2

Characterization of Biodiversity

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CONTENTS

EXECUTIVE SUMMARY

• The recognition and characterization of biodiversity depends critically on the work of three scientific disciplines. *Taxonomy* provides the reference system and depicts the pattern or tree of diversity for all organisms (Chapter 2.1). *Genetics* gives a direct knowledge of the gene variations found within and between species (Chapter 2.2). *Ecology* provides knowledge of the varied ecological systems in which taxonomic and genetic diversity is located, and of which it provides the functional components (Chapter 2.3).

• There appear to be no short cuts to full examination of biodiversity. All three disciplines report in this assessment that, having characterized only part of the world's biological diversity, it will be necessary to undertake similar work to survey the remainder. While predictions can be made, they are no substitute for full enumeration. It is in the nature of biodiversity that surprises and uniqueness abound: predictive methods, such as the use of indicator species, latitudinal gradients, and mapping of hotspots, are of limited value.

• Taxonomy provides the core reference system and knowledge-base on which all discussion of biodiversity hinges: the framework within which biodiversity is recognized and in which species diversity characterization occurs. The most commonly used units of biological diversity are *species*, the basic kinds of organisms.

• Taxonomic characterization of the world's organisms is a mammoth but essential strategic task with which only limited progress has been made: just 1.75 of the estimated 13 to 14 million species have so far been described, and most of these are still poorly known in biological terms. There is not even a comprehensive catalogue of these 1.75 million known species.

• Despite its universal usage as a basic unit of taxonomy, it is difficult to agree on an exact definition of what constitutes a species. As a result there is considerable variation in concept and usage which may be reflected in differing classifications and species totals.

• Taxonomists have the task of enumerating which species exist and placing them in a *taxonomic hierarchy*. This taxonomic hierarchy serves both as a classification used for reference purposes and as a summary of the evolutionary tree. It can also be used to predict properties of certain organisms. The hierarchy is characterized by observation of the patterns of resemblances in comparative features such as morphology, anatomy, chemistry (including molecular data), behaviour and life-history.

• Systematic and evolutionary studies provide valuable knowledge about the evolutionary origins and patterns of life, the scientific map of diversity. This is the map that must be used in planning conservation, prospecting, exploitation, regulation, and sustainable use.

• It is considered important that assessments used in the evaluation of resources and conservation options make adequate use of *taxic diversity* measures which take into account not just numbers of species but their taxonomic positions and the differing contributions that different species make. The map or tree of diversity is occupied by very varied densities of species: in some parts there are thousands of species, in others just one or two. It follows that the very few species in certain parts of the pattern are of exceptionally high scientific value.

• Genetic diversity is the diversity of the sets of genes carried by different organisms: it occurs not only on a small scale between organisms of the same population, but on a progressively larger scale between organisms in different populations of the same species, between closely related species such as those in the same genus, and between more distantly related species, those in different families, orders, kingdoms and domains. Genetic diversity may be characterized by a range of techniques: by observation of inherited genetic traits, by viewing under the microscope the chromosomes that carry the genes, and by reading the genetic information carried on the chromosomes using molecular techniques.

• Genes transmit features from one generation to the next, so determining by inheritance and in interaction with the environment, the pattern of variation realized in features

seen within and between species. Similarly alterations in the genes carried forward to future generations mark the path of evolution. Yet scientists observe that in neither case is there a strictly one-to-one relationship between genetic diversity and the realized diversity of organisms characterized by taxonomists.

• Genetic analysis, including molecular techniques, provides a formidable tool for gaining access to precise gene differences both within and between species. Within species genetic details can characterise the traits and the populations on which natural selection and the process of evolution is acting. Between closely related species gene comparisons can reveal details of speciation and colonization.

• It is selection acting on genetic diversity that carries forward both ecological adaptation and microevolution: to limit or reduce the genetic diversity within a species is to limit or reduce its potential or actual role in the ecological and evolutionary development of the biosphere.

• The food plants, animals, fungi and other micro-organisms on which all humankind depend arise from genetic variants of originally wild organisms. The genetic resources in both wild and domesticated organisms thus represent a patrimony of resources for future use. Even the present well-developed food crops and animal resources are constantly at risk because of the rapid adaptation of pests and diseases: skilful and extensive manipulation of genetic resources is needed even to maintain agricultural productivity.

• Organisms are not evenly distributed: they occur in an intricate spatial mosaic, classified on a world scale into *biogeographic zones*, *biomes*, *ecoregions* and *oceanic realms*, and at a variety of smaller scales within *landscapes* into *ecosystems*, *communities* and *assemblages*.

• In terrestrial systems the community found at any one point can be characterized by the physical environment (ecoregion), the physiognomic type (biome), and the floristic/faunistic (biogeographic) zone in which it occurs. In marine systems communities are characterized in terms of the physical environment and the faunistic (biogeographic) zone.

• The units of classification used on a global scale differ in how they are recognised and consequently in the distinctions between their subdivisions. Biogeographic zones differ taxonomically in the flora and fauna present, even between areas of similar physical environment (e.g. within the same ecoregion) or similar physiognomy (e.g. within the same biome). Conversely, the physiognomic differences between biomes within one biogeographic zone are paralled by those within another.

• All existing global classifications of ecological systems are to some extent inadequate, either in their methodology or in their spatial coverage, or in both. A robust classification of the world's ecosystems which can be used to map the distribution of ecological resources is urgently needed.

• The biodiversity within an area can be characterized by measures of *species richness, species diversity, taxic diversity* and *functional diversity* – each highlighting different perspectives.

(a)   Species richness (also called α-*diversity*) measures the number of species within an area, giving equal weight to each species.

(b)   Species diversity measures the species in an area, adjusting for both sampling effects and species abundance.

(c)   Taxic diversity measures the taxonomic dispersion of species, thus emphasizing evolutionarily isolated species that contribute greatly to the assemblage of features or options.

(d)   Functional diversity assesses the richness of functional features and interrelations in an area, identifying *food webs* along with *keystone species* and *guilds*, characterised by a variety of measures, strategies and spectra.

• A serious limitation on all measures of species diversity in an ecosystem is our inability to survey all organisms at any site: only a few taxonomic groups are sufficiently known for complete field surveys to be made.

• At the smaller scale, landscapes are composed of areas characterised as ecosystems or communities. The diversity between areas is measured as β-*diversity*, the change in species present.

• *Systems diversity* is assessed as the richness of ecological systems in a region or landscape.

2.0 Introduction to the characterization of biodiversity

2.0.1 *What is biodiversity?*

As explained in Section 1, biodiversity means the variability among living organisms from all sources and the ecological systems of which they are a part; this includes diversity within species, between species and of ecosystems. Were life to occur on other planets, or living organisms to be rescued from fossils preserved millions of years ago, the concept could include these as well. It can be partitioned, so that we can talk of the biodiversity of a country, of an area, or of an ecosystem, of a group of organisms, or within a single species.

Biodiversity can be set in a time frame so that species extinctions, the disappearance of ecological associations, or the loss of genetic variants in an extant species can all be classed as losses of biodiversity. New elements of life – by mutation, by natural or artificial selection, by speciation or artificial breeding, by biotechnology, or by ecological manipulation – can similarly be viewed as additions to biodiversity.

2.0.2 *What is meant by characterizing biodiversity?*

The scientific characterization of biodiversity involves what may seem like two different processes, the observation and characterization of the main units of variation (e.g. genes, species and ecosystems), and the quantification of variation within and between them (genetic distance, taxonomic relatedness, etc.). In reality they are part of the same process: the analysis of pattern defines the units as well as characterizing their variation.

In each of the three chapters that follow an assessment is made both of the reference framework and units used, and of the methods for quantifying variation. Chapter 2.1 deals with the central issue of characterizing species or taxonomic diversity. Chapter 2.2 assesses genetic diversity that occurs both within and between species. Chapter 2.3 introduces the diversity of ecological systems in which this species and genetic diversity occurs, a theme further developed in Sections 5 and 6.

A number of techniques described here are of wide application both in characterizing diversity and in topics addressed in later sections. The molecular techniques described as part of genetic diversity (Chapter 2.2) are widely used in taxonomic analysis (2.1) and in biotechnology (Section 10). The taxic diversity measures described in 2.1 are increasingly of interest in the comparison of ecological systems (2.3). No attempt is made to appraise cultural diversity: with its human and cultural dimensions, this is left until Sections 11 and 12.

Lastly, we should comment that this assessment of characterization units and techniques leaves rather a dissected view of biodiversity at different levels of description. It is for other sections to assess our knowledge of how the system works as a whole.

2.1 Biodiversity from a taxonomic and evolutionary perspective

This chapter contains an introduction to the taxonomic and evolutionary characterization biodiversity (2.1.0–2.1.4). This is followed by an overview of the power and utility of taxonomic products in general biodiversity usage (2.1.5), and in the particular context of species diversity assessment (2.1.6).

2.1.0 *Introduction: patterns of living organisms – classification and evolution*

The study of the different kinds of living organisms, the variations among and between them, how they are distinguished one from another, and their patterns of relationship, is known as *taxonomy* or *biosystematics* (see Box 2.1-1 for strict definitions). Taxonomy is thus fundamental in providing the units and the pattern to humankind's notion of species diversity. Indeed, the first estimates of global biodiversity were those made by taxonomists.

At one end of the range of taxonomic studies are rather practical operations such as naming and cataloguing what kinds of organisms exist (including the preparation of checklists, plant Floras, animal handbooks, computerized identification tools, etc.), the information science aspect of taxonomy. At the other end are sophisticated studies of the branching tree and geographic patterns of evolution by descent (known as *phylogeny*) and taxonomic measures of biodiversity. Simple introductory texts are provided by Ross (1974), Jeffrey (1982), Heywood (1976) and Llorente-Bousquets (1990).

Despite the sometimes bewildering complexity of forms observed, biosystematists have succeeded in most major groups in recognizing the patterns of variation and occurrence that are observed. The patterns can be depicted graphically as nested hierarchies, boxes within boxes, or branching trees (Figure 2.1-1) which, as we shall see later, can be thought of either as a nested classification or as a tree of descent. This practice originated simply as a human method of organizing knowledge, as in Aristotle's principle of Logical Division (Turrill 1942), where organisms are divided into contrasted classes: A, not A; useful, not useful; woody, not woody. Similarly, in Diderot's *Encyclopédie* (Diderot 1751–65) all knowledge, including both biology and many other topics, is connected on a hierarchical tree printed inside the book's covers. But since the acceptance of Darwin's theory of evolution by descent with modification (Darwin 1859), the success of using a hierarchy is attributed to organisms having evolved by descent with modification through time, a process that produces a branching tree. The pattern of life actually is intrinsically tree-like and hierarchical in variation pattern.

At the lowest level of this hierarchy are individual organisms which live and die (e.g. a particular dog, a

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Box 2.1-1: Definitions of taxonomy and biosystematics.

A distinction between taxonomy and biosystematics

Taxonomy in the strict sense refers to all information science aspects of handling the different sets of organisms. The word is sometimes used in contexts outside biology so, strictly, one should speak of biological taxonomy. Mayr (1969) defines it thus:

Taxonomy is the theory and practice of classifying organisms.

It can be thought of as having four components (Bisby 1984: Abbott *et al.* 1985; Radford 1986; Hawksworth and Bisby 1988):

    (i) the classification

    (ii) the nomenclature

    (iii) circumscriptions or descriptions

    (iv) identification aids

Biosystematics is a broader topic, which includes taxonomy, but also includes the full breadth and richness of associated biological disciplines, including elements of evolution, phylogeny, population genetics and biogeography (Hawksworth and Bisby 1988; Quicke 1993). In the late 1930s the term systematics was used in Britain to emphasize the move away from classical taxonomy, as in the phrase 'The New Systematics', and the establishment of 'The Systematics Association'. Simpson (1961) and Mayr (1969) define it thus:

Systematics is the scientific study of the kinds and diversity of organisms and of any and all relationships among them.

Again the word is used in non-biological contexts: biosystematics makes clear the biological context.

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particular tree, a particular bacterium). Individuals occur usually as members of more-or-less continuously existing *populations,* which can be variously characterized, depending on their *breeding systems,* either as being related by the process of mating amongst their immediate ancestors (as among humans, among beetles and among palm trees), or as having a common descent from a single recent ancestor (as in the HIV virus). These populations themselves fall into patterns, some being clearly similar and of the same *species,* others being different to varying degrees and thus of different species e.g. species of rats: Norway rat (*Rattus norvegicus*), roof rat (*Rattus rattus*); species of *Prunus*: plum, cherry, peach, apricot; species of large cats: lion, jaguar, leopard, tiger. Even though the exact definition of a species is a matter for debate, the species is used universally as the basic category of the classification.

As the common names sometimes imply, some species are clearly members of recognizable larger aggregations (or the descendants of a common ancestral form) known as *genera* (singular, *genus*): e.g. date palm, canary date palm, dwarf date palm – species in the date palm genus *Phoenix.* This process of aggregating similar or related forms can be continued to form larger aggregations. Genera are aggregated into *families,* families into *orders,* and so on up the hierarchy as shown in Table 2.1-1. The higher categories of the hierarchy, such as families and orders, are vitally important for communication; they permit discussion, generalization and information retrieval about particular sets of organisms. The overall result is a hierarchical classification going the whole way from species (or even *subspecies,* or human-made varieties called *cultivars* or *breeds,* within species) up to the major *kingdoms* such as plants, animals and fungi.

To give some idea of our progress in understanding life on Earth a comprehensive, detailed classification of living organisms on earth compiled into a single work (Parker 1982) recognizes 4 kingdoms, 64 phyla, 146 classes, 869 orders and about 7000 families. However, recent advances in the study of cell organelles and DNA sequences have led to rapid changes in the topmost categories: Whittaker (1969) and Margulis and Schwartz (1982) propose five kingdoms and Woese (1994) places three domains above the kingdoms (as depicted in Figure 2.1-5). The total of 1.75 million species thought to have been described to the present day represents a small fraction of the 13 to 14 million species estimated to exist in total. There is at present no comprehensive catalogue even of these 1.75
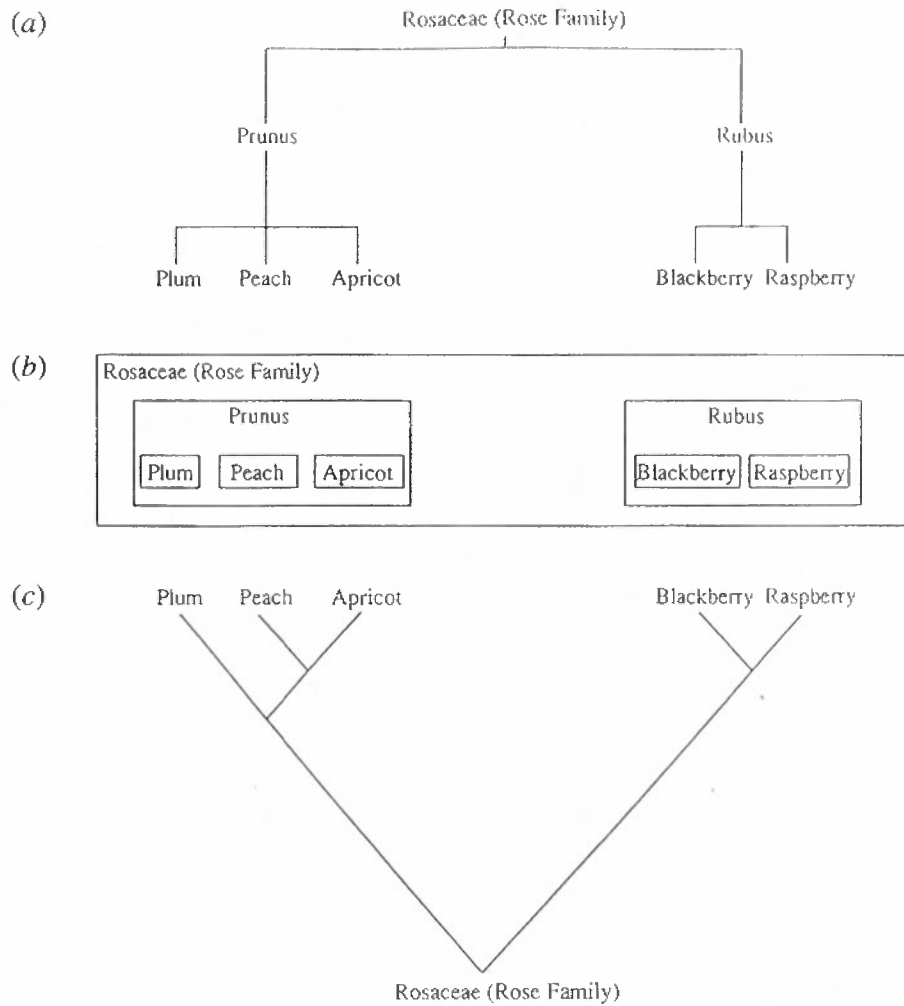
Figure 2.1-1: Three graphical representations of the taxonomic hierarchy of some members of the Rosaceae: (*a*) nested hierarchy; (*b*) box-within-box, and (*c*) a branching tree.

million species (see Chapter 3.1 for further discussion and Tables 3.1.2-1 and 3.1.2-2 for species counts).

Two properties of the taxonomic hierarchy are pivotal to its value in characterizing species diversity. First, the hierarchy provides a reference system that permits the summary, storage and retrieval of information about all organisms (Simpson 1961; Blackwelder 1967; Mayr 1969; Farris 1979; Bisby 1984). Secondly, the hierarchy attempts to be natural, by reflecting the presumed pathway of evolution and the pattern of resemblances among the organisms (Darwin 1859; Haeckel 1866; Cain 1954; Simpson 1961; Mayr 1963; Davis and Heywood 1963; Hennig 1966).

2.1.0.1 Folk classifications and the origin of scientific taxonomy

Throughout history humans have classified organisms. We use our innate classificatory abilities every day: we eat rice in quantity but not peppercorns. In supermarkets many foods are arranged by species. All human societies have *folk taxonomies* – traditional classifications of organisms often associated with cultural, survival and culinary practices (Berlin 1992). The Inuit of East Hudson Bay recognize two major kinds of animals, *umajuq* which are game animals, and *umajuquti* which are domestic ones (Atran 1990). The Tzeltal Indians of Chiapas, Mexico, use four life-forms – trees, herbs, grasses and vines (Table 2.1-2; Berlin *et al.* 1974), a system which contains logical structures (generic taxa) analogous to the genus and species of scientific taxonomy.

It is from these folk classifications that scientific taxonomy emerged, initially in Europe, bringing together the more formalized cataloguing of medicinal herbs, worldwide collecting expeditions, particularly by the seafaring nations, and the dawn of scientific discovery in biology. Mediaeval herbals contained descriptions of herbal extracts

Table 2.1-1: Major taxonomic categories.

Categories (in descending rank)		Examples	
Informal category above kingdom			
Domain	Eucarya	Eucarya	Eucarya
Formal categories recognized			
Kingdom*	Animalia	Plantae	Protoctista
Phylum (Division)*	Chordata	Tracheophyta	Ciliophora
Class (Super-, Sub-)*	Mammalia	Angiospermae	Oligohymenophora
Order (Super-, Sub-)*	Primates	Fabales	Hymenostomatida
Family (Super-, Sub-)*	Hominidae	Leguminosae	Parameciidae
Tribe (Super-, Sub-)*	Hominini	Vicieae	–
Genus (Super-, Sub-)*	*Homo*	*Pisum*	*Paramecium*
Section (Sub-)*	–	–	–
Species (Super-, Sub-)*	*Homo sapiens*	*Pisum sativum*	*Paramecium caudatum*
Variety (also Form)	–	*P. sativum* var. *sativum*	–
Cultivar Group, Cultivar	–	(Sugar Pea Group) cv. 'Olympia'	–
Further informal categories used			
Special form			
Pathovar			
Race			
Breed			

* These categories are often subdivided still further by the addition of the prefixes sub- or super- in addition to the stem ranks themselves, e.g. a superfamily may contain several families, and a family several subfamilies.

Table 2.1-2: Folk taxonomy of the Tzeltal Indians of Chiapas, Mexico (from Berlin et al. *1974).*

Category	Number of generic taxa
te? 'trees'	178
wamal 'herbs'	119
?ak 'grasses'	35
?ak' 'vines'	24
Unaffiliated taxa	97
Ambiguous taxa	18
Total	471

and crude illustrations of the plants from which they came, often with a number of animal extracts and even inanimate items alongside. The thoughtless copying of such works and the attempts to shoe-horn into them new discoveries from all over the world soon led to chaos. It was against this background that the cataloguing energies of the eighteenth century Swedish naturalist Carl Linnaeus, and the first attempts at natural classification by the French naturalists, were so badly needed.

For a long time species were named using a descriptive Latin phrase, but no formal system was widespread. It was Linnaeus who adopted the binomial system in later editions of his master catalogues *Systema Naturae* (Linnaeus 1735) and *Species Plantarum* (Linnaeus 1753), and a system of nomenclature broadly similar to his has continued to the present day. It is now formally embodied in the various

Table 2.1-3: The Codes and Committees that define rules and recommendations for the scientific names of taxa.

Relevant publication or authority	Abbreviation	Latest edition
International Code of Zoological Nomenclature	ICZN	ICZN 1985
International Code of Botanical Nomenclature[1]	ICBN	Greuter *et al.* 1994
International Code of Nomenclature of Bacteria[1,2]	ICNB	Sneath 1992
International Committee on the Taxonomy of Viruses	ICTV	Franki *et al.* 1990; Mayo 1994
International Code of Nomenclature of Cultivated Plants	ICNCP	Brickell *et al.* 1980

1. Blue-green algae (Cyanobacteria) have variously been treated as plants or bacteria, giving rise to confusing applications of both ICBN and ICNB.

2. Fungi are covered by the ICBN/as are Cyanobacteria and certain Protozoa.

international rules for nomenclature and almost universally endorsed as the *scientific names* of organisms. Starting in the same period, much of the classification that we use today was put in place by de Jussieu, Adanson, Cuvier, Lamarck and Geoffroy Saint-Hilaire. It was they who recognized the major natural groupings of animals and plants, albeit without Darwin's insights into evolution or today's understanding of phylogenetic taxonomy. The classification and nomenclature system has developed continuously from that time and now enables workers in all sorts of professions from all over the world to communicate reasonably effectively about the same organisms, be they plants, animals, fungi or other microorganisms.

2.1.1 *The basics of taxonomic characterization: what taxonomists do*

There are common elements to nearly all taxonomic studies despite the different practices relevant to different groups of organisms (Blackwelder 1967; Davis and Heywood 1963). Most studies start from the examination of live or preserved specimens, either because newly discovered specimens do not fit the known patterns, or because specimens are being re-examined to solve a problem in the existing taxonomy. Some specimens are found to belong to already-known species. They are identified and the data associated with the specimen are added to the documentation for the species, possibly adding new localities, or variations in the description. Others prove to be of a previously unnamed organism. After careful research in the literature, and thorough examination of the new taxon, a new species, subspecies or variety is described and named using the international codes of nomenclature (see Table 2.1-3).

Ideally most taxonomic studies would be *revisions* of an entire group of organisms over its complete geographical range – a whole genus, family or order – but this is difficult to achieve both because of the labour involved and because

of the logistics needed to see specimens or cultures and study the organisms over several continents. Depending on the size of the group and its distribution, it may take anything from three to ten years of full-time work, in extreme cases even a lifetime, for a taxonomist to complete. The advantage is that all species can be examined in a comparable way, and that if all have been examined, decisions and descriptions of genera and families will not be confounded by intermediate or more extreme species missed out of the study. Such studies involve examining all available specimens, often by loans from the major collections supplemented by local and specialist collections, followed by the publication of a clear summary of the taxa. It is also important to ascertain the correct name for each taxon plus synonyms where they occur.

2.1.1.1 *The role of specimens in taxonomy*

Collections of biological specimens serve several distinct fundamental functions in the characterization of biodiversity. One of these, discussed here, is as the raw material for taxonomy: all taxonomic research is based on the comparison of large numbers of specimens. Equally important for biodiversity survey and inventory is the use of these same collections of specimens as the raw data for biological recording, discussed in Section 7: the time, the place, and the species for each biodiversity data point come from one of these specimens. We thus think of the collections of living and preserved specimens as fundamental resources for biodiversity assessment world-wide, the subject of Chapter 3.2. A third, specialist, usage is for so-called *type specimens* used to fix the application of names to organisms, discussed in 2.1.1.2.

The specimens needed by taxonomists cover a very wide range: preserved specimens in museums and herbaria; living specimens in zoos, aquaria, botanic gardens, arboreta, germplasm banks and culture collections; and associated data such as descriptions, illustrations, chemical
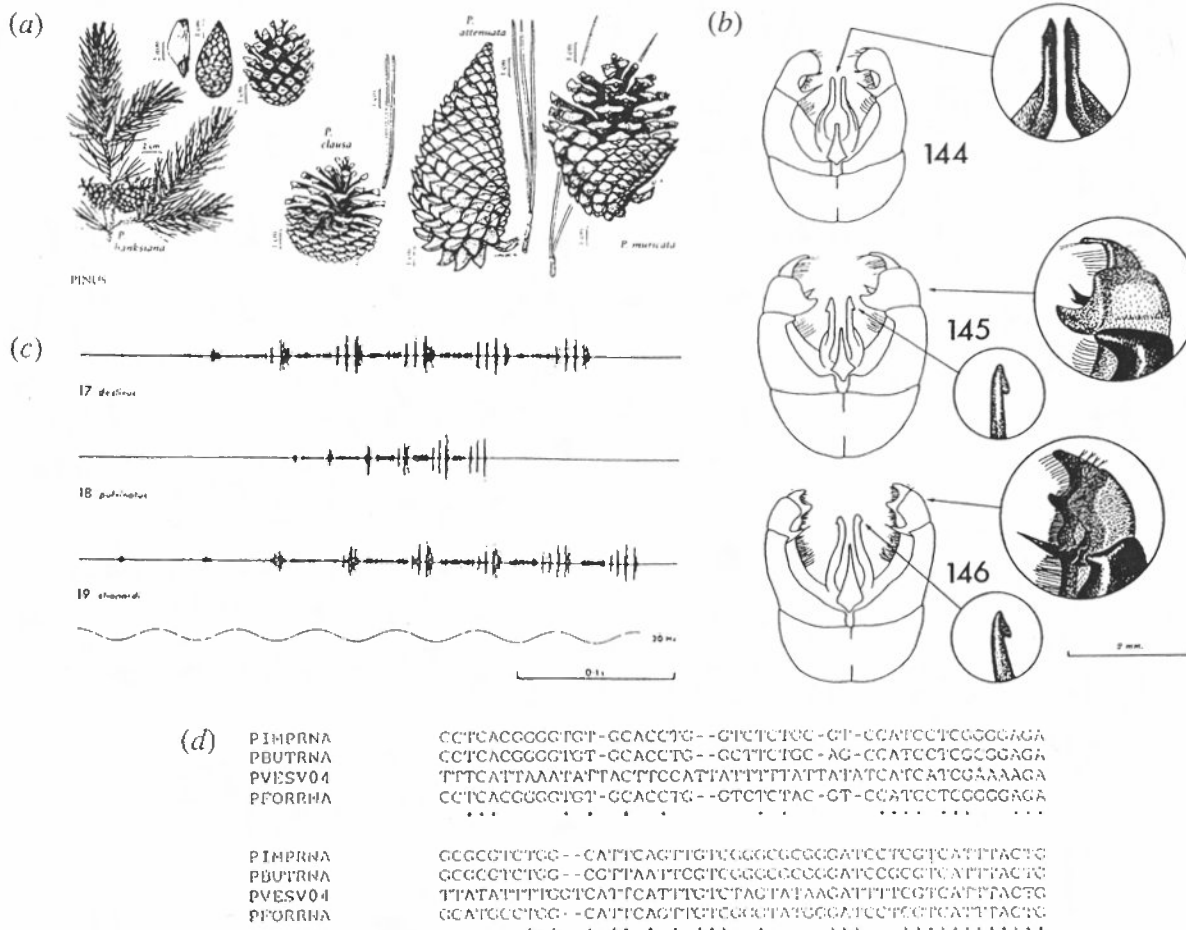
Figure 2.1-2: Comparative data in systematics: (*a*) gross morphological features in pine trees (*Pinus*, Morin *et al.* 1993), (*b*) microscopic features of genitalia in bumble bees (*Bombus*, Alford 1975), (*c*) oscillograms of grasshopper calling songs (*Enchorthippus*, Ragge and Reynolds 1984), and (*d*) 18S ribosomal DNA sequences (from the V4 hypervariable region) in flagellates (*Paraphysomonas imperforata*, *P. butcheri, P. vestita* and *P. foraminifera*, Accession Nos. Z29680, Z29679, Z28335 & Z33646 in the EMBL Sequence Data Library, communicated by J. Rice, 1995).

records, sound recordings and genome sequences stored in libraries, film and tape archives and computer databases. There is a need to marshal large numbers of specimens from the full geographical range side by side for comparison, and to document and preserve evidence of diversity with specimens providing fixed data points.

Taxonomists need to see the widest possible range of specimens for the group of organisms under study. A full geographical and ecological range, plus specimens of differing life stages and temporal variations are needed: juveniles and adults, vegetative and reproductive, male and female, winter and summer plumage, larvae, pupae and adults, seeds, eggs or spores as appropriate to the organism. The specimens used for accessing these vary from entire populations (e.g. a bacterial culture), to individual plants or animals (e.g. a pressed plant or a pinned insect), to fragments such as fruits, skulls, skins or blood samples. Associated data sets such as DNA sequences, oscillograms of animal calls and behavioural recordings may be relevant too. Some different data types are illustrated in Figure 2.1-2.

Ideally the data used for studying each group of organisms will span an immense range of characteristics drawn from different organs, different life stages and different aspects of the biology (see Figure 2.1-2). It is the morphology (physical shape and structure of the organism) and the anatomy (shape and structure of internal organs) that are most easily available and consequently most widely used. Even microscopic details, e.g. of insect genitalia or of fungal spore sculpturing, are often well preserved. Modern techniques such as electron microscopy, phytochemical analyses and DNA sequencing can often be applied to specimens of all ages.

Taxonomic research increasingly involves substantial work in the field to study the living organism *in situ*, or to establish living collections in a laboratory setting. This is an opportunity to collect data that cannot be obtained from preserved specimens, such as physiological measurements. Behaviours such as feeding or food plant preferences, locomotory patterns, microhabitat preferences, timing of sexual or other biological activity (phenology, diurnality

versus nocturnality, migration, circadian rhythms in depth for oceanic plankton), can all contribute to a systematic study. Many species build burrows, nests, brood chambers, retreats, webs, moulting chambers, egg-sacs, and other such constructs. Where these behaviours reflect heritable variation they provide valuable sources of systematic data revealing patterns of variation comparable to those in morphology and anatomy. Samples destined for gene sequencing, particular forms of anatomical comparison, or chemical analysis may require special techniques of preservation. Videotapes of behaviour or audiotapes of calls are obtainable only through fieldwork and must be stored and preserved in special repositories.

Each specimen collected in the field and deposited in one of the public collections is of potential value far beyond the particular study or programme for which it was collected. There is a consequent responsibility on the collector to establish without doubt the minimum parameters: location (increasingly giving precise latitude and longitude using a global positioning device), altitude or depth, date of collection and an identifying unique collector's name and number. Other valuable data are items that cannot be derived from the specimen at a later date – such as substrate, odour, sounds, colours (which often fade), behaviours, and position on a host. Maximum benefit will be obtained if, possibly after immediate usages, every specimen is deposited in a public collection where it can be used many times to contribute to biodiversity knowledge: the resources thus generated are reviewed in Chapter 3.2. For the system of specimen usage to work well amongst taxonomists it is important that at least one duplicate of each specimen, or the single specimen itself, be deposited at a public collection in the country of origin (this is usually a condition of collecting permits), and that such collections should make the specimens available for loan to taxonomists.

2.1.1.2 *Stability of scientific names*
The object of scientific nomenclature is to provide a stable unique name for each organism (Jeffrey 1989). The usage and giving of names is governed by the various international codes of nomenclature which, for historical and biological reasons, are slightly different for certain major groups of organisms (Table 2.1-3). All of the codes provide a mechanism for publishing a new name for a newly recognized taxon, for fixing a name to a particular organism by citing a *type*, and for arbitrating between synonyms where a taxon has accidently been named more than once, or where two taxa have been united into one. The type of a species name is a particular cited specimen in a particular collection, the *type specimen*. The continued preservation of type specimens in public collections is important so that subsequent checks can be made that the right name is being applied to the right organism.

In many cases the giving of names has proved to be a troublesome business (Quicke 1993). On the one hand it is essential that taxonomists continue to map the pattern of variation and descent: this leads to changes in the classification and consequent changes of names, an inevitable price to pay for progress. We do need these changes if modern data and new discoveries are to be incorporated into our view of the taxonomy. More troubling, however, are cases of seemingly unnecessary name changes arising from different interpretations of the rules, or the continual discovery of older names that take priority under some of the codes. Recent discussions have started a move to eliminate such nomenclatural changes, either by permitting certain names to be conserved, or by listing names in current usage and protecting them from the priority of older names (Hawksworth 1991, 1992).

Some problems arise from the existence of different codes for different groups of organisms. Certain organisms, such as the blue-green algae, have even been treated variably under one code or another, leading to ambiguity or duplication (Table 2.1-3). There are also cases of organisms under different codes being given the same name: the names must be unique but only within the domain of one code. Steps are being taken to harmonize the existing codes and a working body of IUBS is now discussing the difficult task of preparing a unified code for all organisms (Hawksworth 1994; Hawksworth *et al.* 1994).

Common or vernacular names, although often used very precisely in a given community, are usually neither unique nor universal. The problem is a tendency to re-use common names for wholly or slightly different organisms as human communities, colonial powers and languages have moved from one place to another. The names *raetam* and *retama*, for instance, cover a wide range of plant species in Arabic-, Spanish- and Portuguese-speaking countries.

2.1.2 *Characterizing flora, fauna and microbiota: preparing Floras, handbooks and keys*
One of the main tasks of taxonomy is to characterize the species of plants, animals and microorganisms so that they can be recognized, used and studied by others. With the exception of the orally communicated folk taxonomies of indigenous peoples, biologists all over the world have, since the eighteenth century, drawn their knowledge on species characterization from the primary catalogues created by the fieldwork and research of an international community of taxonomists. Key elements in these primary works are (1) the classification (what species and higher taxa exist), (2) the nomenclature (unique scientific names for the species and higher taxa), (3) descriptions of the organisms in these species and higher taxa, and (4) identification aids (with which to identify to which species and higher taxon a freshly encountered specimen belongs). Linnaeus called his primary catalogue a *Systema Naturae*

(Linnaeus 1753) and recent electronic publications use phrases such as Species Diversity Information System (e.g. the ILDIS *LegumeLine* database, Zarucchi *et al.* 1994; Bisby *et al.* 1994) and Expert Identification Systems (e.g. the ETI CD-ROM *Linnaeus Protist, Lobsters of the World,* Estep *et al.* 1992: Estep and Rey 1993; Holthius 1994): but the majority are published books called Floras, Faunas, Monographs, Catalogues, Checklists, Handbooks or Keys.

Vascular plant primary catalogues fall into two classes: Floras and monographs. Floras document all of the higher plants in a given land area, such as local Floras, national Floras and regional Floras. National Floras exist for quite a large set of nations (see Frodin (1984) for coverage) and regional Floras have been completed for the former USSR (Komarov *et al.* 1934–60), for Europe (Tutin *et al.* 1964–80) and for West Tropical Africa (Hutchinson and Dalziel 1927–36). Projects are in progress for some other regions (e.g. *Flora of North America,* Morin 1993 *et seq.*; *Flora Malesiana,* van Steenis 1948 *et seq.*) but for many species-rich tropical areas there is still no effective inventory. Botanical monographs document all plants in a given higher taxon world-wide or in a region, as in generic and family monographs.

In practice the study of a major taxon world-wide is often not practicable, so there are few world-wide monographs, mostly of genera, and rather more regional monographs of genera or families. Again, there are no recent monographs of the large or tropical plant families.

For animals, the pattern is much less tidy, and for good reason! The equivalent to the plant scene would be Faunas (all animals of an area) and monographs (all animals in a group, world-wide). But there are so many more animal species, and they belong to widely different groups, each of which may have its own discipline of specialists, such as entomologists, herpetologists, ornithologists, lepidopterists, etc. Most descriptive works are restricted to a single higher taxon and are variously local, national or occasionally regional in scope. The result is an even more patchy coverage than is found in plants with not only some overlaps, but very, very large gaps: many major groups are uncatalogued for large parts of the world. Even the best-covered countries (in Western Europe and North America) have far from complete coverage of all animal groups. Standing way above the other problems is the difficulty in cataloguing insects (over 950 000 world-wide Wilson 1992), of which the beetles, Coleoptera, dominate with 290 000 species. Where Fauna projects have been undertaken, as in the *Faune de France* (FFSSN 1921–66), the work is always segmented into different volumes researched by different authors. There are rather few guides to the coverage of the world's animals: notable are Sims and Hollis (1980), *Animal Identification* in three volumes covering marine and brackish water animals (Vol. 1), land and freshwater animals excluding insects

(Vol. 2) and insects (Vol. 3), and *Key Works for Northwestern Europe* (Sims *et al.* 1988).

Lastly – what is the level of treatment of the other major groups, such as marine and lower plants, marine animals, fungi, bacteria and the viruses? There are some groups that are partially covered: the bryophytes, mosses and liverworts (rather few species and reasonably accessible to field botanists), fish (of economic importance), some bacteria (of medical importance) and some fungal groups (of economic importance). For most of the rest, coverage is sparse indeed: few coherent catalogues exist even for the many species known to taxonomists, let alone the vast numbers of species yet to be discovered.

2.1.2.1 *The amount of research work involved*

The type and amount of research needed to create one of these primary works varies enormously, particularly with how many species are to be covered, whether the group of organisms is well or poorly known, and how well explored is the region to be covered. For poorly-known groups and little-explored areas, years of field exploration may be needed both to accumulate sufficient specimens of each species encountered and to increase the chances that all species in the area have been encountered. Conversely, for well-known groups and much-explored areas there may already be a plethora of material lodged in museums or herbaria: the problems relate more to seeing all this material (borrowing it or visiting it), and to sorting out conflicts in existing taxonomic treatments of the organisms. Depending on how full a treatment is prepared, and particularly on whether all four elements are represented (classification, nomenclature, description and keys), the creator of the work will need to pass the following milestones:

1. Form a concept of the exact set of species being treated, often involving decisions on:

   - what are the species: how are they delimited, how are problems of apparent overlap, intermediacy, hybridization and discontinuity dealt with;
   - how are these species classified, either within the existing published classification, by extending the classification, by adjudicating between alternative views, or by creating a new classification.

2. Form an opinion on the correct (or new) name for each species and each higher taxon, and on the names and taxa from other treatments to be placed in synonymy.

3. Create a description of each species by studying the range of variation within that species as evidenced by field observations or by examining preserved specimens. The range of variability in one area may be greater or

Figure 2.1-3: (*a*) Annual rates of production of the major regional Floras (Polhill 1990).

Flora	Started	First issue	Species published	Total	%	Species/ year	Actual or projected completion
Europaea	1958	1964	11 557	–	100	770	1978
SSR	1931	1933	17 520	–	100	515	1964
Australia	1979	1981	2 631	18 000	15	329	2043
West Tropical Africa	1951	1954	7 349	–	100	387	1972
Neotropica	1968	1968	4 624	90 000	5	220	2397
Southern Africa		1966	2 834	19 500	15	123	2124
Zambesiaca	1956	1960	3 215	9 300	35	110	2044
Tropical East Africa	1949	1952	6 425	10 500	61	173	2013
Malesiana	1947	1954	4 837	25 000	19	138	2135

(*b*) Total number of species treatments published in major regional Floras, in five-year intervals (Polhill 1990).
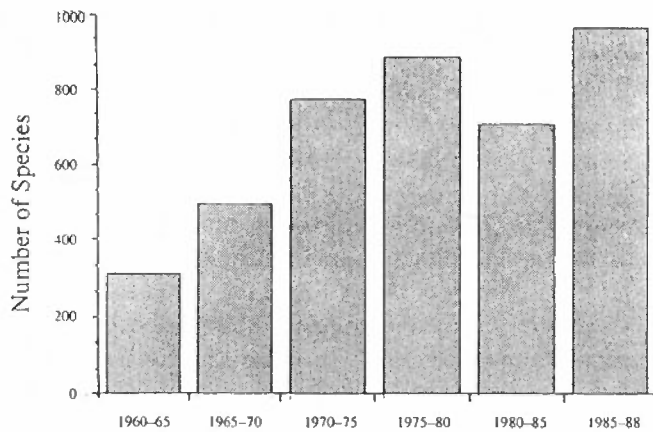
less than that recorded in other works for other areas. Additional descriptive features such as illustrations, distribution maps, ecological features, etc. may be added as well.

4. Create an identification key that leads unambiguously to an identification for freshly encountered specimens. Where possible easily visible, clearly demarcated characters should be used.

To give some idea of the amount of work involved, we cite the successful completion of *Flora Europaea* (Tutin *et al.* 1964–80). Its five volumes, containing a medium (synoptic) rather than full treatment of 11 557 plant species from the well-known, well-collected flora of Europe took 25 years work for a network of full- and part-time specialists to complete. But progress is much slower in the tropical regional Floras where more original research and fieldwork is needed, as illustrated in Polhill's (1990) comparison of nine regional Floras summarized in Figure 2.1–3 *a* and *b*.

Floras, Faunas, monographs, many handbooks, and guides all tend to contain all four elements – classification, nomenclature, descriptions and keys. However, there can be substantial variations in how complete the descriptions are, whether voucher specimens are cited, whether illustrations and maps are included and in the extent of additional ecological, behavioural or economic information given. Checklists normally contain the classification and nomenclature of species, but accompanied by just a geographical distribution – no descriptions or identification aids. They are produced either as quicker projects, or to cover a wider geographical or taxonomic range than could otherwise be contemplated for full treatment. Keys are sometimes published alone, as a preliminary to fuller treatment, as companions to existing works, or to resolve urgent needs for identification in economic or medical contexts.

2.1.2.2 Modern developments: databases and expert identification systems

This is written at a time of unprecedented change in the technology and dissemination of primary and other taxonomic works. Information technology is rapidly

bringing in electronic communication amongst dispersed taxonomic contributors working as teams, the creation of major taxonomic works as databases, and the electronic dissemination of information to users by communications networks such as Internet or by CD-ROM disks. Some of the electronic products are simply electronic versions or compilations from existing primary works, but increasingly major primary projects are being compiled in this way: for instance the ICLARM/FAO FishBase international project on fish (Lourdes *et al.* 1994; Froese and Pauly 1994) incorporates the primary database on fish genera and species (Eschmeyer 1990, 1992), and the ILDIS species diversity system on legume plants is based on a fresh synthesis of the species taxonomy of Leguminosae by a world-wide network of experts (Zarucchi *et al.* 1994; Bisby *et al.* 1994).

A particularly important development is the bringing together of two technologies, the use of descriptive data tables in computer identification routines (Pankhurst 1975, 1978, 1991; Dallwitz 1974, 1980), and the facilities in modern computing environments to use windows containing diagrams, illustrations, photographs and maps. The resulting expert identification systems such as those produced by the Dallwitz school using the DELTA format (*Beetle Larvae of the World*, Lawrence *et al.* 1994; *Families of Flowering Plants*, Watson and Dallwitz 1994) and by ETI, the Expert Centre for Taxonomic Identification (*Linnaeus Protist*, Estep and Ray 1993; *Lobsters of the World*, Holthius 1994) are surely the sign of things to come.

Electronic means are also opening up the possibility of creating master catalogues both of larger and larger groups, and eventually of all known organisms. The IOPI World Plant Checklist (Burnett 1993; Bisby *et al.* 1993) and the BIOTA Terrestrial Arthropods projects (Hodges and Thompson, in press), for instance, propose to list all plants and all terrestrial arthropods. Very many groups of organisms now have rapidly progressing master catalogue systems (Bisby 1993, 1994) and the Species 2000 program of IUBS, CODATA and IUMS is proposing that many of these create a federated system which could lead to an index of all of the world's known organisms.

2.1.3 *Characterizing systematic patterns: the species, their evolution and their classification*

With the publication of Darwin's *On the Origin of Species...* in 1859, a major change was initiated in the way that the hierarchy of life was understood. Darwin's theory of evolution made sense of the natural patterns observed in the variation between organisms. Evolution occurs when organisms experience genetic mutations or recombinations, or when gene frequencies in populations change because of differing rates of reproduction or mortality. Through natural selection or genetic drift these heritable changes may spread throughout the population and over time can

lead to the production of new lineages closely similar to their relatives but differing by the possession of one or more new features (Ridley 1985, 1993; Futuyma 1987; Skelton 1993). If this new lineage continues to diversify throughout evolutionary time-spans, a wholly new higher taxon (lineage or clade) comes into being. Such lineage diversification produces a strictly hierarchical pattern. The roughly 4.5 billion years of biotic evolution has led to an enormous diversity of living forms on Earth. These forms can be grouped as sets within sets (a nested, hierarchical pattern) based on how recently they shared a common ancestor.

Darwin's observations of selective breeding and the way in which characteristics could be inherited, coupled with the immense diversity of different forms, for example of the birds and reptiles he saw on his voyage to the Galapagos, suggested to him that heritable differences between individuals could build up to produce new species and consequently higher taxa over long periods of time. Darwin himself was unaware of the mechanisms of genetics, but later studies have revealed how characters are heritable and mutable. Genetic mutation and recombination can each produce heritable novel characters which either by the process of natural selection or by non-selected random genetic drift lead to populations in different places diverging from one another over time (refer to Chapters 4.2 and 4.3).

Thus the products of evolution are arrayed in natural groups which all people, to a greater or lesser extent, can recognize. The evolutionary explanation of this pattern and diversity is the most important rationale for the taxonomic system used by scientists. This arrangement of the diversity of forms of organisms into a hierarchy serves our goals of communication, and information storage and retrieval, by reflecting the evolutionary process that created these forms in the first place.

2.1.3.1 *Analysing systematic data to reconstruct evolutionary history*

The results of the evolutionary process described above can be reconstructed by careful comparative study of the taxa involved (Hennig 1966; Eldredge and Cracraft 1980; Wiley 1981; Crisci 1983; Forey *et al.* 1992). Evolutionary mutation results in one of three patterns: new features arise, old features are lost, or pre-existing features are transformed to a greater or lesser extent. Any of these patterns are evolutionary changes. In practice, taxonomists find such heritable changes at all levels of the taxonomic hierarchy and at all levels of organismic organization, from single changes in DNA sequences to large changes in skeletal organization or even the entire body plan of the organism.

Because descendants inherit the features of their ancestors, a new mutation that first appeared in the ancestor

tends to be passed to its descendants. The set of all organisms, living and dead, that descended from that original modified ancestor is known as a lineage or clade. The novel mutation is known as a character, trait or feature. The old version of the trait is termed primitive, and the new version is derived. Over immense spans of geological time, speciation may occur so that the lineage splits into several to many species. Subsequently mutations may occur that delimit subsidiary lineages. From a strictly taxonomic point of view, why these changes occur, or whether they are beneficial, neutral or even detrimental to the species in which they occurred is irrelevant. What matters is that any given group of taxa both agree and differ in which characters they possess. Thus spiders are the only Arachnids that have terminal abdominal spinnerets and thoracic poison glands that open through the fang. On the other hand, only some spiders can make viscid, sticky silk; the webs of other species are dry. The simplest hypothesis is that the common ancestor of all spiders had spinnerets and fangs, but that only the common ancestor of a particular subset of spiders made viscid silk. For this simple case it is easy to see how important events in evolutionary history are reconstructed. The evolution of poison fangs and spinnerets marks the origin of spiders, and the invention of viscid silk marks the origin of a particular subfamily of spiders, the Araneoidea.

In evolutionary theory, characters of organisms that are similar because of inheritance from a common ancestor are called homologies. Classic examples are the wings or feathers of birds. No other group has feathers, and close examination of any feather discloses additional complex similarities that substantiate the homology of feathers. Another example is the sting of a wasp, actually the modified female ovipositor. Only some Hymenopteran species have stings, and in all of these species the sting is always the modified female ovipositor.

If evolution consisted only of the gain of complex homologies that were never lost by descendants, reconstructing evolutionary history would be simple indeed. Two processes complicate the issue. First, natural selection is amazingly efficient at moulding what appears to be the same feature from different starting points, a phenomenon termed evolutionary convergence. The wings of birds and bats are so similar that many years ago the homology of the two features was an open question. Detailed comparison, however, revealed substantial differences. The fleshy, spiny stems of some African *Euphorbia* plants are convergent on those of New World cacti. Porpoises are mammals, not fish, despite their fins. However, often the only way to test if two features are convergent or truly homologous is through quantitative analysis.

The second process that complicates systematic analysis is loss of features. Snakes originally had two pairs of limbs like other terrestrial vertebrates, but most have lost all trace of
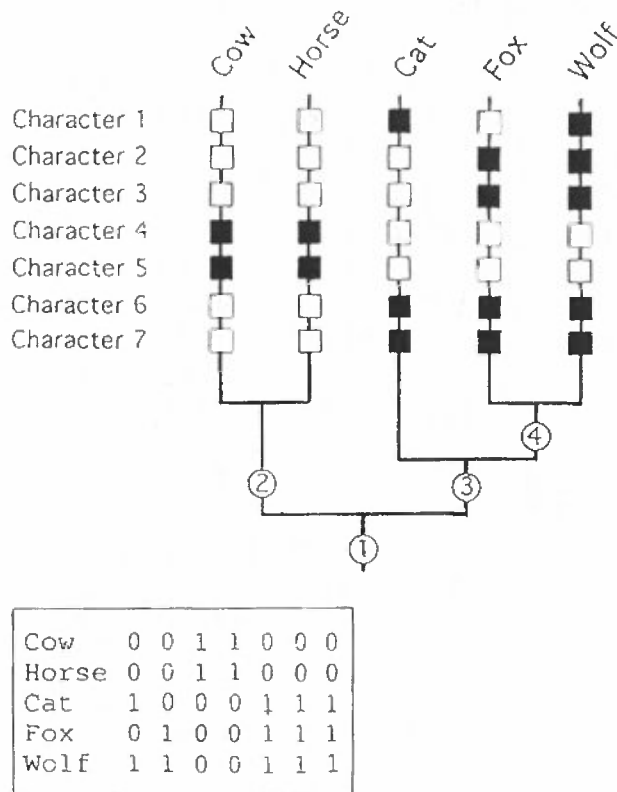

Figure 2.1-4: A simple data matrix and the implied phylogenetic hypothesis of four taxonomic groups.

Cow	0	0	1	1	0	0	0
Horse	0	0	1	1	0	0	0
Cat	1	0	0	0	1	1	1
Fox	0	1	0	0	1	1	1
Wolf	1	1	0	0	1	1	1

them. Fleas may not have wings, but many other features betray their relation to winged insects. Once again, it is frequently impossible to distinguish secondary loss of features from primitive absence except through quantitative analysis.

In practice, systematic data are compiled as a matrix of characters by taxa and analysed quantitatively by computer. By reading across (or down) the matrix, one can either read off all the relevant characters of a particular taxon, or conversely see which of a number of taxa possess a particular feature. The computer analysis is designed to provide the best possible estimate of the phylogeny of the group (as described above), expressed as a branching diagram or evolutionary tree. Such diagrams are often called trees, phylograms, dendrograms, or cladograms (because they indicate relationships between clades of organisms). For simple examples of straightforward data, the best estimate of the phylogeny is often obvious (Figure 2.1-4), but for larger numbers of taxa and characters, computer algorithms are used to produce estimates (Kitching 1992). A number of different algorithms are currently available (e.g. parsimony, maximum likelihood, or neighbour-joining techniques), and the subject of which provides the best estimate under what circumstances is an area of very active research (Swofford and Olsen 1990).

Box 2.1-2: The relationships of the cow, horse, cat, ox and wolf.
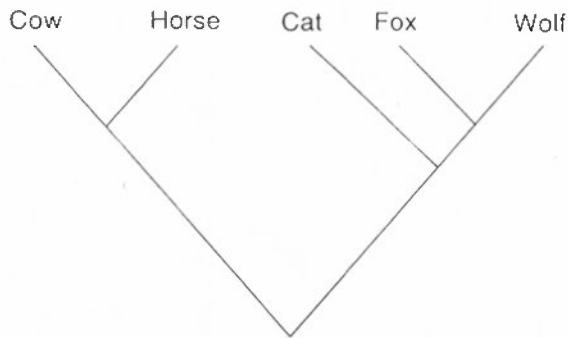
For this tree the groups are:
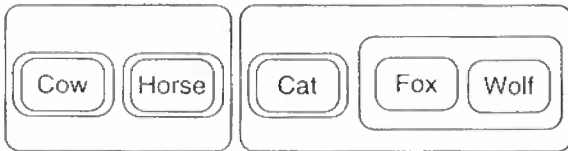
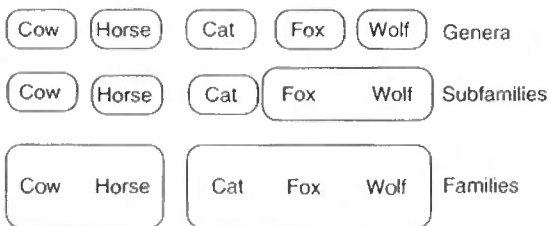and these groups can be converted to taxa in the taxonomic hierarchy:

2.1.3.2 *From phylogenetic trees to formal classifications*

The trees that result from comparing characters in species are usually thought to be a graphic representation of the evolutionary relatedness of the taxa. These trees should be viewed as relative statements of relationship. For example, in Box 2.1-2 the wolf and the fox are hypothesized to share a more recent common ancestor with one another than with the cat, but the cat, wolf and fox all share a more recent common ancestor with one another than with the hoofed mammals such as cow and horse: the tree, therefore, shows a hierarchy of relationships. A tree does not explicitly hypothesize ancestor–descendant relationships. For example, the tree hypothesizes that wolf and fox are related, but not that wolves evolved from foxes or that foxes evolved from wolves.

One of the tasks of a taxonomist is to convert this graphic representation of relationship into the formal hierarchical classification of taxonomic categories such as genus, family, order, etc. In converting the tree to a classification, the systematist gives groups that share a common ancestor the formal taxonomic names. Such groups are called *monophyletic taxa* and they are

recognized because they share unique derived characters. The tree shows several sets of most closely related taxa that are nested within larger sets that contain additional taxa. These larger groups are, in turn, nested within even larger groups. By this process the phylogenetic tree is transformed into the taxonomic hierarchy used as a classification. In creating categories, systematists choose sets that naturally reflect the hierarchy inherent in the tree.

Despite the utility of the traditional taxonomic hierarchy in summarizing diversity and evolutionary relatedness, there are real problems in incorporating elements of the phylogeny into the hierarchy in a precise way. The difficulties relate to the subjectivity in deciding taxonomic rank, and the fact that phylogenies often imply hierarchies with more levels and greater asymmetry than is allowed in the taxonomic hierarchy. A simple example given in Box 2.1-3 makes this clear.

Some biologists (lumpers) stress similarities held in common by the organisms being studied and so tend to group several species into a single genus as in Box 2.1-3 (*a*). Others (splitters) stress differences between the species and so tend to divide the species into several different genera (Corliss 1976) as in Box 2.1-3 (*d*).

As a group of species is studied in more detail, it is not uncommon for it to be ever more finely subdivided or for the group as a whole to be elevated to a higher taxonomic category. This simply reflects the fact that detailed study uncovers more characters that emphasize the differences among the species. Microsporidia, which comprise a unique group of obligate, intracellular parasitic protists, are such a group now receiving increased taxonomic attention. Until recently, their ubiquity did not cause a threat to humans and few systematists worked to describe and classify the species. But since 1985, physicians have documented an unusual rise in worldwide infections in AIDS patients caused by four genera (*Encephalitozoon*, *Nosema*, *Pleistophora* and *Enterocytozoon*), and identifying microsporidian species is impeding diagnosis and effective treatment of patients. As a result, research has been focused on the group and the number and diversity of forms observed have risen sharply.

2.1.3.3 *Why do classification schemes change?*

Scientists working in genetic resources, biotechnology, agriculture, conservation and other disciplines that use existing classifications are often disconcerted to find that systematists change the classification scheme. These changes are, however, just the logical consequences of discovery of new data and new taxa, and correction of two kinds of mistaken interpretation.

New technologies constantly give rise to new sources of character information. New information reveals new similarities and differences among taxa that cause us to revise the placement of a taxon in a tree, or to choose to

Box 2.1-3: A phylogenetic tree which shows relative relatedness between ten species (A–J).
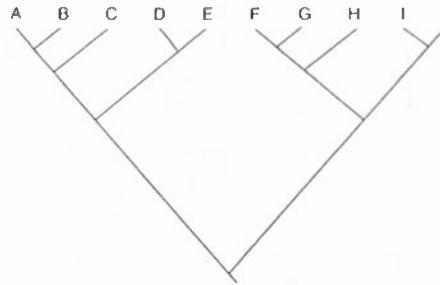
In this tree, A and B share a common ancestor and so are called sister taxa. Examining this tree you see that D and E, F and G, and I and J are also sister taxa. The sister group to species C is the group A + B, and so forth. There are several different ways to sort these species into acceptable, monophyletic genera, shown below. For example, the decision to place taxon C as one of many species in a genus (*a*) or as a single species in its own genus (*d*) is an artificial decision based on the personal preference of the taxonomist.
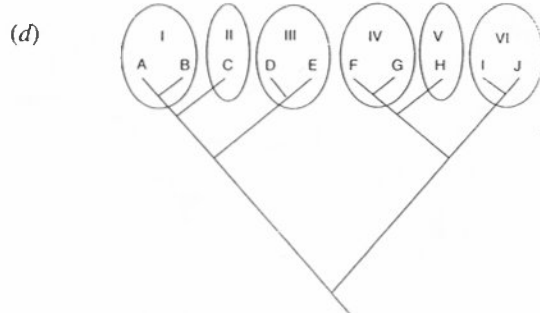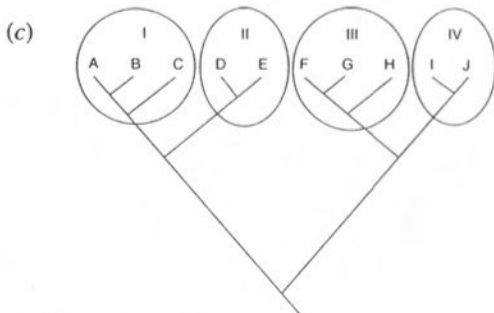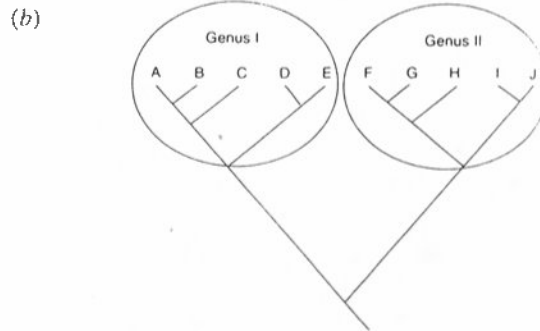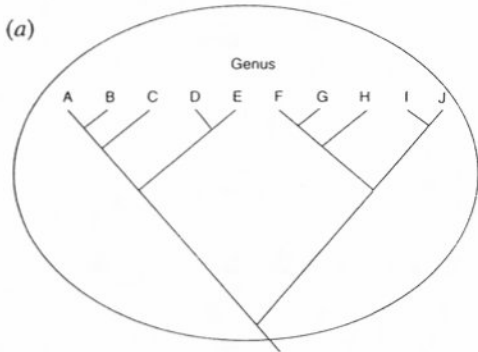
lump or split a taxon within an existing classification. An example of this sort of change is illustrated dramatically by the revision of prokaryote classifications resulting from molecular genetic data that have become available only within the past decade (Figure 2.1-5).

The discovery of previously unknown species will also change classifications. If unique, these species will have to have new taxa created for them. In addition, they have new characters or new combinations of characters whose study revises our hypotheses about evolutionary relationships of all the taxa. There have been some recent spectacular discoveries of new vertebrates such as the plankton-feeding megamouth shark described in 1983, the Vu Quang antelope of Southeast Asia in 1993, and the golden bamboo lemur (*Hapalemur aureus*) from Madagascar in 1986. But

this is only the tip of the iceberg. Many more new species (especially microscopic organisms) are waiting to be discovered. Indeed, we cannot presently say how many species exist on Earth and some people's estimates range over an order of magnitude, from 5 to 80 million species. For most species that have been documented, relatively little is known about their historical relationships, biological characteristics, or distributions within the Earth's habitats and ecosystems.

The first common sort of interpretative mistake that bedevils systematic analysis is the discovery that the defining features of a taxon are convergent rather than homologous (see 2.1.3.1). The taxon then is known to be *polyphyletic* (the taxa do not share a recent common ancestor but instead the group has been defined by a
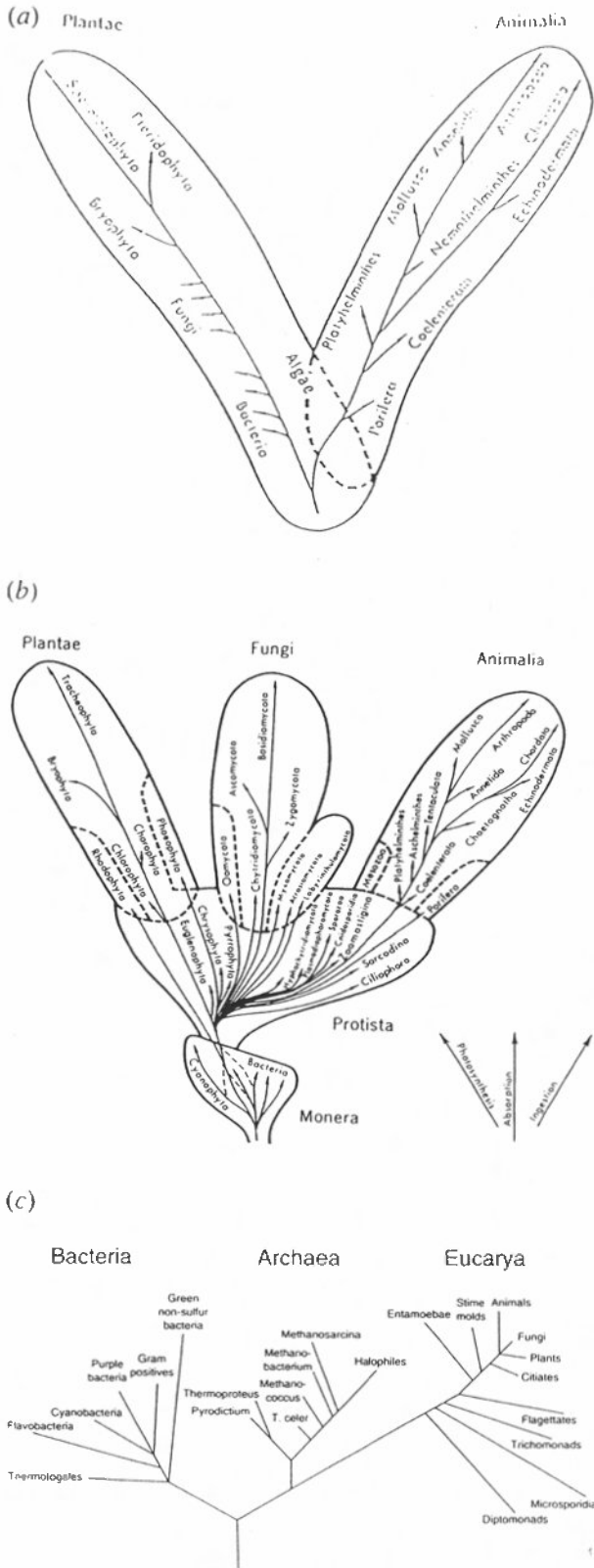
(a) Plantae ... Animalia

(b)

Plantae   Fungi   Animalia

Protista

Monera

(c)

Bacteria   Archaea   Eucarya

Figure 2.1-5: Fundamentally fifferent views of the taxonomy of life based on (*a*) gross morphology (two kingdoms as reconstructed by Whittaker 1969), (*b*) cell structure and organelles (five kingdoms, Whittaker 1969) and (*c*) DNA sequence data (three domains, Woese 1994).

superficial similarity that does not indicate evolutionary relatedness). When this happens, the polyphyletic groups are abandoned and several monophyletic taxa are created in its place. For example, in Figure 2.1-4. the evidence of character 1 conflicts with that of 2 and 3. Either characters 2 and 3 are homologous and 1 is convergent, or the reverse. If scientists did not know of characters 2 and 3, but only of 1 and 4–7, the evidence of character 1 would group the cat with the wolf to the exclusion of the fox. Hence discovery of characters distributed as 2 and 3 can change phylogenetic hypotheses. In practice, most systematists do not change official classifications until the new results have been corroborated and widely accepted, but the pace of taxonomic discovery is so fast that classificatory change is still rather frequent. A real example is the almost complete restructuring of bacterial classification in the last 15 years (Figure 2.1-5).

The second common error found in taxonomic classifications occurs because primitive features of organisms have been mistakenly interpreted as novelties, or derived features, and used to define a group (see 2.1.3.1). In Figure 2.1-4, the cow, horse and cat are alike in characters 2 and 3. However, grouping these three taxa on the basis of characters 2 and 3 would be incorrect because they share no unique common ancestor. The only ancestor that includes cows, horses, and cats also includes foxes and wolves. The implication is that any biological prediction made for cows, horses and cats will either be true also for foxes and wolves (if it evolved at node 1, Figure 2.1-4), or for an even more inclusive group of mammals (if it evolved prior to node 1). Groups defined by primitive features are called paraphyletic because they include only some of the descendants' most recent common ancestors. For example, scientists used to call all animals except vertebrates the Invertebrata. But the only defining trait of invertebrates is the absence of a vertebral column, an absence equally well shared with tomatoes and, for that matter, stones. Aside from the original observation (that some species lack vertebrae), invertebrates as a group share no traits not also present in at least some vertebrates.

2.1.4 Characterizing species

For as long as humans have observed the tremendous diversity of life, they have attempted to sort organisms into recognizable kinds and to give names to them. In all groups of organisms the basic unit of classification is the *species*. The earlier concept of fixed and unchangeable kinds can be traced to the idealism of Plato and Aristotle. Belief in the notion of fixity continued to influence biology into the ninteenth century until destroyed by evolutionary thinking.

Today, species are recognized and conceptualized in three rather different ways. They may be seen to be distinct (the *morphological species concept*); members of the species may be united by shared inheritance from common ancestry (the *phylogenetic species concept*); and there may

be biological processes such as mating, recognition and behaviour that unite members of one species and distinguish them from others (the *biological species concept*). In many groups large numbers of species are easily recognizable, and, if investigated sufficiently, may satisfy all or several of these criteria. But in other groups and in other species, variation patterns may be obscure or insufficient information may be available: in some it may be difficult to find a workable species concept, in others a minority of species are in complexes where the boundaries are uncertain. It is, after all, an amazing achievement even to attempt to categorize into comparable units organisms as different as elephants and bacteria. Despite the universal and successful usage of the species, its precise definition is, and probably always will be, the subject of vigorous debate within the taxonomic discipline. There is no scientifically precise, universally applicable species definition. In practice there is no choice but to pursue a pluralist approach, using where appropriate one or other of the three main concepts given above.

A theoretical view is that each element in the classification is a hypothesis. This illustrates nicely the relation between the three main species concepts. The description of a species on the basis of the morphological concept is interpreted as hypotheses that (1) its unifying characteristics were inherited from common ancestors (the phylogenetic concept) and (2) there is in place some biological mechanism that maintains its distinctness from adjacent species (the biological concept). These hypotheses can then be tested.

The time when the species was considered the smallest unit of variation observed is long past. Detailed observation and knowledge of genetics mean that today biologists are extremely conscious of the range of variation that occurs within each species (see Chapter 2.2), and of the possibilities for classifying subunits within the species – subspecies, varieties and informal races in the wild; or cultivar groups, cultivars and breeds under domestication (see Table 2.1-1). However, the morphological and phylogenetic species concepts do still depend on being the smallest unit that is clearly distinct, or clearly diagnosable.

2.1.4.1 *The morphological species concept*

The most widely used method of recognizing species is referred to as the *morphological species concept*, defined in Box 2.1-4. The term morphological is, however, a misnomer as the concept is applied to any sort of comparative information on heritable characteristics (Davis and Heywood 1963) such as data on behaviour, phytochemistry and microanatomy. In the ideal case there is continuity of variation within and a distinct discontinuity between species. In practice it is the presence of clear discontinuities such as a correlated discontinuity in two or more characters that circumscribes the species (Hedberg 1958; Davis and Heywood 1963). Ideally all members will possess the diagnostic

characters of the species. In reality some species are polythetic, that is, defined by a combination of characters, any one of which might be absent in one member of the species, a property analogous to fuzzy sets in mathematics.

A variant of this concept is the *monotypic species*, widely used in the great Russian schools of taxonomy. Here emphasis has been on the smallest indivisible unit, that is, on uniform homogeneity within the units rather than clear discontinuity between them (Komarov 1944; Juzepczuk 1958). Such a system was considered by some authors to be advantageous in floristic work and in inventorying natural or genetic resources: every recognizably distinct form is named and catalogued separately.

A special case is used in the recognition of bacterial species where there are few morphological features. The DNA/DNA hybridization technique is used to assess the DNA resemblances of different bacterial strains. Strains with DNA resemblances above 70% are treated as members of the same species.

2.1.4.2 *The biological species concept*

In the nineteenth and early twentieth centuries attention turned to species as biological units, giving rise to what we now call the *biological species concept* (defined in Box 2.1-5). The concept emhasizes interconnected populations of interbreeding organisms. The key criterion for delimiting species boundaries is *reproductive isolation* (Vavilov 1931; Mayr 1963, 1970; Zavadsky 1968). The classical literature also refers to the *polytypic concept*, referring to something broadly equivalent to the biological species (Vavilov 1931;

Box 2.1-4: Morphological species concept.

Morphological species concept (Du Rietz 1930; Cain 1954; Mayr 1963; Shaw 1964)

The smallest natural populations permanently separated from each other by a distinct discontinuity in the series of biotypes.

Comment: The concept most commonly used by practising systematists. Many schools of application suggest a minimum of two correlated characters to characterize a sufficient discontinuity.

Criticism: Morphological or comparative criteria may not reflect actual links that hold organisms together into a natural unit. In sexually outbreeding organisms, some morphologically distinctive forms can freely interbreed to produce healthy, fertile offspring while other similar forms do not interbreed. Well known cases include cryptic species, polytypic species and ecophenotypes (Mayr 1963, 1982).

Box 2.1-5: Biological species concepts.

Biological species concept I (Dobzhansky 1937; Mayr 1940, 1969)

> *A species is a group of interbreeding natural populations that are unable to successfully mate or reproduce with other such groups.*

Comment: One of the most popular species concepts because it conforms to the popular view of how evolution occurs. An important point of this definition is that species are not distinguished by degree of difference, but by failure to reproduce with other species. Two species may appear extremely similar, but if they do not interbreed then they are two distinct species.

Criticisms:

(a) It is irrelevant to asexual or parthenogenetic organisms where reproduction occurs without interbreeding even though their role in the ecosystem is the same as sexual species.

(b) Relatedness and ability to reproduce are not always tightly linked (Rosen 1979; Baum 1992).

(c) The amount of interbreeding between groups varies and it is not clear how much is necessary to identify two groups as belonging to the same species or how little indicates that the two are separate species. This question has been particularly troublesome in botany where phenomena such as natural hybridization, polyploidy, apomixis and interspecific introgression (see Chapter 2.2) complicate the delimitation of species (Levin 1979; Grant 1981).

(d) Although the biological species concept may be accepted by biologists as an accurate description of what species are, it may not be used in practice by systematists because it can rarely be applied to real groups of organisms. Often reproductive isolation is inferred (not observed) from the absence of individuals with intermediate characteristics between two groups or by making assumptions about specific evolutionary processes (Mishler and Brandon 1987). Interbreeding is very difficult to observe in nature especially if groups are geographically or temporally separated. The systematist is effectively left having to guess whether groups would interbreed if they were living in the same time and place. Simply bringing the groups together in captivity or cultivation and seeing if they will cross is not sufficient as it is well known that under such artificial conditions many organisms will fail to breed even if they are members of the same species in the wild. Furthermore, separate species may breed in artificial conditions, even if they would not do so in the wild.

Biological species concept II (Mayr 1982)

> *A species is a group of interbreeding natural populations unable to successfully mate or reproduce with other such groups, and which occupies a specific niche in nature.*

Comment: The introduction of 'niche' broadens the original biological species concept to include asexual and parthenogenetic species.

Criticisms: Criticisms b, c, and d of the biological species definition I (above) also apply to this concept. Furthermore, problems with defining 'niche' make this concept hard to apply in natural settings (Hengeveld 1988).

Recognition species concept (Paterson 1978, 1982, 1985; Vrba 1984)

> *A species is a group of organisms that recognize each other for the purpose of mating and fertilization.*

Comment: This concept shifts attention from isolating mechanisms as barriers to breeding, to features that facilitate breeding among members of a species. It is supposed that the systematist is able to determine what features are important to the organisms in mate recognition. If this is possible, one could distinguish natural species in the same manner that the organisms do.

Criticism: Determining whether a feature is used to recognize potential mates is difficult or impossible to do in many wild populations. Furthermore, species that occasionally form hybrids would be considered the same species by this concept (Butlin 1987).

Cohesion species concept (Templeton 1989)

The smallest group of cohesive individuals that share intrinsic cohesion mechanisms.

Comment: Like the biological species concept and the recognition species concept, the cohesion concept accepts interbreeding ability as a mechanism that binds organisms into a group. In addition, it recognizes other mechanisms, such as niche requirement, as causing cohesion too.

Criticism: Cohesion is operationally difficult to recognize and applying this concept to problems of recognizing species in nature is almost impossible. Furthermore, it is not clear how to interpret varying degrees of cohesion between groups (Endler 1989).

Ecological species concept (Van Valen 1976)

A lineage which occupies an adaptive zone different in some way from that of any other lineage in its range and which evolves separately from all lineages outside its range.

Comment: The ecological species concept supposes that niches are discrete adaptive zones with gaps between. If an organism whose attributes adapt it for life in one of the gaps between niches will be maladapted: it will be fit to exploit resources that do not exist, or to avoid non-existent parasites or predators.

Criticism: Adaptive zones may be difficult to define in the real world, making this a difficult concept to apply practically. Furthermore, it is based on the often false premise that two species cannot occupy the same niche even for a short period of time (Wiley 1978).

Zavadsky 1968; Takhtajan 1984; Agaev 1987). In some cases a complex pattern of various forms is bounded by a discontinuity and the taxonomist infers, but without experimental work, that this is one polymorphic biological species.

The biological species concept has functioned well when applied to the major well-known groups of sexually outbreeding organisms. Indeed the link with population genetics and ecology had proved so robust that to many experimental and field biologists this has become the true species that exists as a biological unit, and whose membership can be determined by biological testing (see Chapters 2.2 and 2.3). What are often forgotten, however, are the real limitations on the applicability and functioning of the biological species concept (see Box 2.1-5). By its very definition it can only be applied to organisms with sexual breeding, and a large number of organisms do not fall in this category. Reproductive isolation also proves to be incomplete in some groups: it is particularly in plants that natural hybridization, introgression, the formation of polyploids from hybrids, and hybridization between polyploids (see also Chapter 2.2) all create circumstances where there is no clear demarcation (Stebbins 1950; Grant 1981). Manipulation of these mechanisms is of intense interest to plant breeders (see Chapter 2.2) and has lead to development of the gene-pool concept (Harlan and de Wet 1971), where Gene pool 1, (Figure 2.1-6), Gene pool 2, and Gene pool 3 represent various outer levels of hybridization and ocasional gene flow. But even this eminently practical scheme can be challenged on the basis that in nature there

are many examples of populations separated by only a few kilometres that rarely if ever exchange genes (Ehrlich and Raven 1969; Levin 1979).

2.1.4.3 The phylogenetic species concept

A second set of species concepts views species as the terminal twigs on the evolutionary tree. Speciation is the process by which new lineages originate. Similar
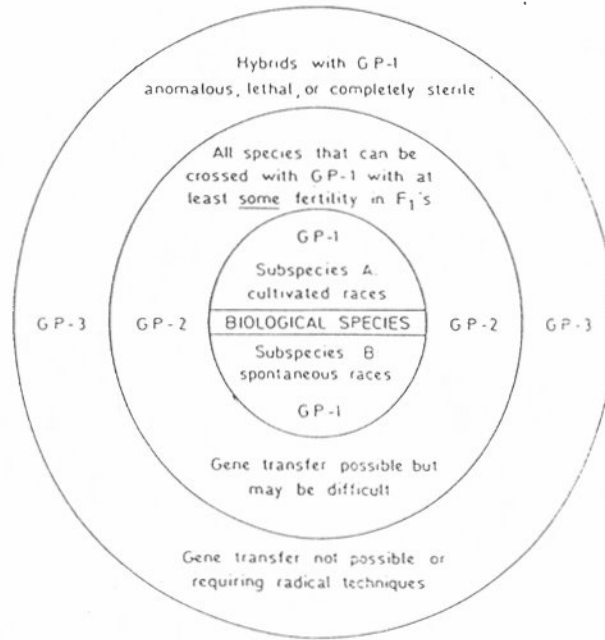

Figure 2.1-6: The gene-pool concept proposed by Harlan and de Wet (1971). Satisfactory only after all the taxa concerned have been intensively studied and satisfactorily classified.

Box 2.1-6: Evolutionary species concepts.

Evolutionary species concept (Simpson 1951, 1961; Wiley 1978)

> *A species is a single lineage of ancestor–descendant populations which is distinct from other such lineages and which has its own evolutionary tendencies and historical fate.*

Comment: This broad definition is intended to define species in terms of the evolutionary process and would thus include living, extinct, sexual and asexual organisms.

Criticism: The concept is difficult to use when trying to identify species in nature because the criteria – evolutionary tendency and historical fate – are vague and difficult to observe (Hecht and Hoffman 1986).

Phylogenetic species concept (Rosen 1979; Eldredge and Cracraft 1980; Nelson and Platnick 1980; Cracraft 1983; Nixon and Wheeler 1990, 1992)

> *A species is the smallest group of organisms that is diagnosably distinct from other such clusters and within which there is a parental pattern of ancestry and descent.*

Comment: This concept focuses on the phylogenetic history of organisms and considers a species to be the last diagnolsable or undivided twig on a phylogenetic tree.

Criticism: As pointed out by Wheeler (1990), application of the phylogenetic species concept would almost certainly give far greater estimates of the total number of species than the more traditional biological species concept. As taxa are examined in more detail (especially with molecular genetic techniques), the chances of finding slight differences between small subgroups increases, and those would be named as separate species under this definition.

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organisms, regardless of mode of breeding, owe elements of their resemblances to inheritance from a common ancestor. We thus have the *evolutionary species concept* (Simpson 1951) and the *phylogenetic species concept* (Cracraft 1983) (see Box 2.1-6). A difficulty, at least in long time-spans, is that an evolving species may eventually become so different that it can be considered a different species. At what point in time is the separation made (Lovtrup 1979)? In practice these concepts again recognize species on the basis of distinguishing characteristics: the results may not be much different from applying the morphological concept, in some cases, the emphasis is placed on the smallest phylogenetic element, so that, as with the monotypic concept, each recognizable unit may become a species.

A special form of the phylogenetic species concept has been adapted (ICTV 1991) for the definition of virus species. A virus species is a polythetic class of virus that constitutes a replicating lineage and occupies a particular ecological niche (Van Regenmortel 1990). The niche of a virus can often be quite clearly demarcated by environmental determinants such as host, tissue and vector tropisms (Franki *et al.* 1991).

2.1.4.4 *The pluralistic approach*

One can argue that for the whole of species diversity to be built on such an uncertain unit as the species is very unsatisfactory. It is, however, the best: the only unit that we have! Because many patterns of variation are found in nature, a pluralistic approach to species demarcation is necessary to answer to the needs of taxonomists and other scientists working with different groups of organisms (Mishler and Donaghue 1982).

The vast majority of species are still recognized by taxonomists on the basis of observed discontinuity (the morphological species concept). Experimental investigation of breeding patterns and careful phylogenetic analysis enrich our knowledge and in many cases clarify species circumscriptions, but they are too expensive to apply to all species. In practice the classical process is cheap, effective and answers most needs.

One practical effect of the debate on species definitions is that the species concepts actually applied may be broader or narrower at different times or between taxonomists in different places. What are described and given the rank of separate species in one treatment may sometimes be aggregated into a single more inclusive species in another. Units given originally as separate species may then be described and named by another author as subspecies or varieties within one broader species. For example, several species of peas (wild species *Pisum elatius* and *Pisum humile*, and cultivated species *Pisum arvense* and *Pisum sativum*) were subsequently found to be interfertile and thus thought of as members of just one species (now *Pisum sativum*) using the biological species concept (Makasheva 1979). However, the originally discernable units are now referred to as botanical varieties within the one species (e.g.

Box 2.1-7: Different layouts for printed classifications. (*a*) is part of a Checklist giving a linear listing of taxa (Corbet & Hill 1991). (*b*) is part of a Flora showing the taxa again in linear sequence but now with descriptions and keys included in the sequence (Tutin *et al.* 1964–80).

(a) Checklist layout.

SUBORDER MICROCHIROPTERA

Family Rhinopomatidae

Mouse-tailed bats (rat-tailed bats, long-tailed bats); 3 species; Morocco, Senegal Thailand, Sumatra; mainly desert and steppe; insectivorous.
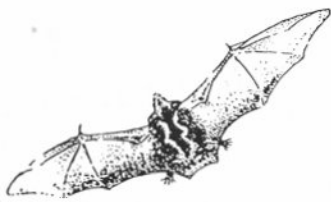
Rhinopoma

R. hardwickii	Lesser mouse-tailed bat	Morocco, Mauretania, Nigeria – Kenya – Thailand
R. microphyllum	Greater mouse-tailed bat	Senegal – India; Sumatra
R. muscatellum		S Arabia – W Pakistan
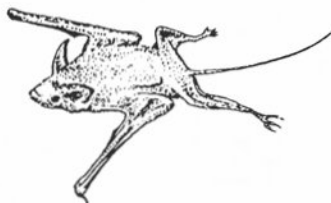
Greater mouse-tailed bat (Rhinopoma microphyllum)

Family Emballonuridae

Sheath-tailed bats (sac-winged bats, pouched bats, ghost bats); *c.* 49 species; tropics and subtropies of world; insectivorous.

Subfamily Emballonurinae

Emballonura; Old-world sheath-tailed bats; Madagascar, S Burma – Pacific Islands.

E. alecto (*rivalis*)	Philippine sheath-tailed bat	Philippines, Borneo – S Moluccas, Tanimbar Is; ref. 4.143
E. atrata	Peters' sheath-tailed bat	Madagascar
E. beccarii	Beccari's sheath-tailed bat	New Guinea, etc.
E. dianae	Rennell Island sheath-tailed bat	New Guinea, New Ireland, Malaita, Rennell Is, Solomons; ref. 4.26

Sac-winged bat (Saccopteryx bilineata)

(b) Flora or Fauna layout.

CLXVII. DIPSACACEAE[1]

Annual to perennial herbs, rarely shrubs. Leaves opposite or verticillate, exstipulate. Florets in a dense, cymose capitulum subtended by involucral bracts, often with marginal flowers radiate, rarely in a spike of verticillasters. Florets hermaphrodite or female, usually zygomorphic, each with a basal epicalyx (*involucel*) of connate bracteoles which may be expanded distally into a *corona*, often subtended by a receptacular scale. Calyx small, cupuliform or divided into 4–5 teeth or of numerous teeth or setae. Corolla-lobes 4–5, subequal, or corolla 2-lipped. Stamens 2 or 4, epipetalous, alternating with corolla-lobes. Ovary inferior, 1-locular; ovule 1, pendent; stigma simple or 2-lobed. Fruit dry, indehiscent, enclosed in epicalyx and often surmounted by persistent calyx; seed 1, endospermic, with straight embryo.

1	Inflorescence a spike of verticillasters	1. Morina
1	Inflorescence of 1 or more capitula	
2	Stems with prickles	3. Dipsacus
2	Stems without prickles	
3	Involucral bracts connate in basal half; calyx-setae present only in central florets of capitulum	10. Pycnocomon
3	Involucral bracts free; calyx-setae present or absent in all florets	
4	Calyx-setae plumose	
5	Fruiting involucel with longitudinal furrows running the whole length	7. Pterocephalus

5	Fruiting involucel with 8 pits in distal half, furrowed below	9. Tremastelma
4	Calyx-setae absent or, if present, not plumose	
6	Calyx-setae or -teeth (6–)8–16(–24); receptacle hairy, without scales	6. Knautia
6	Calyx-setae or -teeth 4–5 or absent; receptacle not hairy, with scales	
7	Marginal florets radiate; corolla 5-lobed	8. Scabiosa
7	Marginal and central florets subequal; corolla 4-lobed	
8	Involucral bracts in more than 3 rows	2. Cephalaria
8	Involucral bracts in 1–3 rows	
9	Calyx-setae 4–5; involucel angled	4. Succisa
9	Calyx-setae absent; involucel ± terete	5. Succisella

1. Morina L.[2]

Perennial herbs. Leaves verticillate, spinose. Inflorescence a spike of many-flowered, bracteate verticillasters. Involucre long, infundibuliform, spiny. Calyx deeply 2-lobed. Corolla with curved tube, distinctly 2-lipped. Fertile stamens 2. Fruit with an oblique apex, rugose.

1. **M. persica** L., *Sp. Pl.* 28 (1753). Robust plant 30–90 cm. Leaves 15–20 × 1–2 cm, linear to elliptical, dentate to pinnatifid, glabrous. Verticillasters rather distant; bracts 2–4·5 × *c.* 1 cm, ovate-triangular, sometimes pinnatifid near base, with marginal spines up to *c.* 1 cm. Calyx-lobes subequal, entire or emarginate.

P. sativum var. *elatius*, etc.; Davis 1970). The reverse process can be seen with the application of phylogenetic species concepts to birds, where recognizably distinct subspecies under the biological species concept, usually geographical races, could be segregated into separate species using the phylogenetic concept. Regional inconsistency in assignment of the species rank by taxonomists can be seen in *Flora Europaea* (Tutin *et al.* 1964–80), where species described by Russian botanists using a monotypic concept have in a few instances been listed alongside wider species described by Western Europeans using the biological species concept. The broom genus *Chamaecytisus* is, for example, given as having a large number of narrow-concept species whose distribution stops abruptly at the boundary of the former Soviet bloc countries, and fewer broad-concept species west of this boundary.

For the vast majority of species the exact definition used makes little difference to the unit circumscribed. Only for the minority, usually where there are clusters of similar forms, can the concept used have the effects described. But users of the taxonomy should be aware that total species numbers may vary from one treatment to another, and in some groups the question of rarity and endemism may interrelate with varying views of what constitutes species.

This brings to an end our introduction to taxonomic and evolutionary characterization (2.1.0–2.1.4). What follows in Section 2.1.5 illustrates the wide and fundamental way in which the taxonomy underpins all knowledge of biodiversity: it provides a rich information structure and a picture of the natural map of diversity. Lastly, Section 2.1.6 highlights the view of many taxonomists and evolutionary biologists that the mere counting of species is a rather uninformative and unrepresentative way of measuring species diversity. The taxonomy provides a map, and species diversity should be characterized as dispersion on this map, with particular value given to distant islands and wide-ranging spans.

2.1.5 *The power of taxonomy and taxonomic products*

2.1.5.1 *Taxonomic products: an essential technological infrastructure for biotechnology, natural resources management, and regulation*

The single most important use of taxonomy is to provide the core reference system for organisms used throughout biology and its associated sciences and industries. The taxonomic classification is similarly the core reference system for biodiversity (Janzen 1993). This reference system is made available through the range of taxonomic products such as the Floras, handbooks and keys already discussed. The dissemination of certain basic information about the organisms is also traditionally incorporated with some of these, such as morphological descriptions and

images of flowers and leaves for plants, maps plus behavioural and song descriptions for birds, etc.

How are these products actually used to disseminate the reference system? Whilst there are many variations in detail, they are composed of just four principal features, each with its own function:

(1) **The classification.** The classification is given either as a concise checklist or by the structure provided by the sequence of organism entries in the book. (see Boxes 2.1-7 and 2.1-8). The classification provides reference information on the existence and taxonomic position of each organism.

Much the commonest starting point is the name of an organism. From the name one can learn what the organism looks like, where it occurs, what other organisms have similar characteristics or are genetically related to it, and much else about its biology and role in the environment: the name and the place in the classification provide a vehicle through which this information is obtained.

What if the enquirer does not know the name? In this case the enquirer must first go to the identification routine: find out the name of the organism under scrutiny. The quest for further information can then be the standard one starting from the name.

(2) **The nomenclature.** The nomenclature provides the scientific names used to label and retrieve organisms and groups of organisms. Users also need to be alerted to cases where an organism or group of organisms has previously been known by other names which can be treated as synonyms for the same. Because the names are needed to label the entries they are presented as part of the classification in products such as handbooks and Floras. Checking what the names are, and checking the spellings and authors are important infrastructure services for those dealing with organisms in many biological professions. Examples are given in Box 2.1-9.

(3) **Descriptions/circumscriptions.** To be logically complete, a taxonomy needs to provide not only a statement about what are the taxa, but also to circumscribe the range of variation among organisms found in each taxon. In practice, detailed circumscriptions are often kept for the technical taxonomic literature, but descriptions giving a word picture of the organism, or images of various sorts are often included as shown in Box 2.1-10. This important feature means that using many taxonomic products a user can find out what the organism listed looks like. So the enquiries illustrated in the boxes above (to find species related to *Vicia serratifolia*, or to check the name of Broom) can lead to a description, illustration and geographical distribution information for the species in question, as illustrated in Box 2.1-10.

(4) **Identification aids.** A variety of devices can be provided so that the user can examine an unknown specimen and determine where it belongs in the

Box 2.1-8: **Examples of factual responses that can be obtained from the classification.**

(1) Position

Where does taxon X fit in the classification? In which order, class or phylum is it to be found? Response, if X = Genus *Apis* (hive bees) –
    in the order Hymenoptera (bees, ants and wasps)
    in the class Insecta (insects)
    in the phylum Arthropoda

(2) Members of a set

What other taxa resemble taxon Y? or What is the complete list of members of the taxon containing Y? Response, if Y = *Vicia serratifolia*
    – one of 7 species in Section Faba of genus *Vicia*
        – the 7 species are:
        Vicia narbonensis
        Vicia serratifolia
        Vicia johannis
        Vicia galilaea
        Vicia kalakhensis
        Vicia hyaeniscyamus
        Vicia faba

(3) Subordinate taxa

What are the members of taxon Z? or Provide a systematic catalogue of all members of taxon Z? Response, if Z = Genus *Acetobacter*
Acetobacter aceti subsp. *aceti*
Acetobacter aceti subsp. *orleanensis*
Acetobacter diazotrophicus
Acetobacter hansenii
Acetobacter liquefaciens
Acetobacter pasteurianus subsp. *ascendens*
Acetobacter pasteurianus subsp. *estunensis*
Acetobacter pasteurianus subsp. *lovaniensis*
Acetobacter pasteurianus subsp. *paradoxus*
Acetobacter pasteurianus subsp. *pasteurianus*
Acetobacter peroxydans
Acetobacter xylinum

Box 2.1-9: **Examples.**

What is the correct (accepted) name for organisms labelled X?

e.g. if X = *Sarothamnus scoparius* (Broom)
response: *Cytisus scoparius*
    (all species formerly known as *Sarothamnus* now usually included in *Cytisus*)

e.g. if X = *Vicia narbonensis* var. *serratifolia*
response: *Vicia serratifolia*
    (now accepted as a separate species)

e.g. if X = *Cytisus scoparius*
response: *Cytisus scoparius*
    (correct as given)

Under what names has taxon Y been known in the past?

e.g. if Y = *Rattus exulans* (Polynesian rat)
response: *Rattus exulans* (accepted name)
    Rattus bocourti (synonym)
    Rattus ephippium (synonym)

classification. The commonest device is the key (see Box 2.1-11) in which the user answers a series of questions about contrasted descriptive features, and by elimination arrives at the identification of what the organism is.

2.1.5.2 As a summary of biodiversity and evolutionary patterns

The taxonomy provides considerably more than the bare bones factual information system described above (the reference system): it also provides a summary of the pattern of diversity and of the pattern of evolution in a group of organisms. The patterns are to be seen in the tree structure of the taxonomic hierarchy. Consider for instance the partial taxonomic hierarchy of gymnosperms shown in Figure 2.1-7.

The hierarchy depicted shows the reader that *Ginkgo biloba* (the maidenhair tree) is the only living representative of the order Ginkgoales, and that it is thus very isolated and distinct in terms of diversity from the nearest other group, the Coniferales (Conifers). Conversely, the Coniferales is made up of seven families, each of which contains several genera and many species, amounting to a total of 610 species (Mabberley 1987). For instance, the Pinaceae (Pine family) contains 10 genera, of which *Pinus* contains about 120 species world-wide and *Abies* 55 (Rushforth 1987). *Pinus* and *Abies* species are thus nowhere near being so isolated as *Ginkgo biloba*: each species has a number of other species so close or similar as to be in the same genus, and a number of close or similar genera exist within the same family and in six related families. This then is the description of a pattern of species diversity. This diversity pattern allows us to quantify the diversity of, say, forests composed of just two species of gymnosperm: the forest whose two species are both pines (*Pinus* spp.) has low diversity (they are both in the same genus), the forest with one *Pinus* and one *Abies* comes next (its species are in related genera of the same family), whilst

Box 2.1-10: Examples of descriptions, illustrations and maps from Greenwood 1987 (a), and Valdes et al. 1987 (b). The description in a) is part of a "diagnosis" or "circumscription", an exact complete technical description of the animal. The description in b) is a brief synoptic description that could be used by botanists in general.

(*a*) Part of a 'diagnosis' and illustrations from Greenwood 1987.
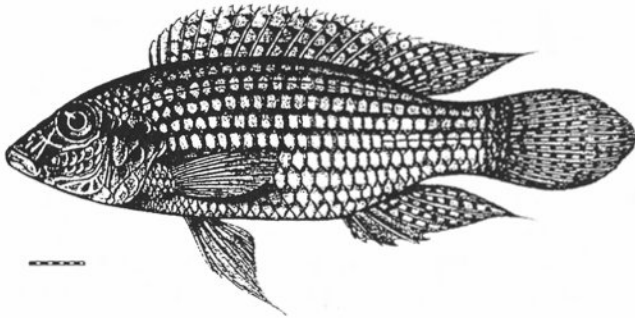

Fig. 21   *Parananochromis longirostris*; holotype. From the original drawing by J. Green. Scale bar in mms.
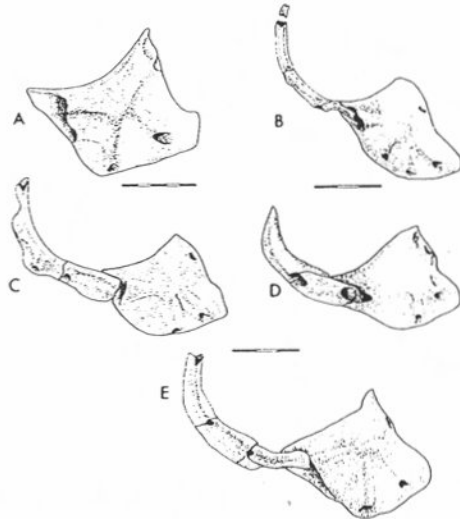
Fig. 5   Right infraorbital bones of: A. *Pelmatochromis buettikoferi* (lachrymal only), B. *Chromidotilapia guntheri* (lachrymal + 4 others); C. *Parananochromis longirostris* (lachrymal + 2 others); D. *Pelvicachromis pulcher* (lachrymal + 2 others); E. *Thysia ansorgii* (lachrymal + 2 others). Scale bar in mms.

(*b*) A description, map and illustration from Valdes *et al.* 1987.

Muy raro. Rupícola. Algeciras. *Distribución general.* Regiones Eurosiberiana y Mediterránea.

3. Polypodium interjectum Shivas, *Journ. Linn. Soc. London (Bot.)* 58: 29 (1961)

P. vulgare subsp. *prionodes* (Ascherson) Rothm., *Mitt. Thüring. Bot. Vereins* 38: 106 (1929)

P. vulgare auct., non L., *Sp. Pl.* 1085 (1753)

Rizoma más o menos largo con escamas densas. Escamas de (2-) 3-6 (-8) mm, linear-lanceoladas. Hojas de (14-) 17-22 (-30) cm; limbo generalmente más largo que el pecíolo, con la anchura máxima hacia la mitad, de ovado a ovado-lanceolado, gradualmente acuminado. Pinnas agudas. Soros elípticos, sin parafisos, a veces con pelos glandulares. Anillo del esporangio con (4-) 7-(-13) células engrosadas y 2-3 células en la base. 2n = 222. *Esporula de Julio a Septiembre.*
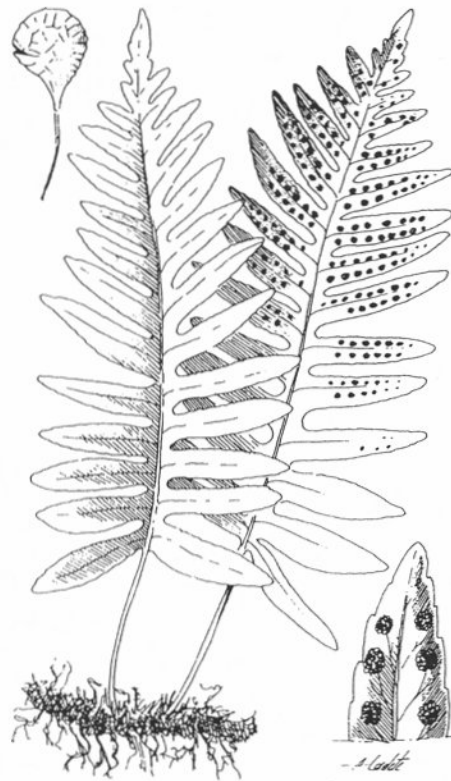
Box 2.1-11: Two examples of printed indentification keys. (*a*) 'indented' type – the first two contrasting leads are labelled '1'; if the lower of these is selected, the next pair labelled '2' are indented, and so on. (*b*) The 'bracketed' type, where the contrasting leads are printed (or sometimes bracketed) one below the other, J2 and its partner, J3 and its partner, etc.

(*a*) Indented key to genera Turkish Gymnospermae (Davis 1970).

SPERMATOPHYTA

GYMNOSPERMAE

Krause, K. 1936. *Türkiyenin Gymnospermleri*. Ankara. Kayacik, H. 1959. *Orman ve Park Ağaçlarinin Özel Sistematiği. 1. Cilt: Gymnospermae (Acik Tohumlar)*. Istanbul.

Key to Genera

1. Leaves reduced to scales at the nodes; equisetoid shrubs (*Ephedraceae*)
                                                  Ephedra
1. Leaves not reduced to scales at the nodes; trees or shrubs, not equisetoid
   2. Mature leaves scale-like, imbricate and adpressed, or linear-lanceolate and articulate at the base (*Cupressaceae*)
      3. All leaves scale-like and imbricate; fruit a woody cone; seeds winged
                                                 Cupressus
      3. At least the juvenile leaves linear-lanceolate, not scale-like and imbricate; fruit fleshy, berry-like; seeds unwinged   **Juniperus**
   2. Mature leaves oblong-linear, not articulate at the base
      4. Leaves without resin canals; fruit surrounded by a fleshy aril (*Taxaceae*)
                                                  Taxus
      4. Leaves with resin canals; fruit a woody cone, exarillate (*Pinaceae*)
         5. Mature leaves borne on short shoots, in whorls or fascicles of two
            6. Leaves in fascicles of two, each fascicle surrounded by a sheath at the base   **Pinus**
            6. Leaves in whorls, without sheaths at the base   **Cedrus**
         5. Mature leaves borne spirally on long shoots; short shoots absent
            7. Branchlets with numerous peg-like projections persisting after leaf-fall; cones pendulous, falling as a whole   **Picea**
            7. Branchlets without such projections; cones erect, the scales falling from the persistent axis   **Abies**

(*b*) Bracketed key to beetle families of Britain (Unwin 1984).

Beetles with elytra covering most of the abdomen. Antennae clubbed, and tarsi with some segments lobed beneath.

J1   Number of tarsal segments:
     Note: in this key, small cylindrical tarsal segments (arrowed) immediately following a bilobed segment are ignored. Claws do not count as segments.
     Tarsal characters may be easier to see if a drop of water is placed on the tarsus

     Tarsi with 5 segments J2
     Tarsi with 4 segments J5
     Tarsi with 3 segments J19

J2   Thorax constricted basally, beetles with a very obvious "waist". Thorax with outstanding long hairs . . . . **CLERIDAE**
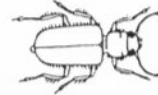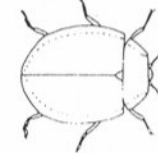
—   Beetles without a distinct "waist" between thorax and elytra J3

J3   Eyes oval, over twice as high as wide, occupying most of the height of the head . . . . **BUPRESTIDAE**

—   Eyes approximately circular J4

J4   Oval beetles with a wide turned-out rim to the elytra and the thorax giving a terrapin-like appearance. Tibiae not flattened and expanded . . . . . . **PELTIDAE**

—   Beetles with at most a narrow "beading" on thorax and elytra. Tibiae flattened and expanded . . . . . . **EROTYLIDAE**

the forest (if such were to exist) with one *Pinus* and *Ginkgo biloba* has a relatively enormous diversity, because its two species are in separate orders. This patterned or qualitative view of diversity provides the basis for taxonomic or taxic measures of diversity discussed in the next section.

The same classification hierarchy can be taken to imply the shape of the evolutionary tree or phylogeny. For instance, two elements of the evolutionary pattern might be:

1. that *Ginkgo* separated from the evolutionary line of conifers at an early date, and

2. that members of the Coniferales are thought to be monophyletic, that is with a common ancestor more recent than the one they share with *Ginkgo* and with all the descendants of that common ancestor included in the Coniferales group.

However, as noted earlier, the taxonomic hierarchy can at best only loosely mirror the branching pattern of the cladistic tree. A more precise view of the hypothesized route of evolution will be obtained by examining in addition any published phylogenies for the group.

2.1.5.3 As a basis for prediction

The natural pattern reflected in the taxonomy enables scientists to make predictions about as yet unobserved features of organisms. These predictions are only probabilistic, but they can provide a powerful and economically important basis for directing future biological research. One example is the successful search for castanospermine-like substances of possible significance in HIV research in South American legume plants of the genus *Alexa*. The substances were first discovered in an Australian plant cultivated in South Africa. This was *Castanospermum australe* (Moreton Bay chestnut), the only species at that time in the genus. When phytochemists wanted to look for the substances in other plants, taxonomists predicted that the highest chance of finding similar properties would be in geographically distant *Alexa*, a South American group but, taxonomically, the closest genus to *Castanospermum*. The prediction was correct and substances related to castanospermine were successfully isolated from the South American plants. In contrast, the chances of locating the substances rapidly by a random (and consequently expensive) search amongst the 280 000 or so Flowering Plants, or indeed amongst the 1.75 million known
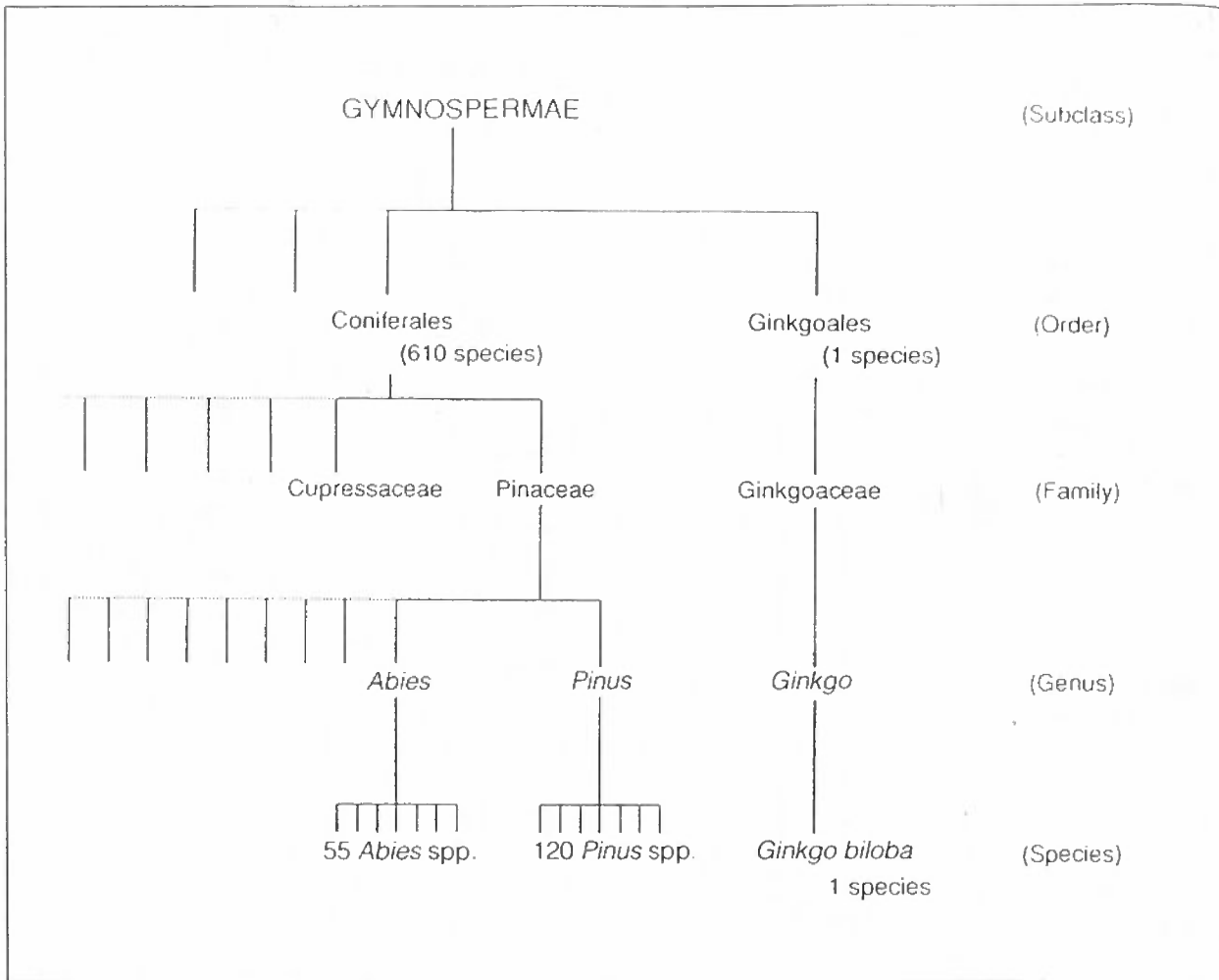
Figure 2.1-7: Partial taxonomic hierarchy of the Gymnosperms.

organisms, would clearly be very small. A similar example is taxol, a drug used to treat ovarian and breast cancer, first discovered in bark extracts of the Pacific yew tree, *Taxus brevifolia*. Unfortunately the yield from one tree is small, so that harvesting sufficient quantities from trees in the wild was likely to endanger the species. But, using the taxonomy to predict which other trees might contain taxol, scientists quickly discovered that the European yew tree, *Taxus baccata*, gave a much higher yield and is easily cultivated in quantity. Harvesting from this species causes no damage.

Another predictive feature relates to the ability to hybridize species or use other means to transfer economically important genes. The taxonomy can predict, again probabilistically, in which organisms we may successfully find genes that can be transferred to a target species, such as a crop, and be found to function successfully within that target species. Thus, in seeking to reduce virus susceptibility of cultivated corn (*Zea mays*), plant breeders turned to the recently discovered related wild species *Zea diploperennis* from Mexico as a source of resistance genes. Resistance to seven viruses was located

and virus-resistant forms incorporating *Z. diploperennis* genes are now grown in South Africa (Raven *et al.* 1992).

2.1.5.4 Other uses of taxonomic techniques

The techniques developed for deducing phylogenetic trees have proved useful in a number of contexts outside the mainstream of biodiversity assessment. One of these is tracking sources of HIV. The HIV virus mutates so rapidly that a reconstructed phylogenetic tree can be used to track both human infections and the passing on of laboratory sources over very short time-scales. One classic case was to determine whether someone was infected from an HIV-positive dentist or from a different source, and another was to show that Robert Gallo's research discoveries in the USA were made on HIV sources from a competing laboratory in France (Wain-Hobson *et al.* 1990). Phylogenetic tree reconstructions of mitochondrial DNA sequences have also been used in the support of the Eve Hypothesis, that all humans originate from Africa (Vigilant and Stoneking 1991). Mitochondrial DNA is maternally inherited, so the tree tracks back through ancestral mothers

to a postulated African female, ancestral to all modern humans. Another use is to reconstruct the evolution of complex molecules where different variants of the molecule are present in the same organism: a classic example is the evolution of globin and haemoglobin molecules (Jeffreys 1982).

2.1.6 *Taxonomic measures of species diversity*

A matter for substantial debate is the question of whether all species, or indeed all higher taxa (families, genera, etc.), are to be valued equally. As described in Chapter 2.3, the most widely used measure of within-area diversity is species richness, a simple count of the number of species present, or the diversity of an ecosystem. All species are thus counted as equal. In contrast, there is a view that individual species vary enormously in the contribution they make to diversity because of their taxonomic position, and that as a consequence measures of ecosystem diversity should include a taxonomic measure of diversity amongst the species contained. Two particular arguments are the widely expressed view (IUCN 1980) that taxonomically isolated species or species of isolated genera are of high value (such as the ginkgo, *Ginkgo biloba*, the tuatara, *Sphenodon*, or the coelocanth, *Latimeria chalumnae*) and that when valuing sets of species, a wide taxonomic range of species encompasses more species diversity than an equal number of closely related species from the same genus. Faith (1992) introduced the concept of *feature diversity* and links this to the discussion on option value and conserving variation for future use (McNeely *et al.* 1990).

Although most taxonomists and evolutionary biologists have clear concepts of taxonomic isolation and of taxonomic diversity, there were until recently no precise measures by which these concepts could be quantified. Initial suggestions by May (1990), Faith and Cawsey (1990) and Vane-Wright *et al.* (1991) led to proposals for a quantitative framework which is further developed, along with examples of application to conservation evaluation, in the symposium volume *Systematics and Conservation Evaluation* (Forey *et al.* 1994).

2.1.6.1 *Evaluating taxonomic isolation of individual species*

The traditional method of referring to isolated species has been to label a taxon in the classification as *monotypic*: a *monotypic genus, monotypic tribe, monotypic family* or *monotypic order* contains just one species. A quantitative scale, analogous to what is called node counting (Faith 1994) is implied in this measure. For instance, use of the phrase monotypic genus implies that the one species is isolated at one level of the taxonomy, but maybe not at the next level, where this and other genera may belong to the same tribe. Monotypic family (one species in a family) means that the tribe and genus levels must also be monotypic, so this family

is monotypic at all three levels. Examples include *Ginkgo biloba*, sole species in the Ginkgoaceae discussed above, the fern *Loxoma cunninghamii* (New Zealand), sole species in the genus *Loxoma*, and many others. The node-counting analogy, however, is obscured by the fact that taxonomists do not bother to name monotypic taxa at many ranks for a single species as it would serve no purpose, whereas in species-rich groups they use many intermediate ranks (subfamily, tribe, subtribe, subgenus, section, subsection). Whether or not a group is monotypic must be seen in relation to a time frame. The Ginkgoaceae, for instance, is monotypic today, but other now extinct species occurred earlier in the fossil record.

The monotypic measure is a measure of isolation from the isolated species to the nearest other species in the classification, or if the tree is derived from a phylogeny, from the closest related species. Several authors (Faith and Cawsey 1990; Crozier 1992; Faith 1992; Weitzman 1992) have proposed quantitative measures of species distinctiveness. The method of Faith (1992) measures spanning sub-tree length (distance along branches of the phylogenetic tree) between an isolated species and its closest related species, ideally measured on a fully worked phylogeny. Where a phylogenetic tree is not available Faith suggests using the distances along branches of the classification tree, effectively node counting as with traditional monotypic statements.

These measures may be used in conservation evaluation where a set of species is already protected (e.g. by law, within other reserves, in other countries), to evaluate which is the most isolated species whose additional protection would add most to the set already conserved. Faith (1992)


Figure 2.1-8: A map of Australia showing botanic regions. Numbered regions are those making high contributions to phylogenetic diversity (from Faith 1994).
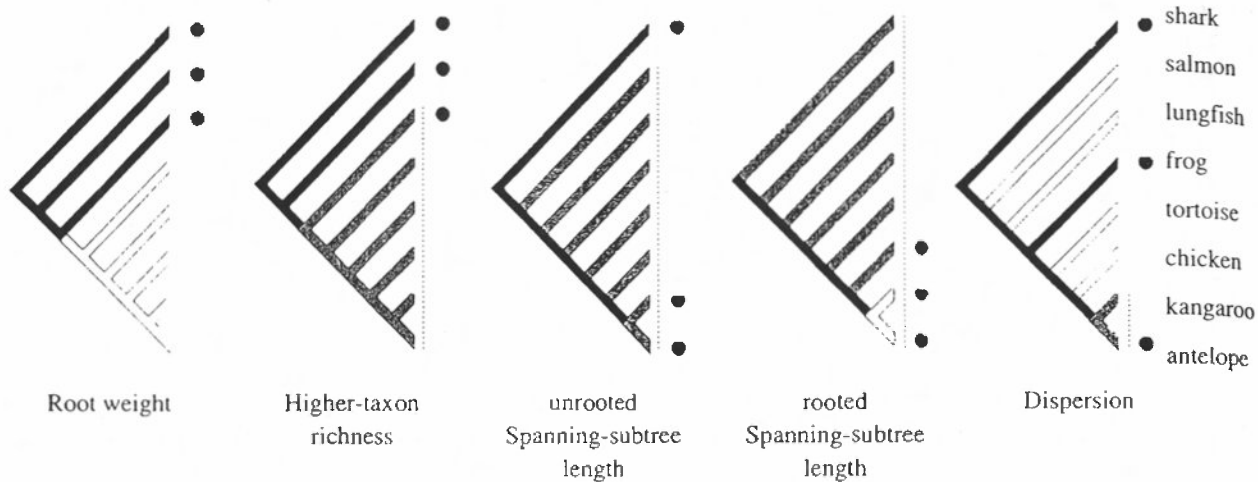
Figure 2.1-9: Classification of eight surviving species showing which biotas of just three species would score most highly when using each of the measures of taxonomic diversity. The selected species are shown by black spots, with any equally highly scoring alternatives for each choice shown bracketed by dotted lines. The groups within the classification that are essential to represent high diversity value using each measure are shown in black, groups which remain alternative choices are shown stippled, and groups which are of low diversity value are shown in white outlined in black (from Williams & Humphries 1994).

describes using his measure to evaluate orchid floras in Australia. Thirty-two species and two endemic genera, *Trichoglottis* and *Aphyllorchis*, occur in the Cape York region (Region 40 in Fig. 2.1-8). He applies his measure (to the albeit poorly known phylogeny of orchids) to evaluate which of the 71 regions contains other orchid species whose degree of taxonomic isolation would add most if added to the protected set. Region 63 (Central Coast, New South Wales) and Region 1 (SW Western Australia) add

most, followed by Regions 53, 66, 67 and 71. The result is interesting both because of the evident complementarity implied (Regions 40, 63 and 1 are at diametrically opposite corners of Australia with widely different habitats), and because the ranking of evaluations was different from that obtained by valuing numbers of endemic species, the species traditionally thought of as valuable or at risk. Complementarity means that effective conservation of a valuable subset of taxa requires attention to conserving
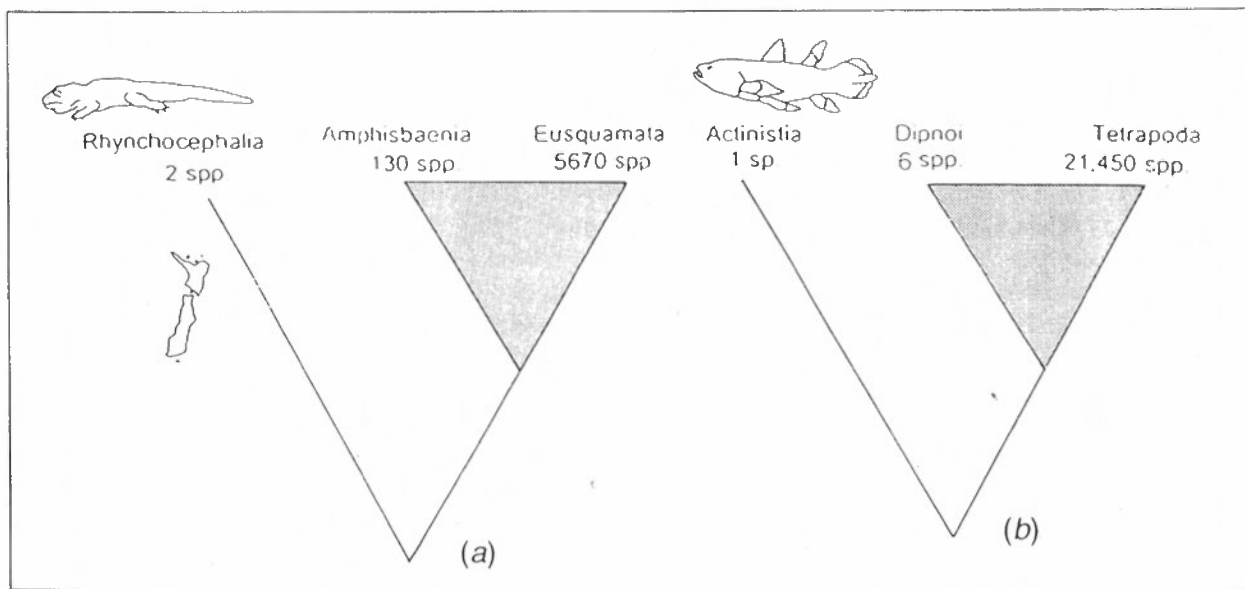
Figure 2.1-10: (a) Systematic position of *Sphenodon* (see Daugherty *et al.* 1990). Inset indicates geographical distribution of *Sphenodon*, restricted to the islands of New Zealand. (b) Systematic position of *Latimeria* (see Rosen *et al.* 1981). Inset indicates the geographical distribution of *Latimeria*, restricted to deep water habitats off the islands of Grande Comore and Anjouan.

taxonomically different, complementary taxa often in different habitats, rather than focusing on single species hot-spots or areas of endemism.

2.1.6.2 *Measuring taxonomic diversity of biota or ecosystems*

Williams and Humphries (1994) review the methods proposed for measuring the taxonomic spread or diversity covered by a set of species, such as those in a single ecosystem or biota. They too assume that the methods will be most widely applied to the taxonomic hierarchy itself, although in some cases a phylogeny may be available. The differences between the measures are illustrated in Figure 2.1-9, taken from their paper, which illustrates how different measures would lead to the selection of different species for conservation in an example set.

It has been suggested that a key element in taxonomic diversity is the number of higher taxa present, or to focus on the *basal taxa* in a phylogeny or cladistic tree (Williams *et al.* 1991; Stiassny 1992). Stiassny and de Pinna (1994) have reported an intriguing number of cases of high-level phylogenetic asymmetry where the basal taxa on a tree are both monotypic or bi-typic relict species, *and* endemic, *and* rare, such as *Sphenodon* and *Latimeria* illustrated in Figure 2.1-10. Endemism and rarity are eco-geographic features, however, largely unrelated to taxonomic isolatedness. Two of the measures that take into account higher taxa, the root weighted method of evaluation (Vane-Wright *et al.* 1991) and the higher taxon richness method (Williams *et al.* 1991), are illustrated in the comparisons in Figure 2.1-10.

Versions of a direct measure of taxonomic spread have been proposed by Faith (1992), as the node-counting version of phylogenetic diversity, and by Williams *et al.* (1993) as cladistic path length. Both can be referred to as *spanning-subtree length* measures. The number of nodes on the taxonomic tree needed to link the taxa is counted, each node being counted only once.

Finally, Williams and Humphries (1994) have attempted to refine spanning sub-tree length with their *cladistic dispersion* measure which values an even representation, or evenly dispersed taxa where alternative biotas would otherwise tie on spanning sub-tree length. The method is again visualized in Figure 2.1-9.

2.1.7 *Conclusion*

1. Taxonomy provides the core reference system and knowledge base on which all discussion of biodiversity hinges, providing the framework within which biodiversity characterization occurs. Taxonomic characterization for all known organisms is a mammoth but essential infrastructure task with which only limited progress is being made: just 1.75 of the estimated 13 million species have so far been described, and most of these are still poorly known in biological terms. There is not even a comprehensive catalogue of these 1.75 million known species.

2. Systematic and evolutionary studies are now providing valuable knowledge about the phylogeny of life, the scientific map of diversity. This is the map on which conservation, prospecting, exploitation, regulation and sustainable use must be planned and, indeed, without which all might be lost. It is important that assessments used in the evaluation of resources and conservation options make adequate use of taxonomic diversity measures that do take into account the positions and differing contributions made by different species.

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2.2 Genetic diversity as a component of biodiversity

2.2.0 Introduction

In this Chapter we outline various aspects of biological diversity within the species. This diversity is variously termed subspecific (meaning below the species level), intraspecific or infraspecific (both meaning within the species, but the former term apparently more favoured by zoologists and the latter by botanists). A major aspect of this is obviously what is termed genetic diversity (see below), but it should be borne in mind that within biology, genetics and systematics are, or at least should be, intimately linked and that there are a considerable number of groupings below the species level which have taxonomic or systematic implications without necessarily being clearly defined in genetic terms. A number of the subspecific groupings more commonly referred to are outlined in Box 2.2-1. Some of these (e.g. subspecies, varieties) are or have been used as straightforward subspecific taxa. Others (e.g. ecotypes, chemotypes) imply differences based upon other than conventional systematic characters or (e.g. cytotypes, hybrids) have mainly genetic implications. The explanations suggested for these terms are not intended to be strict definitions and for many of them the intended meaning differs, often subtly, between authors and between fields of research and some, like the organisms they describe, have evolved with time and may no longer be used in precisely the same sense as they were by earlier workers. However, irrespective of meaning and usage, such intraspecific groupings generally can be assumed to imply some, albeit imprecise, level of genetic differentiation or genetic biodiversity.

Genetic diversity is a critical component to issues of biodiversity. It is the genetic diversity within species that allows a species the opportunity to evolve under changing environments and selection pressures. This section will overview the main fields of evolutionary genetics as applied to the assessment of biodiversity and introduce briefly various techniques available to assay genetic diversity within and between species.
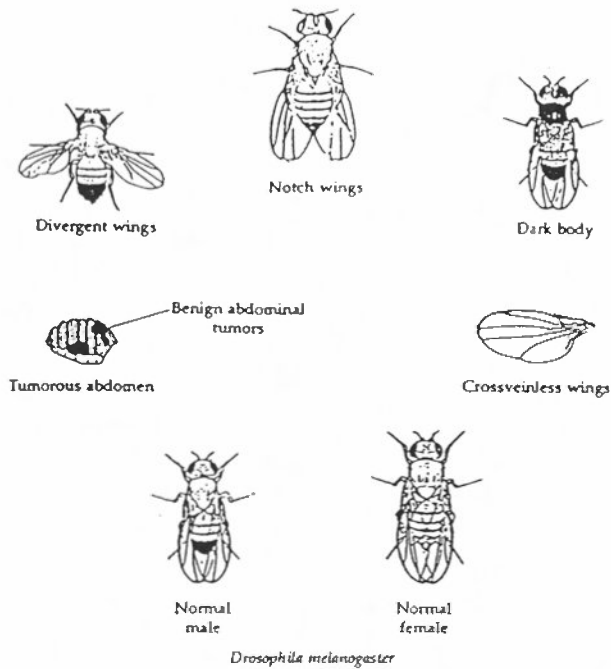

Figure 2.2-1: Examples of some phenotypic variants found in natural *Drosophila melanogaster* populations: sketches of normal flies are presented for comparison. A relatively small proportion of such abnormal flies owe their abnormality to single mutant genes (from Hartl and Clark 1989).

The variability that we observe among individuals (*phenotype*) results partly from the interaction of genetic differences (*genotype*) with their surrounding environments. Genetic diversity both within species and among higher taxonomic groups can be assayed directly by surveying the actual genetic material (i.e. the genotype). The genetic diversity occurs in the form of nucleotide variation within the genome. When this variation causes a change in a given protein, the variants are termed *alleles*. Allelic variation occurs at various genetic *loci*, or gene positions within a chromosome. Genetically variable loci are termed *polymorphic* or are said to show *polymorphism*. Genetic diversity can also be assayed indirectly by measuring a phenotype with a presumed or demonstrated underlying genetic basis (Figure 2.2-1). As one moves up the taxonomic hierarchy, genetic diversity tends to increase with increasing taxonomic diversity, both within organismal groups (Figure 2.2-2a) and across groups as a whole (Figure 2.2-2b).

The recognition that natural populations have high levels of genetic variation is something comparatively recent and followed from the application of allozyme electrophoresis to population genetics (Hubby and Lewontin 1966). This resulted in debate as to the factors responsible for the maintenance of these high levels of variation: the 'neutralists' claimed that genetic variation accumulated through mutation to form new alleles, which remained in