylocode*

Catalán, P., Kellogg, E. A. and Olmstead, R. G. 1997 Phylogeny of Poaceae subfamily Pooideae based on chloroplast ndhF gene sequences. *Molecular Phylogenetics and Evolution,* 8: 150-166

Charles, M. 1998 Fodder from dung: the recognition and interpretation of dung-derived plant material from archaeological sites. *Environmental Archaeology,* 1: 111-122

Charles, M., Jones, G. and Hodgson, J. G. 1997 FIBS in archaeobotany: functional interpretation of weed floras in relation to husbandry practices. *Journal of Archaeological Science,* 24: 1151-1161

Charles, M., Bogaard, A., Jones, G., Hodgson, J. G. and Halstead, P. 2002 Towards the archaeobotanical identification of intensive cereal cultivation: present-day ecological investigation in the mountains of

Asturias, northwest Spain. *Vegetation History and Archaeobotany*: 133-142

Chase, M. W., Soltis, D. E., Olmstead, R. G., Morgan, D. R., Les, D. H., Mishler, B. D., Duvall, M. R., Price, R. A., Hills, H. G., Qiu, Y.-L., Kron, K. A., Rettig, J. H., Conti, E., Palmer, J. D., Manhart, J. R., Sytsma, K. J., Michaels, H. J., Kress, W. J., Karol, K. G., Clark, W. D., Hedrén, M., Gaut, B. S., Jansen, R. K., Kim, K.-J., Wimpee, C. F., Smith, J. F., Furnier, G. R., Strauss, S. H., Xiang, Q.-Y., Plunkett, G. M., Soltis, P. S., Swensen, S. M., Williams, S. E., Gadek, P. A., Quinn, C. J., Eguiarte, L., Golenberg, E., Learn, G., Graham, S. W., Barrett, S. C. H., Dayanandan, S. and Albert, V. A. 1993 Phylogenetics of seed plants: an analysis of nucleotide sequences from the plastid gene rbcL. *Annals of the Missouri Botanical Garden,* 80: 528-580

Clapham, A. R. 1956 Autecological studies and the 'Biological Flora of the British Isles'. *Journal of Ecology,* 44: 1-11

Clapham, A. R., Tutin, T. G. and Warburg, E. F. 1952 *Flora of the British Isles.* Cambridge, Cambridge University Press

Clapham, A. R., Tutin, T. G. and Moore, D. M. 1987 *Flora of the British Isles.* Cambridge, Cambridge University Press

Clark, L. G., Weiping, Z. and Wendel, J. F. 1995 A phylogeny of the grass family (Poaceae) based on ndhF sequence data. *Systematic Botany,* 20: 436-460

Clarke, D. L. 1973 Archaeology: the loss of innocence. *Antiquity,* 47: 6-18

Clutton-Brock, T. H. and Harvey, P. H. 1978 Primate ecology and social organization. In Clutton-Brock, T. H. and Harvey, P. H. (eds) *Readings in sociobiology.* Reading, W. H. Freeman and Company: 342-383

Cronquist, A. 1968 *The evolution and classification of flowering plants.* Boston, Houghton Mifflin

Daubenmire, R. F. 1974 *Plants and the environment - a textbook of plant autecology.* New York, John Wiley and Sons

Davies, M. S. and Hillman, G. C. 1988 Effects of soil flooding on growth and grain yield of populations of tetraploid and hexaploid species of wheat. *Annals of Botany,* 62: 597-604

Davis, M. B. 1983 Holocene vegetation history of the eastern United States. In Wright, H. E. (ed.) *Late Quaternary environments of the United States, 2. The Holocene.* Minneapolis, University of Minnesota Press

Delacourt, P. A. and Delacourt, H. R. 1987 *Long-term forest dynamics of the temperate zone with particular reference to late-Quaternary forest history.* New York, Springer

Díaz, S. and Cabido, M. 1997 Plant functional types and ecosystem function in relation to global change. *Journal of vegetation science,* 8: 463-474

Díaz, S., Cabido, M. and Casanoves, F. 1998 Plant functional traits and environmental filters at a regional scale. *Journal of Vegetation Science,* 9: 113-122

Downie, S. R. 1998 Molecular systematics of Apiaceae subfamily Apioideae: phylogenetic analyses of nuclear ribosomal DNA internal transcribed spacer and plastid rpoC1 intron sequences. *American Journal of Botany,* 85: 563-591

Downie, S. R. and Palmer, J. D. 1994 A chloroplast DNA phylogeny of the Caryophyllales based on structural and inverted repeat restriction site variation. *Systematic Botany,* 19: 236-252

Downie, S. R., Katz-Downie, D. S. and Cho, K.-J. 1997 Relationships in the Caryophyllales as suggested by phylogenetic analyses of partial chloroplast DNA ORF2280 homology sequences. *American Journal of Botany,* 84: 253-273

Doyle, J. J., Doyle, J. L., Ballenger, J. A., Dickson, E. E., Kajita, T. and Ohashi, H. 1997 A phylogeny of the chloroplast gene rbcL in the Leguminosae: taxonomic correlations and insights into the evolution of nodulation. *American Journal of Botany,* 84: 541-554

Dytham, C. 1999 *Choosing and using statistics - a biologists guide.* Oxford, Blackwell Science

Edwards, S. and Naeem, S. 1993 The phylogenetic component of cooperative breeding in perching birds. *American naturalist,* 141: 754-89

Eldenäs, P., Källersjö, M. and Anderberg, A. A. 1999 Phylogenetic placement and circumscription of tribes Inuleae s. str. and Plucheeae (Asteraceae): Evidence from sequences of chloroplast gene ndhF. *Molecular Phylogenetics and Evolution,* 13: 50-58

Ellenberg, H. 1950 *Landwirtschaftliche Pflanzensoziologie 1: Unkrautgemeinschaften als Zeiger für Klima und Boden.* Stuttgart, Eugen Ulmer

Ellenberg, H. 1974 Zeigerwerte der Gefässpflanzen Mitteleuropas. *Scripta Geobotanica,* 9: 1-79

Ellenberg, H., Weber, H. E., Düll, R., Wirth, V., Werner, W. and Paulissen, D. 1992 Keigerwerte von Pflanzen in Mittleuropa. *Scripta Geobotanica,* 18: 1-258

Eriksson, T., Donoghue, M. J. and Hibbs, M. S. 1998 Phylogenetic analysis of Potentilla using DNA sequences of nuclear ribosomal internal transcribed spacers (ITS), and implications for the classification of Rosoideae (Rosaceae). *Plant Systematics and Evolution,* 211: 155-179

Etherington, J. R. 1975 *Environment and plant ecology.* London, John Wiley and Sons

Evans, J. G. 1978 *An introduction to environmental archaeology.* London, Paul Elek

Faegri, K. and Iversen, J. 1989 *Textbook of pollen analysis.* Chichester, John Wiley

Feinbrun-Dothan, N. 1978 *Flora Palaestina - Part 3: Ericaceae to Compositae.* Jerusalem, Israel Academy of Sciences and Humanities

Feinbrun-Dothan, N. 1986 *Flora Palaestina - Part 4: Alismataceae to Orchidaceae.* Jerusalem, Israel Academy of Sciences and Humanities

Felsenstein, J. 1985 Phylogenies and the comparative method. *The American Naturalist,* 125: 1-15

Gaillard, M.-J., Birks, H. J. B., Emanuelsson, U. and Berglund, B. E. 1992 Modern pollen/land-use relationships as an aid in the reconstruction of past land-uses and cultural landscapes: an example from south Sweden. *Vegetation History and Archaeobotany,* 1: 3-17

Gaillard, M.-J., Birks, H. J. B., Emanuelsson, U., Karlsson, S., Lageräs, P. and Olausson, D. 1994 Application of modern pollen/land-use relationships to the interpretation of pollen diagrams - reconstructions of land-use history in south Sweden, 3000-0 BP. *Review of Palaeobotany and Palynology,* 82

Garcia-Jacas, N., Susanna, A., Garnatje, T. and Vilatersana, R. 2001 Generic delimitation and phylgoeny of subtribe Centaurinae (Asteraceae): a combined nuclear and chloroplast DNA analysis. *Annals of Botany,* 87: 503-515

Gitay, H. and Nobel, I. R. 1997 What are functional types and how should we seek them? In Smith, T. M., Shugart, H. H. and Woodward, F. I. (eds) *Plant functional types - their relevance to ecosystem properties and global change.* Cambridge, Cambridge University Press: 3-19

Gittleman, J. L. and Luh, H.-K. 1992 On comparing comparative methods. *Annual Review of Ecology and Systematics,* 23: 383-404

Givnish, T. J. 1987 Comparative studies of leaf form: assessing the relative roles of selective pressures and phylogenetic constraints. In Rorison, I. H., Grime, J. P., Hunt, R., Hendry, G. A. F. and Lewis, D. H. (eds) *Frontiers of comparative plant ecology.* London, Academic Press: 131-160

Godwin, H. 1975 *History of the British Flora.* Cambridge, Cambridge University Press

Green, F. J. 1976 Collection and interpretation of botanical information from Medieval urban excavations in southern England, in Festschrift Maria Hopf (ed. U Körber-Grohne). *Archaeo-Physika,* 8: 39-55

Green, F. J. 1982 Problems of interpreting differentially preserved plant remains from excavations of medieval urban sites. In Hall, A. and

Kenward, H. K. (eds) *Environmental archaeology in the urban context.* London, Prometheus Books: 27-36

Greig, J. R. A. 1976 The plant remains. In Buckland, P. (ed.) *The environmental evidence from the Church Street Roman sewer system.* London, Council for British Archaeology: 23-28

Greig, J. R. A. 1988 Some evidence of the development of grassland plant communities. In Jones, M. (ed.) *Archaeology and the flora of the British Isles.* Oxford, Oxford University Committee for Archaeology: 39-54

Greuter, W., McNeill, J., Barrie, F., Burdet, H. M., Demoulin, V., Filgueiras, T., Nicolson, D. H., Silva, P. C., Skog, J., Trehane, P., Turland, N. and Hawksworth, D. L. 2000 International Code of Botanical Nomenclature (Saint Louis Code) adopted by the Sixteenth International Botanical Congress St. Louis, Missouri, July - August 1999. *Regnum Vegetabile,* 138: 1-474

Grime, J. P. 1974 Vegetation classification by reference to strategies. *Nature,* 250: 26-31

Grime, J. P. 1979 *Plant strategies and vegetation processes.* Chichester, John Wiley and Sons

Grime, J. P. 1984 The ecology of species, families and communities of the contemporary British flora. *New Phytologist,* 98: 15-33

Grime, J. P. 1985 Factors limiting the contribution of pteridophytes to a local flora. *Proceedings of the Royal Society of Edinburgh,* 86B: 403-421

Grime, J. P. and Lloyd, P. S. 1973 *An ecological atlas of grassland plants.* London, Edward Arnold

Grime, J. P. and Hodgson, J. G. 1987 Botanical contributions to contemporary ecological theory. In Rorison, I. H., Grime, J. P., Hunt, R., Hendry, G. A. F. and Lewis, D. H. (eds) *Frontiers of comparative plant ecology.* London, Academic Press: 283-295

Grime, J. P., Mason, G., Curtis, A. V., Rodman, J., Band, S. R., Mowforth, M. A. G., Neal, A. M. and Shaw, S. 1981 A comparative study of

germination characteristics in a local flora. *Journal of ecology,* 69: 1017-1059

Grime, J. P., Hodgson, J. G. and Hunt, R. 1988 *Comparative plant ecology - a functional approach to common British species.* London, Unwin Hyman Ltd

Grime, J. P., Hodgson, J. G., Hunt, R., Thompson, K., Hendry, G. A. F., Campbell, B. D., Jalili, A., Hillier, S. H., Diaz, S. and Burke, M. J. W. 1997a Functional types: testing the concept in Northern England. In Smith, T. M., Shugart, H. H. and Woodward, F. I. (eds) *Plant functional types - their relevance to ecosystem properties and global change.* Cambridge, Cambridge University Press: 122-150

Grime, J. P., Thompson, K., Hunt, R., Hodgson, J. G., Cornelissen, J. H. C., Rorison, I. H., Hendry, G. A. F., Ashenden, P. W., Askew, A. P., Band, S. R., Booth, R. E., Bossard, C. C., Campbell, B. D., Cooper, J. E. L., Davison, A. W., Gupta, P. L., Hall, W., Hand, D. W., Hannah, M. A., Hillier, S. H., Hodkinson, D. J., Jalili, A., Liu, Z., Mackey, J. M. L., Matthews, N., Mowforth, M. A. G., Neal, A. M., Reader, R. J., Reiling, K., Ross-Fraser, W., Spencer, R. E., Sutton, F., Tasker, D. E., Thorpe, P. C. and Whitehouse, J. 1997b Integrated screening validates primary axes of specialisation in plants. *Oikos,* 79: 259-281

Grubb, P. J. 1985 Plant populations and vegetation in relation to habitat disturbance and competition: problems of generalization. In White, J. (ed.) *The population structure of vegetation, handbook of vegetation science part III.* Dortrecht, W. Junk: 595-621

Hall, A., Kenward, H. K. and Williams, D. 1980 *Environmental evidence from Roman deposits in Skeldergate.* London, Council for British Archaeology

Halstead, P. and Jones, G. 1989 Agrarian economy in the Greek islands: time, stress, scale and risk. *Journal of Hellenic Studies,* 109: 41-55

Harper, J. L. 1982 After description. In Newman, I. E. (ed.) *The plant community as working mechanism.* London, Blackwell: 11-25

Harvey, P. H. and Mace, G. M. 1982 Comparisons between taxa and adaptive trends: problems of methodology. In King's College Sociobiology Group, C. (ed.) *Current Problems in Sociobiology.* Cambridge, Cambridge University Press: 343-361

Harvey, P. H. and Clutton-Brock, T. H. 1985 Life history variation in primates. *Evolution,* 39: 559-581

Harvey, P. H. and Pagel, M. D. 1988 Recent developments in the analysis of comparative data. *The Quarterly Review of Biology,* 63: 413-440

Harvey, P. H. and Pagel, M. D. 1991 *The comparative method in evolutionary biology.* Oxford, Oxford University Press

Harvey, P. H., Read, A. F. and Nee, S. 1995a Why ecologists need to be phylogenetically challenged. *Journal of Ecology,* 83: 535-536

Harvey, P. H., Read, A. F. and Nee, S. 1995b Further remarks on the role of phylogeny in comparative ecology. *Journal of ecology,* 83: 733-734

Havinga, A. J. 1964 Investigation into the differential corrosion susceptibility of pollen and spores. *Pollen et Spores,* 4: 621-635

Hennig, W. 1966 *Phylogenetic systematics.* Urbana, University of Illinois Press

Herrera, C. M. 1992 Historical effects and sorting processes as explanations for contemporary ecological patterns: character syndromes in Mediterranean woody plants. *The American Naturalist,* 140: 421-446

Hickey, L. J. 1971 Revised classification of the architecture of dicotyledonous leaves. In Metcalfe, C. R. and Chalk, L. (eds) *Anatomy of the dicotyledons. Vol 1: systematic anatomy of leaf and stem, with a brief history of the subject.* Oxford, Clarendon Press: 25-39

Hicks, S. 1988 The representation of different farming practices in pollen diagrams from northern Finland. In Birks, H. H., Birks, H. J. B., Kaland, P. E. and Moe, B. (eds) *The cultural landscape, past, present and future.* Cambridge, Cambridge University Press

Hicks, S. 1992 Modern pollen deposition and its use in interpreting the occupation history of the island Hailuoto, Finland. *Vegetation History and Archaeobotany,* 1: 75-86

Hicks, S. and Birks, H. J. B. 1996 Numerical analysis of modern and fossil pollen spectra as a tool for elucidating the nature of fine-scale human activities in boreal areas. *Vegetation History and Archaeobotany,* 5: 257-272

Hillman, G. C. 1973 Crop husbandry and food production: modern basis for the interpretation of plant remains. *Anatolian studies,* 23: 241-244

Hillman, G. C. 1981 Reconstructing crop husbandry practices from charred remains of crops. In Mercer, R. (ed.) *Farming practice in British prehistory.* Edinburgh, Edinburgh University Press: 123-162

Hillman, G. C. 1984 Interpretation of archaeological plant remains: the application of ethnographic models from Turkey. In van Zeist, W. and Casparie, W. (eds) *Plants and ancient man: studies in palaeoethnobotany.* Rotterdam, Balkema: 1-41

Hillman, G. C. 1991 Phytosociology and ancient weed floras: taking account of taphonomy and changes in cultivation methods. In Harris, D. R. and Thomas, K. D. (eds) *Modelling Ecological Change.* London, Institute of Archaeology, University College London: 27-40

Hilu, K. W., Alice, L. A. and Liang, H. 1999 Phylogeny of Poaceae inferred from matK sequences. *Annals of the Missouri Botanical Garden,* 86: 835-851

Hodgson, J. G. 1986 Commonness and rarity in plants with special reference to the Sheffield flora. Part III: taxonomic and evolutionary aspects. *Biological conservation,* 36: 276-296

Hodgson, J. G. 1990 The role of autecological accounts. In Hillier, S. H., Walton, D. W. H. and Wells, D. A. (eds) *Calcareous grasslands - ecology and management.* Huntingdon, Bluntisham: 161-168

Hodgson, J. G. 1991 The use of autecological datasets in studies of endangered plant and animal species and communities. *Pirineos*, 138: 3-28

Hodgson, J. G. and Mackey, J. M. L. 1986 The ecological specialization of dicotyledonous families within a local flora: some factors constraining optimization of seed size and their possible evolutionary significance. *New Phytologist,* 104: 479-515

Hodgson, J. G., Colosanti, R. and Sutton, F. unpub.-a FIBS (Functional Interpretation of Botanical Surveys), 1 - General methods.

Hodgson, J. G., Hillier, S. H., Grime, J. P., Band, S. R., Spencer, R. and Sutton, F. unpub.-b FIBS (Functional Interpretation of Botanical Surveys), 2 - Changes in the semi-natural grasslands of Central England 1965-1990.

Hodgson, J. G., Halstead, P., Wilson, P. J. and Davis, S. 1999 Functional interpretation of archaeobotanical data: making hay in the archaeological record. *Vegetation History and Archaeobotany,* 8: 261-271

Hodgson, J. G., Colosanti, R., Alberto, F., Martí, G. M. and Díez, A. R. 1993 *Plant strategies and other functional attributes from the arid lands: Monegros.* Zaragoza, Instituto Pirenaico de Ecologia.

Holzner, W. 1978 Weed species and weed communities. *Vegetatio,* 38: 13-20

Hoot, S. B. 1995 Phylogeny of the Ranunculaceae based on preliminary stpB, rbcL and 18S nuclear ribosomal DNA sequence data. *Plant Systematics and Evolution,* 9

Hoot, S. B., Kadereit, J. W., Blattner, F. R., Jork, K. B., Schwarzbach, A. E. and Crane, P. R. 1997 Data congruence and phylogeny of the Papaveraceae s.l. based on four data sets: atpB and rbcL sequences, trnK restriction sites, and morphological characters. *Systematic Botany,* 22: 575-590

Hoppé, C. 1999 *A thousand years of farming: agricultural practices from the Byzantine to early Ottoman period at Khirbet Furis, the Kerak Plateau,*

Jordan. Unpublished PhD, Department of Archaeology and Prehistory, University of Sheffield

Hort, A. 1916 *Enquiry into plant and minor works on odours and weather signs. (By Theophrastus, trans. by A. Hort)*. London, Methuen

Hsiao, C., Chatterton, N. J., Asay, K. H. and Jensen, K. B. 1995 Phylogenetic relationships of the monogenomic species of the wheat tribe, Triticeae (Poaceae), inferred from nuclear rDNA (internal transcribed spacer) sequences. *Genome,* 38: 211-223

Hubbard, R. and al Azm, A. 1990 Quantifying preservation and distortion in carbonised seeds; and investigating the history of friké production. *Journal of Archaeological Science,* 3: 257-265

Huntley, B. and Birks, H. J. B. 1983 *An atlas of past and present pollen maps of Europe 0-13,000 years ago*. Cambridge, Cambridge University Press

Hüppe, J. and Hofmeister, H. 1990 Syntaxonomische Fassung und Übersicht über die Ackerunkrautgesellschaften der Bundsrepublik Deutschland. *Berichte der Reinhardt Tüxen-Gesellschaft,* 2: 61-81

Iversen, J. 1941 Landnam i Danmarks Stenalder. *Danmarks Geologiske Underscgelse, 2 rk,* 66: 1-68

Iversen, J. 1949 The influence of prehistoric man on vegetation. *Danmarks geologiske underscgelse, 4 rk,* 3: 1-25

Jansen, R. K., Holsinger, K. E., Michaels, H. J. and Palmer, J. D. 1990 Phylogenetic analysis of chloroplast DNA restriction site data at higher taxonomic levels: an example from the Asteraceae. *Evolution,* 44: 2089-2105

Jensen, U., Hoot, S. B., Johansson, J. T. and Kosuge, K. 1995 Systematics and phylogeny of the Ranunculaceae - a revised family concept on the basis of molecular data. In Jensen, U. and Kadereit, J. W. (eds) *Plant Systematics and Evolution, supplementum 9: systematics and evolution of the Ranunculiflorae*. New York, Springer-Verlag: 273-280

Johansson, J. T. 1995 A revised chloroplast phylogeny of the Ranunculaceae. In Jensen, U. and Kadereit, J. W. (eds) *Plant Systematics and Evolution,*

supplementum 9: systematics and evolution of the Ranunculiflorae. New York, Springer-Verlag: 253-261

Johansson, J. T. 1998 Chloroplast DNA restriction site mapping and the phylogeny of Ranunculus (Ranunculaceae). *Plant Systematics and Evolution,* 213: 1-19

Johansson, J. T. and Jansen, R. K. 1993 Chloroplast DNA variation and phylogeny of the Ranunculaceae. *Plant Systematics and Evolution,* 187: 29-49

Jones, G. 1983 The ethnoarchaeology of crop processing: seeds of a middle-range methodology. *Archaeological review from Cambridge,* 2: 17-26

Jones, G. 1984 Interpretation of archaeological plant remains: ethnographic models from Greece. In van Zeist, W. and Casparie, W. (eds) *Plants and ancient man: studies in palaeoethnobotany.* Rotterdam, Balkema: 43-61

Jones, G. 1992 Weed phytosociology and crop husbandry: identifying a contrast between ancient and modern practice. *Review of Palaeobotany and Palynology,* 73: 133-143

Jones, G. 1998 Distinguishing food from fodder in the archaeobotanical record. *Environmental Archaeology,* 1: 95-98

Jones, G. and Halstead, P. 1995 Maslins, mixtures and monocrops: on the interpretation of archaeobotanical crop samples of heterogeneous composition. *Journal of Archaeological Science,* 22: 103-114

Jones, G., Wardle, K., Halstead, P. and Wardle, D. 1986 Crop storage at Assiros. *Scientific American,* 254: 96-103

Jones, G., Straker, V. and Davis, A. 1991 Early medieval plant use and ecology. In Vince, A. G. (ed.) *Aspects of Saxon and Norman London, 2: Finds and environmental evidence. London and Middlesex Archaeological Society Special Paper 12*: 347-385

Jones, G., Charles, M., Colledge, S. and Halstead, P. 1995 Towards the archaeobotanical recognition of winter-cereal irrigation: an investigation of modern weed ecology in northern Spain. In Kroll, H. and Pasternak, R.

(eds) *Res Archaeobotanicae - 9th Symposium IWGP.* Kiel, Institut für Ur- und Frühgeschichte der Christian-Albrecht-Universität: 49-68

Jones, G., Bogaard, A., Halstead, P., Charles, M. and Smith, H. 1999 Identifying the intensity of crop husbandry practices on the basis of weed floras. *Annual of the British School at Athens,* 94: 167-189

Jones, G., Bogaard, A., Charles, M. and Hodgson, J. G. 2000 Distinguishing the effects of agricultural practices relating to fertility and disturbance: a functional ecological approach in archaeobotany. *Journal of Archaeological Science,* 27: 1073-1084

Jones, M. 1981 The development of crop husbandry. In Jones, M. and Dimbleby, G. (eds) *The environment of man: the Iron Age to the Anglo-Saxon period.* Oxford, BAR British Series, 87: 95-127

Jones, M. 1988 The arable field: a botanical battleground. In Jones, M. (ed.) *Archaeology and the flora of the British Isles.* Oxford, Oxford University Committee for Archaeology: 86-92

Jones, S. B. and Luchsinger, A. E. 1987 *Plant systematics.* New York, McGraw-Hill International Editions

Judd, W. S., Campbell, C. S., Kellogg, E. A., Stevens, P. F. and Donoghue, M. J. 2002 *Plant systematics: a phylogenetic approach. 2nd edition.* Sunderland, Massachusetts, Sinauer Associates, Inc.

Kadereit, J. W. and Sytsma, K. J. 1992 Disassembling Papaver: a restriction site analysis of chloroplast DNA. *Nordic Journal of Botany,* 12: 205-217

Kadereit, J. W., Blattner, F. R., Jork, K. B. and Schwarzbach, A. E. 1994 Phylogenetic analysis of the Papaveraceae s.l. (including Fumariaceae, Hypecoaceae, and Pteridophyllum) based on morphological characters. *Botanische Jahrbücher für Systematik und Pflanzengeographie,* 116: 361-390

Kadereit, J. W., Schwarzbach, A. E. and Jork, K. B. 1997 The phylogeny of Papaver s.l. (Papaveraceae): polyphyly or monophyly? *Plant Systematics and Evolution,* 204: 75-98

Kelly, C. K. and Woodward, F. I. 1996 Ecological correlates of plant range size: taxonomies and phylogenies in the study of plant commonness and rarity in Great Britain. *Philosophical Transactions of the Royal Society of London, Series B,* 351: 1261-1269

Kim, K.-J. and Jansen, R. K. 1995 ndhF sequence evolution and the major clades in the sunflower family. *Proceedings of the National Academy of Science, USA,* 92: 10379-10383

Kim, S.-C., Crawford, D. J., Jansen, R. K. and Santos-Guerra, A. 1999 The use of a non-coding region of chloroplast DNA in phylogenetic studies of the subtribe Sonchinae (Asteraceae: Lactuceae). *Plant Systematics and Evolution,* 215: 85-99

Knörzer, K. 1971 Urgeschichtliche Unkraüter im Rheinland. Ein Beitrag zur Entstehungs geschichte der Segetalgesellschaften. *Vegetatio,* 23: 89-111

Körber-Grohne, U. 1967 *Geobotanische Untersuchengen aug der Feddersen Wierde.* Wiesbaden, Steiner

Körber-Grohne, U. 1991 Identification methods. In van Zeist, W., Wasylikova, K. and Behre, K.-E. (eds) *Progress in Old World palaeoethnobotany.* Rotterdam, Balkema: 3-24

Küster, H. 1991 Phytosociology and archaeobotany. In Harris, D. R. and Thomas, K. D. (eds) *Modelling ecological change.* London, Institute of Archaeology, University College London: 17-26

Lee, B.-Y. and Downie, S. R. 1999 A molecular phylogeny of Apiaceae tribe Caucalideae and related taxa: inferences based on ITS sequence data. *Systematic Botany,* 24: 461-479

Lee, B.-Y. and Downie, S. R. 2000 Phylogenetic analysis of cpDNA restriction sites and rps16 intron sequences reveals relationships among Apiaceae tribes Caucalideae, Scandiceae and related taxa. *Plant Systematics and Evolution,* 221: 35-60

Lee, S. and Wen, J. 2001 A phylogenetic analysis of Prunus and the Amygdaloideae (Rosaceae) using ITS sequences of nuclear ribosomal DNA. *American Journal of Botany,* 88: 150-160

Links, D. D. 1993-1996 *Aequitas IDA: image database and image archive management system, Version 1.5x.* Cambridge

Loconte, H., Campbell, L. M. and Stevenson, D. W. 1995 Ordinal and familial relationships of Ranunculid genera. In Jensen, U. and Kadereit, J. W. (eds) *Plant Systematics and Evolution, supplementum 9: systematics and evolution of the Ranunculiflorae.* New York, Springer-Verlag: 99-118

Lowe, J. J. and Walker, M. J. C. 1984 *Reconstructing Quaternary environments.* Harlow, Longman Scientific and technical

Manen, J.-F., Natali, A. and Ehrendorfer, F. 1994 Phylogeny of Rubiaceae-Rubieae inferred from the sequence of a cpDNA intergene region. *Plant Systematics and Evolution,* 190: 195-211

Martins, E. P. and Garland, T. 1991 Phylogenetic analyses of the correlated evolution of continuous characters: a simulation study. *Evolution,* 45: 534-557

McIntyre, S., Lavorel, S., Landsberg, J. and Forbes, T. D. A. 1999 Disturbance response in vegetation - towards a global perspective in functional traits. *Journal of Vegetation Science,* 10: 621-630

Miles, D. B. and Dunham, A. E. 1993 Historical perspectives in ecology and evolutionary biology: the use of phylogenetic comparative analyses. *Annual Review of Ecology and Systematics,* 24: 587-619

Minitab 2000 *MINITAB 13.1.* State College, PA

Moore, P. D. 1990 Vegetation's place in history. *Nature,* 347: 710

Moore, P. D. and Webb, J. A. 1978 *An illustrated guide to pollen analysis.* London, Hodder and Stoughton

Moore, P. D., Webb, J. A. and Collinson, M. E. 1991 *Pollen analysis.* Oxford, Blackwell Scientific Publications

Morgan, D. R., Soltis, D. E. and Robertson, K. R. 1994 Systematic and evolutionary implications of rbcL sequence variation in Rosaceae. *American Journal of Botany,* 81: 890-903

Natali, A., Manen, J.-F. and Ehrendorfer, F. 1995 Phylogeny of the Rubiaceae-Rubioideae, in particular the tribe Rubieae: evidence from a non-coding chloroplast DNA sequence. *Annals of the Missouri Botanical Garden,* 82: 428-439

Natali, A., Manen, J.-F., Kiehn, M. and Ehrendorfer, F. 1996 Tribal, generic and specific relationships in the Rubioideae-Rubieae (Rubiaceae) based on sequence data of a cpDNA region. *Opera Botanica Belgica,* 7: 193-203

Nesbitt, M. 2000 *Identification guide for Near Eastern grass seeds.* London, Institute of Archaeology

Nickrent, D. L., Duff, R. J., Colwell, A. E., Wolfe, A. D., Young, N. D., Steiner, K. E. and dePamphilis, C. W. 1998 Molecular phylogenetic and evolutionary studies of parasitic plants. In Soltis, D. E., Soltis, P. S. and Doyle, J. J. (eds) *Molecular systematics of plants.* New York, Chapman and Hall. Vol 2

Oberdorfer, E. 1954 Über Unkrautgesellschaften der Balken-halbinsel. *Vegetatio,* 4: 379-411

Olmstead, R. G. and Reeves, P. A. 1995 Evidence for the Polyphyly of the Scrophulariaceae based on chloroplast rbcL and ndhF sequences. *Annals of the Missouri Botanical Garden,* 82: 176-193

Olmstead, R. G., Kim, K.-J., Jansen, R. K. and Wagstaff, S. J. 2000 The phylogeny of the Asteridae sensu lato based on chloroplast ndhF gene sequences. *Molecular Phylogenetics and Evolution,* 16: 96-112

O'Rourke, M. K. and Lebowitz, M. D. 1984 A comparison of regional and atmospheric pollen with pollen collected at and near homes. *Grana,* 23: 55-64

Oxelman, B., Lidén, M. and Berglund, D. 1997 Chloroplast rps16 intron phylogeny of the tribe Sileneae (Caryophyllaceae). *Plant Systematics and Evolution,* 206: 393-410

Palmer, C. 1998 An exploration of the effects of crop rotation regime on modern weed floras. *Environmental Archaeology,* 2: 35-48

Peat, H. J. and Fitter, A. 1994a A comparative study of the distribution and density of stomata in the British flora. *Biological Journal of the Linnean Society,* 52: 377-399

Peat, H. J. and Fitter, A. 1994b Comparative analyses of ecological characteristics of British angiosperms. *Biological Review of the Cambridge Philosophical Society,* 69: 95-115

Plunkett, G. M., Soltis, D. E. and Soltis, P. S. 1996 Higher level relationships of Apiales (Apiaceae and Araliaceae) based on phylogenetic analysis of rbcL sequences. *American Journal of Botany,* 83: 499-515

Pradhan, A. K., Prakash, S., Mukhopadhay, A. and Pental, D. 1992 Phylogeny of Brassica and allied genera based on variation in chloroplast and mitochondrial DNA patterns: molecular and taxonomic classifications are incongruous. *Theoretical and Applied Genetics,* 85: 331-340

Prentice, I. C. 1986 Vegetation responses to past climatic variation. *Vegetatio,* 67: 131-141

Raunkiaer, C. 1934 *The life forms of plants and statistical plant geography.* Oxford, Clarendon Press

Rees, M. 1995 EC-PC comparative analyses? *Journal of ecology,* 83: 891-892

Rettig, J. H., Wilson, H. D. and Manhart, J. R. 1992 Phylogeny of the Caryophyllales - gene sequence data. *Taxon,* 41: 201-209

Ro, K.-E., Keener, C. S. and McPheron, B. A. 1997 Molecular phylogenetic study of the Ranunculaceae: utility of the nuclear 26S ribosmal DNA in inferring intrafamilial relationships. *Molecular Phylogenetics and Evolution,* 8: 117-127

Rodman, J., Price, R. A., Karol, K. G., Conti, E., Sytsma, K. J. and Palmer, J. D. 1993 Nucleotide sequences of the rbcL gene indicate the monophyly of mustard oil plants. *Annals of the Missouri Botanical Garden,* 80: 686-699

Rodman, J., Soltis, P. S., Soltis, D. E., Sytsma, K. J. and Karol, K. G. 1998 Parallel evolution of glucosinolate biosynthesis inferred from congruent nuclear and plastid gene phylogenies. *American Journal of Botany,* 85: 997-1006

Rodwell, J. S. (ed.) 1991a *British plant communities. Vol. 1: woodlands and scrub.* Cambridge, Cambridge University Press

Rodwell, J. S. (ed.) 1991b *British plant communities. Vol. 2: mires and heaths.* Cambridge, Cambridge University Press

Rodwell, J. S. (ed.) 1992 *British plant communities. Vol. 3: grasslands and montane communities.* Cambridge, Cambridge University Press

Rodwell, J. S. (ed.) 1995 *British plant communities. Vol. 4: aquatic communities , swamps and tall-herb fens.* Cambridge, Cambridge University Press

Rodwell, J. S. (ed.) 2000 *British plant communities. Vol. 5: maritime communities and vegetation of open habitats.* Cambridge, Cambridge University Press

Root, R. B. 1967 The niche exploitation of the blue-gray gnatcatcher. *Ecological monographs,* 37: 317-350

Rothmaler, W. 1995 *Excursion flora von Deutschland.* Stuttgart, Gustav Fischer Verlag Jena

de Rougemont 1989 *A field guide to the crops of Britain and Europe.* London, Collins

Rowlands, D. G. 1959 A case of mimicry in plants - *Vicia sativa L.* in lentil crops. *Genetica,* 30: 435-446

Salisbury, E. J. 1927 On the causes and ecological significance of stomatal frequency, with special reference to the woodland flora. *Philosophical Transactions of the Royal Society of London, Series B,* 216: 1-65

Semenova, G. and van der Maarel, E. 2000 Plant functional types - a strategic perspective. *Journal of vegetation science,* 11: 917-922

Shannon, C. E. 1948 A mathematical theory of communication. *Bell System Technical Journal,* 27: 379-423, 623-656

Shugart, H. H. 1997 Plant and ecosystem functional types. In Smith, T. M., Shugart, H. H. and Woodward, F. I. (eds) *Plant functional types - their relevance to ecosystem properties and global change.* Cambridge, Cambridge University Press: 20-43

Silvertown, J. and Dodd, M. 1996 Comparing plants and connecting traits. *Philosophical Transactions of the Royal Society of London, Series B,* 351: 1233-1239

Simberloff, D. and Dayan, T. 1991 The guild concept and the structure of ecological communities. *Annual Review of Ecology and Systematics,* 22

Sivarajan, V. V. and Robson, N. K. P. 1991 *Introduction to the principles of plant taxonomy.* Cambridge, Cambridge University Press

Smilauer, P. 1992 *CANODRAW 3.0 user's guide.* New York

Smith, T. M., Shugart, H. H. and Woodward, F. I. 1997 *Plant functional types - their relevance to ecosystem properties and global change.* Cambridge, Cambridge University Press

Snaydon, R. W. and Bradshaw, A. D. 1961 Differential responses to calcium within the species Festuca ovina L. *New Phytologist,* 60: 219-34

Sneath, P. H. A. and Sokal, R. R. 1973 *Numerical taxonomy: the principles and practice of numerical classification.* San Francisco, W. H. Freeman

Sokal, R. R. and Sneath, P. H. A. 1963 *Principles of numerical taxonomy.* San Francisco, W. H. Freeman

Sokal, R. R. and Rohlf, F. J. 1995 *Biometry – the principles and practice of statistics in biological research.* New York, W.H. Freeman and Company

Soltis, D. E. and Soltis, P. S. 1998 Choosing an approach and an appropriate gene for phylogenetic analysis. In Soltis, D. E., Soltis, P. S. and Doyle, J. J. (eds) *Molecular systematics of plants II: DNA sequencing.* Boston, Kluwer Academic Publishers: 1-42

Soltis, D. E., Soltis, P. S., Chase, M. W., Mort, M. E., Albach, D. C., Zanis, M., Savolainen, V., Hahn, W. H., Hoot, S. B., Fay, M. F., Axtell, M., Swensen, S. M., Prince, L. M., Kress, W. J., Nixon, K. C. and Farris, J. S. 2000 Angiosperm phylogeny inferred from 18S rDNA, rbcL, and atpB sequences. *Botanical Journal of the Linnean Society,* 133: 381-461

Soreng, R. J. 1990 Chloroplast-DNA phylogenetics and biogeography in a reticulating group: study in Poa (Poaceae). *American Journal of Botany,* 77: 1383-1400

Stace, C. 1989 *Plant taxonomy and biosystematics.* Cambridge, Cambridge University Press

Stace, C. 1991 *New Flora of the British Isles.* Cambridge, Cambridge University Press

Stace, C. 1997 *New Flora of the British Isles.* Cambridge, Cambridge University Press

Stammers, M., Harris, J., Evans, G. M., Hayward, M. D. and Forster, J. W. 1995 Use of random PCR (RAPD) technology to analyse phylogenetic relationships in the Lolium/Festuca complex. *Heredity,* 74: 19-27

Stebbins, G. L. 1971 *Chromosomal evolution in higher plants.* London, Edward Arnold

Stebbins, G. L. 1972a Research on the evolution of higher plants: problems and perspectives. *Canadian journal of genetics and cytology,* 14: 453-462

Stebbins, G. L. 1972b Ecological distribution of centres of major adaptive radiation in angiosperms. In Valentine, D. H. (ed.) *Taxonomy, phytogeography and evolution*: 7-34

Stebbins, G. L. 1974 *Flowering plants - evolution above the species level.* London, Edward Arnold

Strid, A. and Tan, K. 1997 *Flora Hellenica.* Königstein, Koeltz

Sukopp, H. and Scholz, H. 1997 Herkunft der Unkräuter. *Osnabrücker Naturwissenschaftliche Mitteilungen,* 23: 327-333

Susanna, A., Garcia-Jacas, N., Soltis, D. E. and Soltis, P. S. 1995 Phylogenetic relationships in tribe Cardueae (Asteraceae) based on ITS sequences. *American Journal of Botany,* 82: 1056-1068

Tauber, H. 1965 Differential pollen dispersion and the interpretation of pollen diagrams. *Danmarks Geologiske Underscgelse, Series II,* 89: 1-69

ter Braak, C. J. F. 1986 Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology,* 67: 1167-1179

ter Braak, C. J. F. 1987 The analysis of vegetation-environment relationships by canonical correspondence analysis. *Vegetatio,* 69: 69-77

ter Braak, C. J. F. and Smilauer, P. 1997-1999 *Canoco for Windows version 4.02.* Wageningen

Thompson, K., Band, S. R. and Hodgson, J. G. 1993a Seed size and shape predict persistence in soil. *Functional Ecology,* 7: 236-241

Thompson, K., Hodgson, J. G., Grime, J. P., Rorison, I. H., Band, S. R. and Spencer, R. 1993b Ellenberg numbers revisited. *Phytocoenologia,* 23: 1-13

Tomlinson, P. 1985 An aid to the identification of fossil buds, bud scales and catkin-bracts of British trees and shrubs. *Circaea,* 3: 45-130

Tomlinson, P. 1991 Vegetative plant remains from waterlogged deposits identified at York. In Renfrew, J. M. (ed.) *New light on early farming - recent developments in palaeoethnobotany.* Edinburgh, Edinburgh University Press

Tomlinson, P. and Hall, A. 1995a *The archaeobotanical computer database for the British Isles (ABSC) v.95.1.* York, Environmental Archaeology Unit

Tomlinson, P. and Hall, A. 1995b The archaeological computer database (ABCD): a guide for users. *Reports from the Environmental Archaeology Unit York,* 95/52

Tutin, T. G., Heywood, V. H., Burges, N. A., Moore, D. M., Valentine, D. H., Walters, S. M. and Webb, D. A. (eds) 1968 *Flora Europaea Volume 2 - Rosaceae to Umbelliferae.* Cambridge, Cambridge University Press

Tutin, T. G., Heywood, V. H., Burges, N. A., Moore, D. M., Valentine, D. H., Walters, S. M. and Webb, D. A. (eds) 1972 *Flora Europaea Volume 3 - Diapensiaceae to Myoporaceae.* Cambridge, Cambridge University Press

Tutin, T. G., Heywood, V. H., Burges, N. A., Moore, D. M., Valentine, D. H., Walters, S. M. and Webb, D. A. (eds) 1976 *Flora Europaea Volume 4 - Plantaginacea to Compositae (and Rubiaceae).* Cambridge, Cambridge University Press

Tutin, T. G., Heywood, V. H., Burges, N. A., Moore, D. M., Valentine, D. H., Walters, S. M. and Webb, D. A. (eds) 1980 *Flora Europaea Volume 5 - Alismataceae to Orchidaceae (Monocotyledons).* Cambridge, Cambridge University Press

Tutin, T. G., Burges, N. A., Chater, A. O., Edmundson, J. R., Heywood, V. H., Moore, D. M., Valentine, D. H., Walters, S. M. and Webb, D. A. (eds) 1993 *Flora Europaea Volume 1 - Psilotaceae to Platanaceae.* Cambridge, Cambridge University Press

van der Veen, M. 1987 The plant remains. In Heslop, D. H. (ed.) *The excavation of an Iron Age settlement at Thorpe Thewles, Cleveland, 1980-1982.* London, Council for British Archaeology, Research Report No. 65: 93-99

van der Veen, M. 1992 *Crop husbandry regimes: an archaeobotanical study of farming in Northern England, 1000BC-AD 500.* Sheffield, J.R. Collis Publications

Wagstaff, S. J. and Olmstead, R. G. 1997 Phylogeny of Labiatae and Verbenaceae inferred from rbcL sequences. *Systematic Botany*, 22: 165-179

Wagstaff, S. J., Hickerson, L., Spangler, R., Reeves, P. A. and Olmstead, R. G. 1998 Phylogeny in Labiatae s.l., inferred from cpDNA sequences. *Plant Systematics and Evolution,* 209: 265-274

Warwick, S. I. and Black, L. D. 1994 Evaluation of the subtribes Moricandiinae, Savignyinae, Vellinae, and Zillinae (Brassicaceae, tribe Brassiceae) using chloroplast DNA restriction site variation. *Canadian Journal of Botany,* 72: 1692-1701

Wasylikova, K. 1981 The role of fossil weeds for the study of former agriculture. *Zeitschrift für Archäologie,* 15: 11-23

Wasylikova, K. 1986 Analysis of fossil fruits and seeds. In Berglund, B. E. (ed.) *Handbook of Holocene palaeoecology and palaeohydrology.* Chichester, John Wiley and Sons: 571-590

Watson, L. E., Sayed-Ahmed, H. and Badr, A. 2000 Molecular phylogeny of Old World Trifolium (Fabaceae), based on plastid and nuclear markers. *Plant Systematics and Evolution,* 224: 153-171

Westhoff, V. and van der Maarel, E. 1973 The Braun-Blanquet approach. In Whittaker, R. H. (ed.) *Ordination and classification of communities. Handbook of vegetation science, part V.* The Hague, Junk Publishers: 617-726

Westoby, M. 1998 A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and soil,* 199: 213-227

Westoby, M. 1999 Generalization in functional plant ecology: the species sampling problem, plant ecology strategy schemes, and phylogeny. In Pugnaire, F. I. and Valladares, F. (eds) *Handbook of functional plant ecology.* New York, Marcel Dekker, Inc: 847-872

Westoby, M. and Leishman, M. R. 1997 Categorizing plant species into functional types. In Smith, T. M., Shugart, H. H. and Woodward, F. I.

(eds) *Plant functional types - their relevance to ecosystem properties and global change.* Cambridge, Cambridge University Press: 104-121

Westoby, M., Leishman, M. R. and Lord, J. M. 1995a On misinterpreting the 'phylogenetic correction'. *Journal of Ecology,* 83: 531-534

Westoby, M., Leishman, M. R. and Lord, J. M. 1995b Further remarks on phylogenetic correction. *Journal of ecology,* 83: 727-730

Westoby, M., Leishman, M. R. and Lord, J. M. 1995c Issues of interpretation after relating comparative datasets to phylogeny. *Journal of ecology,* 83: 727-730

Wilkinson, H. P. 1979 The plant surface. Part one: stomata. In Metcalfe, C. R. and Chalk, L. (eds) *Anatomy of dicotyledons.* Oxford, Clarendon Press. 1: 97-116

Willerding, U. 1978 Paläo-Ethnobotanische Befunde an mittelalterliche Pflanzenreste aus Süd-Niedersachsen, Nord-Hessen und dem östlichen Westfalen. *Berichte der Deutsche Botanische Gesellschaft,* 91: 129-160

Willerding, U. 1980a Zum Ackerbau der Bandkerarmiker. In Krüger, T. and Stephan, H.-G. (eds) *Beiträge zur Archäologie Nordwestdeutschlands und Mitteleuropas.* Hildesheim, August Lax: 423-456

Willerding, U. 1980b Anbaufrüchte der Eisenaeit und des frühen Mittelalters, ihre Anbauformen, Standortsverhältnisse und Erntemethoden. In *Untersuchungen zur eisenzeitlichen und frühmittelalterlichen Flur in Mitteleuropa und ihrer Nutzung.* Göttingen: 126-196

Wilsie, C. P. 1962 *Crop adaptation and distribution.* San Fransisco, W H Freeman and company

Wilson, D. G. 1984 The carbonization of weed seeds and their representation in macrofossil assemblages. In van Zeist, W. and Casparie, W. (eds) *Plants and ancient man: studies in palaeoethnobotany.* Rotterdam, Balkema: 201-206

Wink, M. and Kauffman, M. 1995 Phylogenetic relationships between some members of the subfamily Lamioideae (Family Labiatae) inferred from Nucleotide Sequences of the rbcL gene. *Botanica Acta,* 109: 139-148

Woodward, F. I. and Kelly, C. K. 1995 The influence of CO2 concentration on stomatal density. *New Phytologist,* 131: 311-327

Yasui, Y. and Ohnishi, O. 1996 Comparative study of rbcL gene sequences in Fagopyrum and related taxa. *Genes and Genetic Systems,* 71: 219-224

Zar, J. H. 1999 *Biostatistical Analysis.* Upper Saddle River New Jersey, Prentice Hall International Inc.

van Zeist, W. 1974 Palaeobotanical studies of settlement sites in the coastal area of The Netherlands. *Palaeohistoria,* 16: 223-371

van Zeist, W. 1981 Plant remains from Iron Age Noordbarge, Province of Drenthe, the Netherlands. *Palaeohistoria,* 23: 169-193

van Zeist, W. and Palfenier-Vergter, R. M. 1979 Agriculture in medieval Gasselte. *Palaeohistoria,* 21: 267-299

van Zeist, W. and Bakker-Heeres, J. A. H. 1982 Archaeobotanical studies in the Levant, 1. Neolithic sites in the Damascus basin: Aswad, Ghoraifé, Ramad. *Palaeohistoria,* 24: 165-256

van Zeist, W., de Roller, G. J., Palfenier-Vergter, R. M., Harsema, O. H. and During, H. 1986 Plant remains from medieval sites in Drenthe. *Helinium,* 26: 226-274

Zohary, D. and Hopf, M. 1994 *Domestication of plants in the old world - the origin and spread of cultivated plants in West Asia, Europe, and the Nile Valley.* Oxford, Clarendon Press

Zohary, M. 1966 *Flora Palaestina - Part 1: Equisetaceae to Moringaceae.* Jerusalem, Israel Academy of Sciences and Humanities

Zohary, M. 1972 *Flora Palaestina - Part 2: Platanaceae to Umbelliferae.* Jerusalem, Israel Academy of Sciences and Humanities

Zunk, K., Mummenhoff, K. and Hurka, H. 1999 Phylogenetic relationships in tribe Lepideae (Brassicaceae) based on chloroplast DNA restriction site variation. *Canadian Journal of Botany,* 77: 1504-1512