Taxonomy and fossils: a critical appraisal

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Many compendia at the species, genus and family levels document the fossil record, but these are not standardized, nor usually critical in content, and few are available on the World Wide Web. The sampling of the available record is good for organisms with fossilizable parts, but preservational constraints on the entire morphology, life history and geographical distribution lead to difficulties in recognizing and naming species. We recommend abandoning some of the palaeontological species concepts such as chronospecies and stratospecies, and we advocate species recognition based on unique combinations of characters. The compilation of species lists is extremely time consuming, and given the inherent problems we suggest that compilation of generic lists is a more achievable goal because genera are recognized by definitive morphological characters. In calculating taxon duration, care must be taken to distinguish between mono-, para- and polyphyletic groups, the first being the only reliable unit for use in calculating diversity curves. We support the inclusion of fossils into classifications based on Recent organisms, but we recognize some of the problems this may pose for standard Linnaean classifications. Web-based taxonomy is the way forward, having the advantages of speed and currency of information dissemination, universal access with links to primary literature and increasingly sophisticated imagery. These advantages over conventional outlets will only be realized with careful Web design and a commitment to maintenance.

Keywords: completeness of the fossil record; diversity; species; parataxa; classification; World Wide Web

1. INTRODUCTION

We have been asked to address the challenges surrounding the classification of extinct taxa, how these relate to the taxonomy of extant organisms and our vision of future taxonomy from the palaeontological perspective. We do so by starting from what we know; that is, by assessing what information is currently available. From there we proceed to discuss how well we know the fossil record so as to gain some idea of biases that may influence any comparison between the extinct and extant worlds (May *et al.* 1995). Those biases fall into two areas: (i) the nature of the geological record and how well it yields species counts faithful to reality; and (ii) the nature of the species that are named by palaeontologists, including the influence of taxonomy on our estimations of species numbers. Following this, we consider some of the issues surrounding the use of hierarchical data above the species level. Finally, we offer some suggestions that may enable palaeontological data to be used more easily.

2. THE STATE OF OUR KNOWLEDGE

Palaeontologists do not face the extreme problem confronting neontologists who struggle to describe species before they go extinct. Additionally, palaeontologists have always paid attention to documenting genera and species,

and this is due, in part, to the use of fossils for stratigraphic zonation and correlation. Of course, new finds of fossils will lead to the discovery of new species and perhaps provide a check for the validity of others. Description and taxonomic revision are at the heart of palaeontology, and this has always been so. Many compendia exist, such as *The Fossil record* (Harland *et al.* 1967) and its successor, *The Fossil record 2* (Benton 1993), *The treatise on invertebrate paleontology* (Moore 1953–) and Sepkoski's family and genus level databases (1982, 1992, 2002). These databases are not independent of one another, but collectively they do supply a reasonably comprehensive coverage of fossil taxa above the species level. However, the detail of coverage and means of disseminating that information do vary considerably. Table 1 documents a few of the most commonly used major taxonomic databases for fossil taxa with some details of their content.

Certain observations on the information contained in table 1 are pertinent. Virtually none are Web-based and/or updated on a regular basis. If updated, it is more usual for wholesale revisions to replace earlier attempts. Because most are hard copy, any information is always immediately outdated. Generally, wholesale revisions are performed by new authors. Because of this there can be different concepts of species and genera and, in particular, very different ideas of higher classification leading to minimal continuity between revisions. For example, two of the major sources of information on the diversity of foraminera are Haynes (1981) and Loeblich & Tappan (1988). The former recognizes 99 families, the latter 288. The discrepancy is due largely to differing perceptions of rank, and this may have significant consequences in estimations

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Table 1. Some of the major databases, compendia and lists of fossils with some indication of their information content.

group	most exclusive taxonomic level	most exclusive level of diagnosis	species listed	synonymy included	higher classification	stratigraphic resolution	geographic location	hard/CD/Web	updated	reference
all taxa	family	n/a	no	no	yes	stage	yes	hard/Web	no	Benton (1993)
marine animals	genus	n/a	no	part	part	stage	no	hard/CD	?	Sepkoski (2002)[a]
marine animals'	family	n/a	no	no	yes	stage	no	hard	no	Sepkoski (1992)
fungal spores and mycelia	species	species	yes	yes	no	stage	no	hard	yes	Kalgutkar & Jansonius (2000)
dinoflagellates	s (var)	n/a	yes	yes	no	variable to stage	no	hard	yes	Williams et al. (1998)[b]
dinoflagellates	species	species	yes	yes	no	variable to stage	yes	hard	yes	Cramer & Diez (1979)[c]
acritarchs	species	n/a	yes	yes	no	variable to stage	no	hard	no	Fensome et al. (1990)
palynomorphs	species	species	yes	yes	yes	stage	yes	hard	yes	Jansonius & Hills (1978–)[d]
foraminifera	genus	genus	yes	yes	yes	stage	yes	hard	no	Loeblich & Tappan (1988)
invertebrates	species	genus	type	yes	yes	stage	yes	hard	yes	Moore (1953–)[e]
echinoids	species	genus	yes	yes	yes	stage	yes	Web	yes	www.nhm.ac.uk/science/echinoids[f]
echinoids	species	no	yes	no	yes	stage	yes	hard	no	Kier & Lawson (1978)[g]
fishes	species	genus	yes	part	yes	stage	yes	hard	no	Schultze (1978–)[h]
'reptiles'	species	species	yes	yes	yes	stage	yes	hard	no	Kuhn (1969–)[i]
birds	species	no	yes	yes	yes	epoch	yes	hard	no	Brodkorp (1963–1978)
mammals	genus	no	no	yes	yes	epoch	yes	CD	no	McKenna & Bell (1997)
land plants	species	species	yes	no	yes	variable to stage	yes	hard	no	Boureau (1964–1975)
plants	species	species	yes	yes	yes	stage	yes	Web	no	http://ibs.uel.ac.uk/ibs

[a] Sepkoski (2002). A compendium of fossil marine genera. This volume has been edited by D. Jablonski and M. Foote after the death of Jack Sepkoski (in 1999). The core of the database comes from Moore (1953–) for invertebrates, Romer (1966) for vertebrates and Loeblich & Tappan (1988) on forams, with many emendations (e.g. synonymy, stratigraphic updates) and additions from primary literature. The genera are assigned to order, class, phylum and kingdom but not to family. This is unfortunate because it is not possible to relate this database with the earlier and much used family-level database (Sepkoski 1992).

[b] Williams et al. (1998). This is updated approximately every 5 years. Plans are to issue CDs for future editions. This series, begun in 1973, lists genera and species. It is in part complementary to Stover & Evitt (1978) and Stover & Williams (1987) who give synoptic descriptions at generic level and list species.

[c] Cramer & Diez (1979). Known as the 'Eisenack Catalogue' (started by A. Eisenack). Contains illustrations of type specimen. This is a catalogue that translates papers describing species into a common style giving species information. It is constantly updated by addition rather than revision.

[d] Jansonius & Hills (1978–). Deals with fossil spores and has been issued on cards, with supplements still continuing to appear, sometimes with additional authors. Contains not only diagnoses but also those features distinguishing a species from those presumed close relatives.

[e] Moore (1953–) *Treatise on invertebrate paleontology*. This is the major compendium for fossil invertebrates. Published in 23 parts that correspond to taxonomic groups. The parts have been produced irregularly over the years; some have been revised while others have yet to appear for the first time. A Web-based version is planned under the name of PaleoBank (Kaesler et al. 2001).

[f] Smith. This Web-based directory lists the type species and as many species as the author has seen and assessed as valid.

[g] Kier & Lawson (1978). This directory lists the names of all species of echinoids and builds on that produced by Lambert & Thiery (1909–1925). Although the geographical location is given this is only valid for the type specimen. There is no attempt to reassess earlier generic assigments.

[h] Schultze (1978–). This series was begun in 1978, scheduled for 10 volumes, of which five have appeared and one is currently being revised. This series appears at irregular intervals. It may be of significance that all those that have appeared have been single-authored, whereas those remaining are scheduled as multi-authored.

[i] Kuhn (1969–). This series appears at irregular intervals and there is no plan for updating. However, all of the 'reptile' groups are covered and diagnoses are given to species level.

of family diversity through time, when foraminiferan data are included with those of marine organisms in general.

It is quite common for individuals to continue annotating existing compendia for their own use. For example, Woodward's *Catalogue of fossil fishes* (1889–1901) had been annotated by different workers at the Natural History Museum throughout much of the twentieth century. Such annotation is, however, only available to a few: a difficulty that may be alleviated by creating a digital facsimile.

The level to which taxa are identified varies between the family and variety and very few include diagnoses/descriptions at more than one Linnaean rank. Species-level compendia do exist for many invertebrate groups but they are usually uncritical listings of everything that has been published. For example, Kier & Lawson (1978) list every echinoid species described between 1925 and 1970 (supplementing an earlier compendium of echinoid species by Lambert & Thiery 1909–1925), but they make no assessment of whether these are valid taxa and the original generic assignment is retained whether correct or not.

It is rare that full synonymies at any more than one hierarchical level are included in the modern compendia, although reference to primary literature is frequently given. Nearly all of the compendia, or at least very large taxonomic partitions, were single-authored, a fact reflecting the expertise/taxon distribution. Those compendia containing illustrations do so in very different forms. *The treatise on invertebrate paleontology* (Moore 1953–), makes extensive use of photographs, whereas the *Handbook of paleoichthyology* (Schultze 1978–) and *Handbuch der Paläoherpetologie* (Kuhn 1969–) use mostly line drawings.

Another consideration concerns the ease of tracing names back to specimens—the bedrock of taxonomy. For some compendia (e.g. Sepkoski 1992, 2002; Benton 1993) there is no intention to do so. For most of the remainder, the literature citation to the original author of species and genera is given, thus enabling backtracking. The problem here is that the original literature may be difficult to access. In some cases (e.g. most of the parts of Kuhn 1969–; table 1) individual holotype specimen numbers and institutional locations are given, making it very easy for researchers to isolate their collections of nomenclatural interest. Increasingly, major holders of type and figured material are placing information, including photographs, on the Web, and we see this as a welcome and indispensable aid. However, the task has barely begun.

Therefore, although we can claim that palaeontologists are competent at documenting the fossil record, we have to admit that there is little interlinking between compendia. They seem to stand alone, to be used by groups of workers who have historically sorted themselves to special disciplines within palaeontology. This alone may make it difficult for a neontologist to use several of these compendia to answer broad questions of past diversity.

3. THE MAGNITUDE OF THE PROBLEM FACING TAXONOMISTS IN PALAEONTOLOGY: HOW MANY SPECIES REMAIN UNDESCRIBED?

In some ways palaeontologists face a less daunting task than neontologists in taxonomy. The fossil record is very heavily biased towards animals with a robust or resistant

skeleton and plants that are woody, so large parts of the tree of life are simply absent from the geological record. Nichol (1977) estimated that *ca.* 8% of living animal species had a skeleton and were therefore likely to be preserved. However, if we also acknowledge that scattered through the geological record there are special deposits (Konservat-Lagerstätten) where soft-bodied organisms are fossilized, it is not unreasonable to assume that *ca.* 10% of the biota might have entered the fossil record (Paul 1998).

There are some palaeoenvironments that are unlikely to be preserved in the fossil record. Taxa from such sites will rarely be sampled, because they have low fossilization potential. Montane environments may have high biodiversity today, but being in predominantly erosional settings their fossil equivalents are infrequent. Oceanic crust is exceptionally preserved in the record before the break-up of Pangaea during the Jurassic, so the fossil occurrences of, for example, mid-ocean ridge biota depend on the rare obduction of ancient ocean floor. Nonetheless, there are occasional 'snapshots' of this habitat as far back as the Devonian (Little 2001). By contrast, habitats ranging from alluvial plain and rift valley to continental slope have a better record, from which a good proportion of skeletonized species that once existed can in principle be recovered as fossils (Jablonski 1995).

A more pertinent question is how well palaeontologists have sampled the fossil-bearing rock record for those groups whose skeleton provides them with a high preservation potential and which were living in suitable environments? Several methods can be used to estimate this, including cumulative collection curves, gap analysis, analysis of stratigraphic ranges (FreqRat), and these all provide a relatively reassuring picture (Paul 1998). Furthermore, estimates of genus- and family-level diversity through time appear robust against sampling error. Sepkoski (1993) compared his original 1982 compilation of marine family diversity in the Phanerozoic with one compiled 10 years later, after considerable addition and correction. Although the absolute numbers had changed, the overall shape of the diversity graph through time remained remarkably stable. Furthermore, an independent compilation of families through time (Benton 1995) produced a similarly shaped diversity plot. Although 10 years is a rather short time for significant changes to have accumulated, many palaeontologists feel that our knowledge of taxonomic diversity through time, though not perfect, is a reasonable representation of the true record.

A similar view emerges from an assessment of the tetrapod fossil record by Maxwell & Benton (1990; see also Benton 1998). They used cumulative collection curves to demonstrate that for better-studied parts of the world a large proportion of the fauna has now been collected, identified and described.

Others have looked at specific fossil assemblages to try to obtain an estimate of how well sampled the rock record is. The FreqRat method of Foote & Raup (1996) uses the ratio of taxa confined to one, two and three stratigraphical time-units to obtain a measure of the proportion of the observed to predicted taxonomic range. Applied to specific monographic studies of trilobites, bivalves and mammals they concluded that possibly 60% of the actual species diversity has been recorded. Paul (1998) looked at the proportion of new species in monographs that
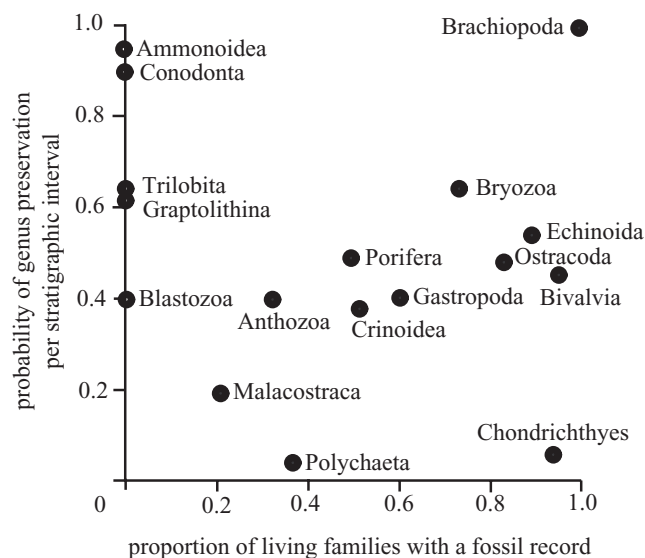
Figure 1. Estimates of completeness of the fossil record at genus level based on two measures: (i) the proportion of living families with a fossil record, and (ii) the probability of genus preservation per stratigraphic interval based on a 107-interval time-scale. (Modified from figs 1 and 3 in Foote & Sepkoski (1999).)

represented genuinely new finds as opposed to the reinterpretation of earlier collected material and concluded that only *ca.* 40% of new species were the result of new collections. Foote & Sepkoski (1999) applied two independent methods to estimate how complete a fossil record major taxonomic groups had at the genus level. As expected, some groups such as polychaetes have a very poor record indeed, but taxa with a robust skeleton are often well sampled (figure 1).

Finally, Kidwell & Flessa (1996) have investigated details of how faithful are the death assemblages that palaeontologists have to work with compared with those seen in original communities today. Reassuringly, their work suggests that most species with preservable hard parts are in fact represented in local death assemblages and commonly in the correct rank importance. Time averaging on individual bedding planes is a problem but does not obscure a good record of the natural range of community composition and structure.

Of course, the rock record that has been preserved and is accessible to palaeontologists is only a small proportion of what once existed. Thus, a major complicating factor is that, although most organisms enter the geological record, over time degradation of this record leads to the loss of taxa. Furthermore, such degradation is not randomly distributed through time, but is driven by cycles in Earth history, particularly by sea-level cycles (Smith 2001). This leads to a very heterogeneous distribution of well-sampled and poorly sampled time-intervals as the proportion of environments represented in the geological record varies over time. Fossil preservation is also far from random over time (e.g. Cherns & Wright 2000). An equally important question therefore, is what proportion of the original fossilizable biota is captured by the geological record that we have access to?

Following on from the pioneering work of Raup (1976*a*,*b*), the recent finding that the diversity of fossils

through time is correlated with the amount of rock available for sampling (Smith 2001; Peters & Foote 2001) raises the possibility that our view of species diversity over time is, in large part, a reflection of a species/area effect. Alroy *et al.* (2001) have started addressing this question and found worrying evidence that raw taxon counts may not be giving an accurate picture of biological diversity over time, even for groups with a high preservation potential. A sizeable, and as yet unquantified, proportion of the 10% of taxa that begin with some reasonable potential of being fossilized therefore are lost through destruction of the geological record.

In summary, although only maybe 1–5% of species are preserved in the geological record that survives today, the specific palaeoenvironments that are represented have generally been sampled efficiently, especially in the Northern Hemisphere. Recent studies suggest that more than 50% of the species in rocks available at outcrop are now documented. Furthermore these biotas provide a generally accurate snapshot of community structure and diversity.

Palaeontological taxonomists are not generally faced with vast numbers of undescribed species waiting to be plucked from the rock, except in the few parts of the world that remain poorly explored palaeontologically. For macrofossils, at least, it is more likely that new species will come from the revision of existing material in museum collections (Paul 1998). However, palaeontologists do have to be aware of the large gaps that exist in coverage that cannot simply be filled by better collecting.

4. NAMING SPECIES IN THE FOSSIL RECORD

In modern biodiversity studies it is common practice to estimate both the amount of biodiversity that survives as well as the probabilities of species extinction (Mace 1995; May *et al.* 1995). These, in turn, are compared with extinction rates and species longevity calculated from the fossil record (e.g. Raup 1991; Jablonski 1995). In making such comparisons there is the underlying assumption that Recent and fossil species are, in some way (phylogenetically, morphologically and geographically) the same. In some cases this may be true. Coope (1995), in documenting the extinction of Quaternary insects, specifically makes the point that such studies are precise because the nature of the material is the same. Hence, the same species concepts and recognition criteria can be used in entomology and palaeoentomology. There are also other cases of exceptional preservation where sufficient characters are preserved to enable the same criteria to be used to distinguish fossil species as are used in the living fauna. Amber, for example, preserves details of wing venation, setae and genitalia in fossil insects in such detail that they may be described with the same confidence as their living relatives (e.g. bees; Engel 2001). In other cases the *kinds* of characters used to define fossil species are commensurate with those used in Recent taxonomy even though the biological relationship may be distant. Among trilobites with acute vision, for example, closely related species are often distinguished by radical differences in surface ornament, in a comparable manner to living decapod crustaceans.

However, from the broader palaeontological perspective this may not be generally true. There are many species

concepts and recognition criteria used in palaeontology and this leads to the named entities (species) representing very different biological units. Such variability needs to be taken into consideration when, for instance, tabulating average species longevities in the fossil record (e.g. May *et al.* 1995; table 1).

At one level, problems of species recognition are the same as in the Recent world, even though they may be more extreme in the fossil record. At another level there are problems unique to recognizing fossil species.

Recent species concepts lead to different ways of delimiting species (Wheeler & Meier 2000). The biological species concept of Ernst Mayr (1942) is favoured by most neontologists. However, most modern species are not recognized on reproductive criteria. Instead, some measure of morphological, behavioural or ecological difference is used as a surrogate for genetic incompatibility. Thus, palaeontological species, recognized almost exclusively on morphological differences, are in practice equally as valid as modern species. However, there are several problems and special cases.

(a) Recognition of species in the fossil record

(i) *Fragmentary nature of fossils*

Only a small part of the morphology is preserved, usually the skeleton, and this means that our view of total morphological difference is both incomplete and distorted. Extreme examples in the fossil record are belemnites, conodonts and fish scales. Belemnites and conodonts represent a tiny fraction of the total morphology of the animal and, as there are no Recent close relatives, we do not know what range of skeletal morphology to expect in any one palaeospecies. Belemnites show relatively little morphological variation and it is likely that we are severely underestimating the number of species at any one stratigraphic level.

For conodonts, rare and fortuitously preserved assemblages demonstrate that very differently shaped conodonts, formally belonging to very different form taxa belong to the same species (e.g. Klapper & Philip (1971) were able to combine up to six nominal species to one morphospecies). Although these assemblages are very useful in associating some conodont 'species' it is likely that we have considerably overestimated the numbers of conodonts. Sweet (1988) estimated the number of named conodont species to be almost 5000. However, after adjusting for multi-element taxonomy this reduced to 1446 species (246 genera). Species erected on isolated fish scales, or holothurian body-wall spiculation, suffer from similar problems. Isolated conodonts and, at least, Palaeozoic fish scales are also similar because they are used for stratigraphic zonation and correlation and this leads to inflation of species names, which can only be halted by finding complete individuals. Indeed, some recently discovered articulated thelodonts showed a body that included scales previously identified on isolated scales as belonging to two separate orders (Wilson & Caldwell 1998). Fortunately, the practice of recognizing species on isolated scales dramatically decreases for Mesozoic and Cenozoic fishes.

The fragmentary and isolated nature of fossils sometimes leads to extreme complications where individual parts have been described as separate species, placed in completely different higher taxa. The Middle Cambrian Burgess Shale of British Columbia has yielded several enigmatic fossils. The giant arthropod predator *Anomalocaris* was known originally from its raptatory limbs. An enigmatic 'jellyfish' named *Peytoia* was described from the same rock formation. Briggs (1979) finally proved that the latter 'organism' was actually the mouthparts of what was probably the largest predatory animal in the Cambrian.

Perhaps the most extreme cases of fragmentary fossils are seen in plants. Plants by their nature produce disposable organs with a lifespan that is often much shorter than the life of the individual. Organs such as leaves, cones and flowers can be produced on an annual basis or continuously throughout the year. In addition to these short-lived parts, plants generate enormous amounts of pollen and seeds or spores as part of their normal life cycle. Together these organs and reproductive propagules are broadcast into the environment in vast quantities providing by far the greatest source of material for the plant fossil record. The main difference therefore between species named for living plants and those for fossils is that the former are based on a connected set of organs that approximate to a 'whole organism' whereas the latter are, for the most part, based on single organs and the nomenclature is designed to deal with this. To this we must add an additional level of complexity. Plant organs can be preserved in different ways, and these can have quite different appearances. A compressed specimen of a cone may look quite different to one that is petrified, and more importantly it may preserve a different but complimentary set of characters. With fossil plants the mode of preservation is therefore also a consideration, whereas this is irrelevant for their living counterparts. These key distinctions have implications for nomenclature (Chaloner 1986, 1999; Collinson 1986; Meyen 1987; Greuter *et al.* 2000) as well as impacting on how we interpret the meaning of named species of fossil plants.

The problems of fragmentation and the vagaries of preservation inherent in the fossil record of plants have been acknowledged by special provision through the many editions of the International Code of Botanical Nomenclature (Botanical Code). In the current edition (Greuter *et al.* 2000) fossil plants may be treated as morphotaxa—a fossil taxon that, for nomenclatural purposes, comprises only the parts, life-history stages or preservational states represented by the corresponding nomenclatural type (Botanical Code article 1.2). In other words, plant parts or different preservation states are recognized as distinct taxa. For example, the genus *Alethopteris* is used as the name for the foliage of certain Carboniferous seed ferns, *Laurocarpum* is the name applied to a type of fossil endocarp (part of a seed) in the Eocene London Clay flora, and *Lagenicula* is a genus of Carboniferous megaspore. One consequence of morphotaxa is that different organs of the same plant when found detached from one another are assigned to different genera (Chaloner 1999). The roots might receive one name, the bark another, cones, leaves, wood, and spores or seeds yet more. The giant clubmosses of the Carboniferous period provide a familiar example. The bark and leafy branches may be called *Lepidodendron* or *Lepidoploios*, the roots *Stigmaria*, the detached leaves *Cyperites* or *Lepidophylloides*, and the fallen cones *Achlamydocarpon* (female) or *Lepidostrobus* (male). Cones
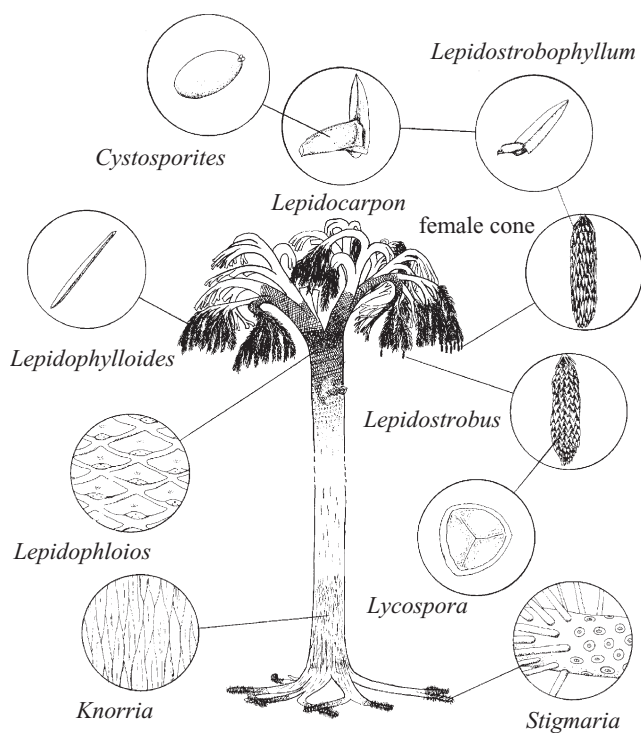
Figure 2. The naming of parts. Fossil plants exemplify well the practice of naming different parts by different names. *Lepidodendron* is a Carboniferous lycopod found as at least nine kinds of morphotaxon, each given its own name (Thomas 1981). (Reproduced, with permission, from Dr Barry Thomas.)

may further fragment to give individual sporophylls (fertile leaves) called *Lepidostrobophyllum*. The propagules come in two types: megaspores might be called *Cystosporites* and microspores *Lycospora*. Similarly, preservation state may determine the genus to which a fossil can be assigned (Chaloner 1999). The cones of the tree lycopod *Sigillaria* are called *Sigillariostrobus* (compression) and *Mazocarpon* (permineralization). The two states of preservation reveal a different range of characters, and so they are defined in different terms. The use of morphotaxa will inevitably inflate the absolute number of plant species recorded in fossil floras (figure 2).

The taxonomic status of a morphotaxon and its ability to be placed within the hierarchy of plant life depend upon the quality and quantity of information it displays. Some morphotaxa are sufficiently well characterized to be placed within families. These were formerly termed 'organ genera' (Chaloner 1999). Others are insufficiently well characterized to be placed within a family, but it may be possible to assign them to higher-level groups. *Carpolithes* is a name used for certain types of dispersed seed. The plants that produced *Carpolithes* can be placed in the class Spermatophyta (seed plants), but the affinities within this group are diverse. Previous codes of botanical nomenclature named these 'form genera', a term that is now also subsumed in the concept of morphotaxon (Greuter *et al.* 2000). Still other morphotaxa are clearly unnatural groups. *Dadoxylon* is a morphogenus of fossil woods that contains wood species from conifers in the Araucariaceae as well as species from conifer-like plants in the extinct Cordaitales. Based on wood anatomy alone, it may not be

possible to know to which family a species of *Dadoxylon* belongs. Likewise, species of leafy shoots assigned to the genus *Brachyphyllum* are attributable to conifers in the Araucariaceae (extant) or Cheirolepidiaceae (extinct). The specimens on which many species of *Brachyphyllum* are based do not contain enough information to allow them to be assigned to a family. Thus, some generic entities of fossil plants are not uniquely assignable to a family either because they are insufficiently well characterized or because they contain species from more than one family. The latter are, for the most part, either polyphyletic or paraphyletic groups.

The names of morphotaxa based on different organ types can never be synonymized even when found to belong to the same organism because morphotaxa can only compete with those representing the same part, life-history stage or preservational state (Botanical Code article 11.7). The morphogenus *Sigillaria*, which was established for bark fragments of a Carboniferous tree clubmoss may, in part, represent the same biological taxon as the morphogenus *Mazocarpon*, which was established for permineralized cones. These generic entities can be used concurrently. Furthermore, there is evidence that genera that overlap conceptually have somewhat different ranges in time, indicating that one suite of characters became extinct or modified before the other. *Lepidodendron acutum* bore cones of *Flemingites russellianus* containing megaspores called *Lagenicula rugosa*. These three genera do not, however, have the same stratigraphic ranges (figure 3).

The first occurrence of *Lagenicula* predates significantly that of *Flemingites*. We cannot assume that species of all three genera were borne on the same type of plant and we cannot simply treat them as synonyms (Chaloner 1986). Following current practice therefore, synonymy cannot come to the rescue, correcting for taxonomic inflation by cutting out surplus species names. Furthermore, in most instances, the plant that produced the parts—the conceptual whole organism—does not have its own formal name.

In a further wrinkle to a complex nomenclature, not all isolated plant parts are assigned to morphotaxa. Many leaf fossils of the Tertiary Period can be placed in extant genera. These genera are, of course, based on extant types housed in herbaria. The practice of assigning fossil plants to extant genera has had a chequered history that is plagued by inconsistencies (Collinson 1986). Some authors prefer not to place fossils in extant genera because the fossil is only a part of the plant. How do we know that the rest of the plant would conform in all its particulars to the diagnosis? Carried to its logical conclusion, this would mean that extant genera do not have a fossil record. Others argue that one should use extant genera if the plant part is consistent with this placement, even though most of the organism remains unknown. The living genus *Equisetum* is seen by many as recognizable in the Late Mesozoic. Others assign Mesozoic species to the extinct genus *Equisetites*, even though no morphological distinction is recognized between the two. This latter practice might also lead to taxonomic inflation.

In palaeobotany, the nomenclature that has been developed to deal with the fragmentary nature of fossil plants and the different preservation states yields taxonomic units that are mostly fundamentally different to those of living plants. It is rare that the holotype of a fossil
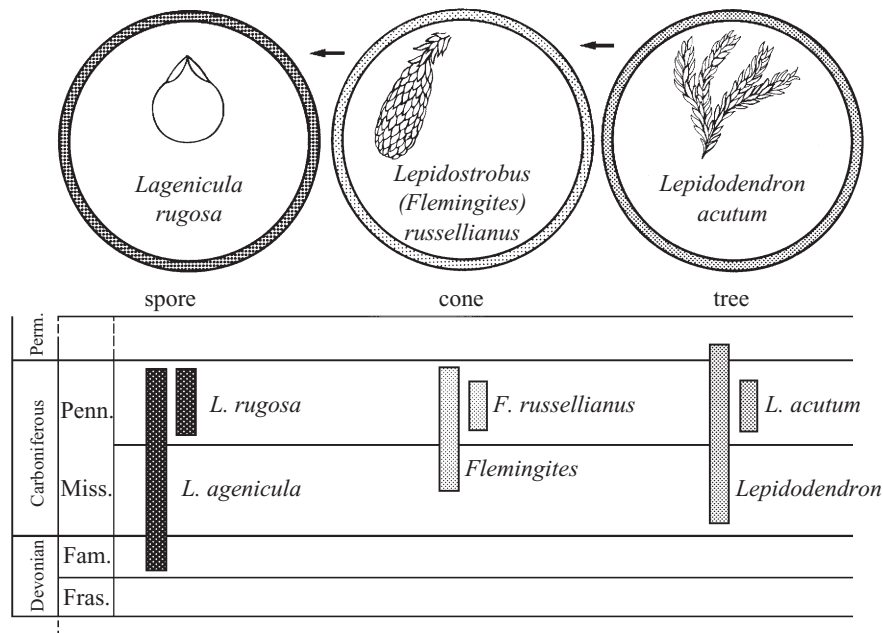
Figure 3. The relationships among three morphotaxa (genera and species) of fossil plants and their stratigraphic ranges. The species are believed to represent parts of a single species. Note that the three genera have different stratigraphic ranges. If these ranges are correct, the genera cannot be regarded as synonyms. (Reproduced from Chaloner (1986) with the permission of the author.)

resembles the holotype of a living species. For the most part, fossil taxa are based on plant parts or organs. The use of morphotaxa tends to inflate the absolute number of plant species recorded in fossil floras. All things being equal, one might expect similar levels of inflation throughout the fossil record, so it is conceivable that the overall shape of broad changes in plant diversity through time might remain largely unaffected. However, in some cases using separate parts may give rise to different diversity curves as has been found, for instance, by Crane & Lidgard (1990) when they compared the pattern of angiosperm diversification as measured by macroflora (leaves, etc.) and by palynofloras (pollen). At the very least, one can see how the diversity of large plants producing many parts might be overestimated. Also, by comparison, species diversity might be underweighted before periods of exceptional innovation, such as the Devonian period when many new organ systems first appeared.

(ii) *Lack of spatial continuity*

Fossils do not provide us with the same level of geographical continuity as Recent organisms. Therefore, it is not possible to recognize clinal variation and, consequently, geographically isolated finds are often interpreted as different species, whereas in reality they may only represent geographical varieties of a single species. This is also a problem in the modern world but here neontologists do have the theoretical possibility of checking for this.

(iii) *Lack of ontogenetic continuity*

Palaeontologists, in general, are hampered by the lack of knowledge of ontogenetic variation. Growth stages of individual taxa have received separate names, which may spuriously increase apparent diversity. Trilobites grow from larvae a millimetre long to adults some centimetres in length, during which ontogeny most of the features

change. The Ordovician trilobite genus *Asaphoon* Hutchison & Ingham, 1975 was demonstrated to be no more than a growth stage of a well-known form *Asaphellus* by Fortey & Owens (1991). The Middle Cambrian trilobite *Sao* acquired no less than seven synonyms in this manner. Once again, this can, and indeed has, happened in the modern world, particularly where there are morphologically and ecologically distinct larval stages, but the problem is far more acute in the fossil record and can only be solved by fortuitous finds.

(iv) *Parataxonomies*

Other more specialized types of species taxonomy have developed in the area of trace fossils including footprints, burrows, borings, coprolites, enterospirae, etc. (ichnotaxonomy). Currently the names of ichnotaxa are binomials and are covered by the International Code of Zoological Nomenclature (Zoological Code) (ICZN 1999) up to the genus level, although the species, genera, etc. are not based on patterns of evolutionary descent and sometimes can cross major biological boundaries. Nevertheless, some consider that Linnaean taxonomy should be applied (Rindsberg 1998). It is universally recognized that such taxonomy is artificial and such species are not used in species counts or diversity indices. They are, however, extremely useful in palaeoecological and sedimentological studies.

(v) *Virtual species*

In very recent times a new kind of species has surfaced in palaeontology—the virtual species. There are exceptional cases in which an image—and one readily available on the Web—has become the description of a fossil taxon. Reconstruction of superbly preserved three-dimensional fossils from the Silurian of the Welsh borderland has been based upon computer reconstructions from serial sections

Figure 4. The virtual fossil of a supposed aplacophoran mollusc *Acaenoplax hayae* (Sutton *et al.* 2001), *ca.* 16 mm long, from the Silurian of the Welsh Borderland. This image was prepared from computer reassembly of serial sections. (Courtesy of D. J. Siveter.)

that destroy the original specimen; the result is an image that exists only virtually (Sutton *et al.* 2001). The intact holotype specimen is retained for nomenclatural purposes but the diagnosis is realized by the virtual image (figure 4).

(b) *Species and time*

The fact that the fossil record allows sampling through time raises a whole set of taxonomic issues and problems that are unique to palaeontology. These revolve around how lineages are partitioned into taxonomic units and what this means for extinction studies.

(i) *Time and species recognition*

The evolutionary species concept of Simpson (1961, p. 153) recognizes a species as an ancestor–descendent sequence of populations changing through time with its own trends and tendencies. Here, a succession of sampled populations each encompassing a slightly different range in morphology follow one another. Such continua are often divided into segments called species. Sometimes these segments are delimited by comparison with the amount of morphological variation expected in modern representatives (Simpson 1961, p. 165) although clearly this will only work with taxa having close Recent representatives. Sometimes they are delimited by arbitrary segments of time (e.g. every 5 million years)—the chronospecies (e.g. Gingerich 1979). More commonly, the continuum is divided by stratigraphic occurrence and this is particularly so in those organisms taken from strata that accumulated in oceanic environments. Here, the palaeontologist has an increased likelihood of complete sampling of fossil populations through geological time. Planktonic organisms are naturally preserved in such

environments, and the taxonomic treatment of their fossil representatives has emphasized stratigraphical order and statistical characteristics of successive populations in their species concepts. 'Lineages' of such 'species' are routinely and successfully used for stratigraphic correlation of strata. Planktonic foraminiferans in Palaeogene and Neogene strata and coccoliths are typically treated this way. The planktonic, colonial graptolites typical of Ordovician and Silurian deep-water strata exhibit similar chronostratigraphic 'lineages' (figure 5; Cooper & Ni 1986).

In yet other instances the species are recognized because of the breaks in stratigraphic sequence due to non-deposition/erosion. All of these ways of recognizing species are very different from species recognition in the modern world. Thus the entities to which we give names may not be comparable, either from one palaeontological study to another or when comparing the Recent world and the fossil record. At the very least, the different ways of recognizing species may have implications for our estimates of species longevity.

(ii) *Species extinction*

Biologists are sometimes faced with the problem of deciding whether an organism has truly gone extinct or not, with uncertainty revolving around whether a remnant population may be persisting unseen in some remote part of the world. A similar problem of sampling also complicates the interpretation of first and last occurrences of species in the geological record, although it is possible to calculate appropriate confidence intervals to range ends (see Marshall 1998).

However, palaeontologists interested in extinction patterns face a much more serious problem: not all last occurrences in the fossil record represent biological extinction. This arises because of the way in which taxonomists have subdivided lineages into chronospecies (see above). When the fossil record is patchy, species are often known from just a few specific horizons, and the gaps in their stratigraphical distribution create convenient break points. A good example of such a lineage is provided by the species of the sea urchin *Hagenowia* from the Upper Cretaceous Chalk (figure 6).

Here, a succession of species each slightly different in morphology, follow one another through time. Because each morphospecies is effectively confined to a short time-horizon, it is likely that we are dealing here with samples of a single, continuously evolving lineage. Consequently, all but the terminal species end by taxonomic convention, because genetic continuity is obviously maintained. Species that disappear as a result of taxonomists partitioning of a lineage are lost through pseudoextinction, which should not be confused with genuine biological extinction—the loss of a genetic line.

Pseudoextinction is not confined to taxa at species level but can occur wherever a monophyletic clade has been abstracted from a larger clade so as to leave a plesiomorphic basal remnant. Historically, paraphyletic groups abound in the taxonomic literature, and where such groups end stratigraphically earlier than the first appearance of their derived sister group their termination marks a pseudoextinction.
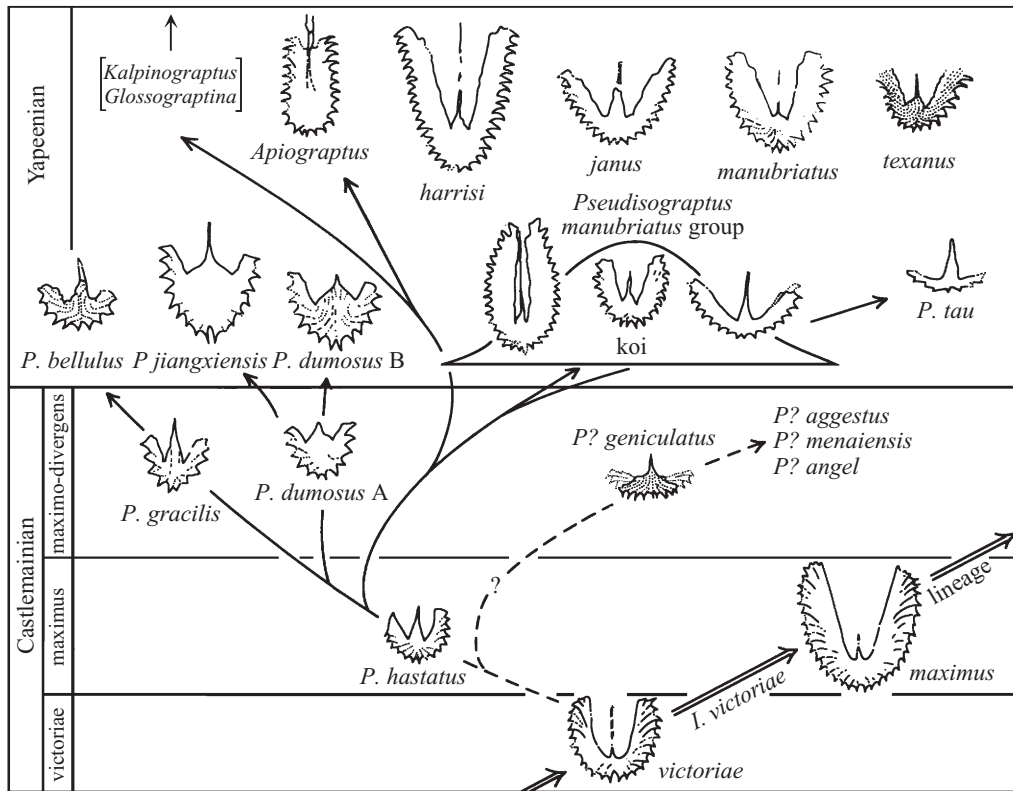
Figure 5. Stratigraphic species. Collections of graptolites in successive strata showing gradual changes in modal morphology give rise to phyletic lineages, which are named here as separate species according to the stratigraphic horizon in which they occur. (Redrawn from Cooper & Ni (1986).)
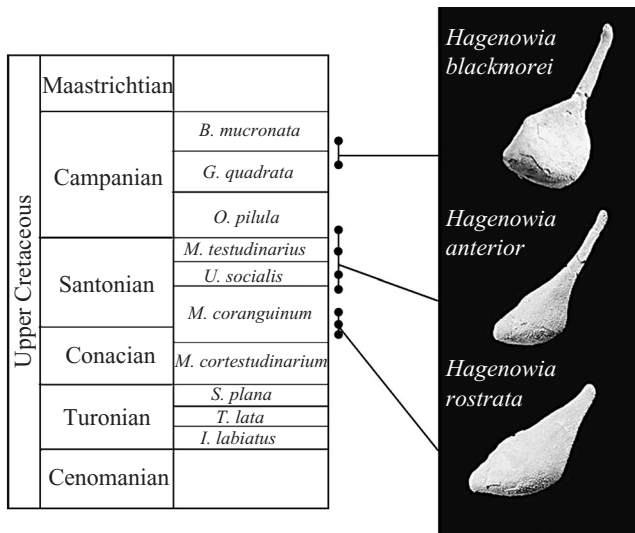

Figure 6. The succession of species of the echinoid *Hagenowia* in the chalk of western Europe. Fossil populations come from only a small number of discrete horizons and the two lower species end through pseudoextinction.

Thus, simply counting last occurrences of taxonomic names from the literature is likely to grossly overestimate extinction levels, and an understanding of the phylogenetic relationships of taxa is required to estimate true levels of biological extinction in the geological past.

5. THE USE AND MISUSE OF TAXONOMIC RANK IN PALAEONTOLOGY

In this section we highlight some of the problems of using supraspecific fossil taxa as data for diversity studies. Most of the problems concern the use of ranks in classifications and how those ranks may be affected by our changing ideas of relationships between taxa.

(a) *Comparison of ranks and species durations*

The preamble to the Botanical Code is clear about the purpose of naming groups: 'The purpose of giving a name to a taxonomic group is not to indicate its characters or history, but to supply a means of referring to it and to indicate its taxonomic rank.' (Greuter *et al.* 2000, preamble, p. 1). Few would dispute the need for a name for reference purposes, but the need to allocate taxonomic rank is altogether a more controversial issue, particularly at hierarchical levels above the genus (see de Queiroz & Gauthier 1992; Mishler 2000). The taxonomic rank of a group specifies its level in the Linnaean hierarchy according to a rank order convention, which needs to be matched to the underlying pattern of taxonomic groups as they are discovered. Straightforward as this may seem, several problems emerge. Taxonomic ranks within the Linnaean hierarchy are arbitrary, meaning that they cannot be used as comparable (objective) entities. A family of beetles and a family of primates can represent very different concepts. The rank given to a clade depends upon a complex set of factors, including perceived morphological difference from its close relatives, numbers of included species,

stratigraphical distance from closest relatives, extent of work carried out on the group, etc. Assigning different groups to similar Linnaean ranks may falsely imply historical equivalence. For instance, class Reptilia and class Aves are very different entities, the former being paraphyletic—with some of its members (e.g. crocodiles) genealogically more closely related to members of the class Aves than they are to other members of the class Reptilia. Unfortunately, in palaeontology the non-equivalence in morphological diversity, species numbers, stratigraphic duration and genealogical history is often overlooked, and diversity analyses that are based on counts of supraspecific taxa make the unfounded assumption that taxa of similar rank are directly equivalent units. Most of the compendia include higher classifications that are of very variable content, with named monophyletic, paraphyletic, and even polyphyletic groups, and these represent groupings of variable scope in terms of both morphological and taxonomic diversity.

Misuse of taxonomic rank data abounds in the palaeontological literature. For example, counts of families recorded per geological time-interval are often used as proxies for species diversity, and the percentage drop of recorded families is used as a measure of the proportion of species loss at mass extinctions (Raup & Sepkoski 1982). However, this assumes that 100 families in the Ordovician, on average, encompass the same number of species as a 100 families in the Miocene. Yet we know that species and family diversity curves follow different trajectories over the Phanerozoic, with families in the Neogene containing considerably more species, on average, than families in the Palaeozoic (Flessa & Jablonski 1985). This temporal bias means that family diversity at different times in the geological record does not, on average, encompass equivalent levels of basal (species) diversity.

It is important to realize that even at the species level there are no grounds for considering taxonomic entities as objectively equivalent in palaeontology. As discussed above (§ 4) morphospecies boundaries are, to a large extent, dictated by the amount of morphological complexity that is preserved, and a 'species' of belemnite for example represents a very different level in the biological hierarchy than a 'species' of amber-entombed insect. The more complex the hard-part morphology a clade displays, the more potential there is to create a more finely subdivided taxonomy. This is important because some people (e.g. Stanley 1979) have used mean species duration in the fossil record as a measure of biological species duration and evidence of a *scala naturae*. The fact that corals and bivalves have a mean species duration of 15–20 Myr whereas trilobites, insects and mammals have a mean species duration of less than 5 Myr, however, probably tells us more about the complexity of the preservable hard-part morphology and the limitations facing taxonomists than about biological species duration.

(b) *Problems of instability in naming taxa*

The importance of using only monophyletic groups for studies of patterns of past diversity has been demonstrated by Patterson & Smith (1987) and Smith & Patterson (1988). However, even acknowledging the desirability of monophyletic groups there remain problems of naming them as a result of changing ideas of phylogenetic relationships and/or the introduction of newly discovered fossils into an existing phylogeny. As sampling of diversity improves, and as knowledge of the relationships among both living and extinct organisms advances, the hierarchy of relationships that one might need to express in a classification increases.

In comparing his two compendia of families of marine organisms Sepkoski (1993, 2002) noted the substantial differences in supraspecific classification that had occurred during the intervening 10 years. In part, this was due to changes in phylogenetic hypotheses, which were reflected in the erection of new names of higher taxa as well as the very different content of named groups. In other cases, new names were erected to embrace knowledge of newly discovered fossils. Such instability in classifications causes difficulties when making comparisons between different databases. Of course, this is a problem associated with neontological as well as palaeontological taxa. However, classifications involving fossils are particularly prone to instability. The inclusion of new fossils often places them in stem positions; that is, as sister groups to already existing named clades. To reflect this in a standard Linnaean-ranked classification a new rank and name may be required and can have a cascade effect, demanding changes in the more inclusive ranks. Taxonomic changes at one level may force a cascade of rank changes further up or down the hierarchy. These ripples in the nomenclature by themselves do not convey any useful information. They are simply a necessary consequence of the rank order convention. No new group is circumscribed; no information is added to the classification.

There have been a variety of suggestions to lessen the impact of classificatory instability caused by relying on Linnaean rank. Farris (1976) devised a system of prefixes for the standard Linnaean ranks (family, order, etc.) which, when used in combination (e.g Mega/hyper/sub/super Family), could provide an almost limitless number of ranks. Comparable suggestions have been to switch to a numbering system whereby numbers could be inserted to signify additional ranks (Hennig 1966; Løvtrup 1977). Both of these systems, however, although logical, really only exacerbate the problem of rank proliferation. Another suggestion is to ignore the rank and use a sequencing convention (Nelson 1972) in combination with the rankless modifier 'plesion' (Patterson & Rosen 1977). Plesion can be associated with any Linnaean rank and simply means that it is to be considered as the extinct primitive sister taxon to the taxon listed below in the written classification. In other words, they considered the rank of the fossil group to be decoupled from that of the rest of the hierarchy. A third way is to abandon the Linnaean rank order convention and simply give names to groups (nodes on a phylogenetic tree) as and when required (for example, if one wished to discuss the evolution of a character complex or biogeographic history) (see also Finlay 2004). Name endings would no longer have a meaning. Classes, orders, families, etc. would disappear from the taxonomists' vocabulary and from the various codes. Grouping would be expressed either by reference to a cladogram or in a tabular form using indentation. This approach was adopted by Crane & Kenrick (1997) in their classification of fossil and Recent land plants. A fourth way is to abandon Linnaean rank and to construct names

(a)

Elopocephala
Hiodontiformes
Osteosglossidae
Notopteridae
Mormyroidei

(c)

division Teleostei
  superorder Elopocephala
  superorder Osteoglossomorpha
  order Hiodontiformes
   family Hiodontidae
  order Osteoglossiformes
  suborder Osteoglossoidei
   family Osteoglossidae
   family Notopteridae
  suborder Mormyroidei

(e)

division Teleostei
  superorder Elopocephala
  superorder Osteoglossomorpha
  †plesion genus *Lycoptera*
  order Hiodontiformes
   family Hiodontidae
  suborder Mormyroidei
  †plesion genus *Lycoptera*
  suborder Osteglossidae
   family Osteoglossidae
   family Notopteridae

(b)

Elopocephala
Hiodontiformes
Osteosglossidae
Notopteridae
Mormyroidei
†*Joffrichthys*
†*Lycoptera*

(d)

division Teleostei
  magnaorder Elopocephala
  magnaorder Osteoglossomorpha
  †superorder Lycopteromorpha
   family Lycopteridae
   genus *Lycoptera*
  superorder Osteoglossomorpha
  grandorder Hiodontiformes
   family Hiodontidae
  grandorder Osteoglossiformae
  order Osteoglossiformes
  †suborder Joffrichthyidei
   family Joffrichthyidae
   genus *Joffrichthys*
  suborder Osteoglossoidei
   family Osteoglossidae
   family Notopteridae
  order Mormyriformes
  suborder Mormyroidei

(f)

division Teleostei [L]
  superorder Elopocephala [L]
  Osteoglossomorpha [P(stem-based)]
   †*Lycoptera*
  order Hiodontiformes [L]
   family Hiodontidae [L]
  Osteoglossiformes [L]
  Osteoglossoidei [P(stem-based)]
   †*Joffrichthys*
   family Osteoglossidae [L]
   family Notopteridae [L]
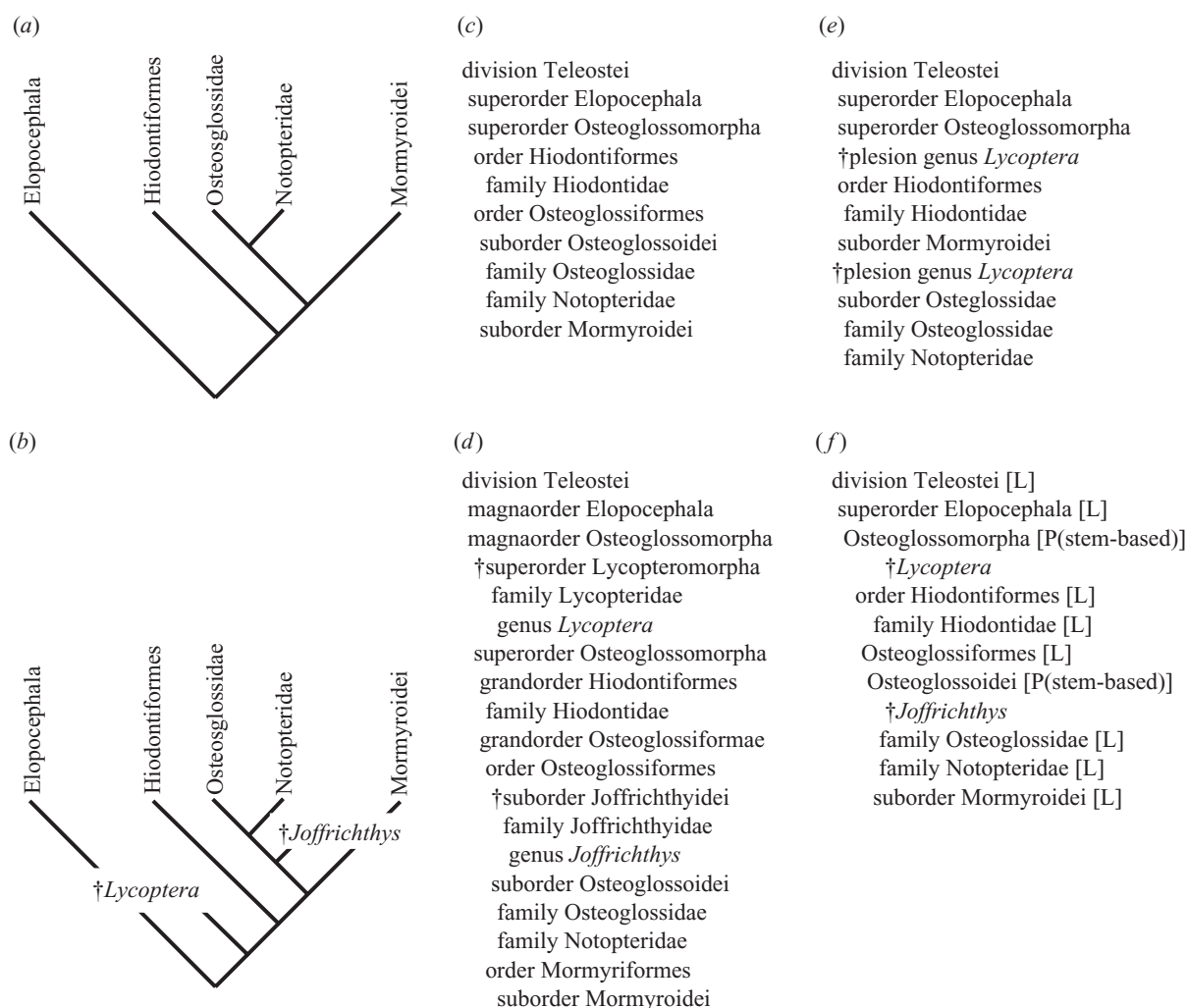 suborder Mormyroidei [L]

Figure 7. Effects on introducing fossils into classifications. Fossils often occupy stem positions in phylogenies leading to difficulties in classifying the whole group. (*a*) Phylogeny of a primitive living group of teleost fishes—the Osteoglossomorpha with the sister group, Elopocephala. (*b*) The introduction of two genera (in this case the fossil monospecific genera *Lycoptera* and *Joffrichthys*) can cause difficulties if the classification is to reflect the phylogeny. (*c*) A standard ranked Linnaean classification of the living taxa. (*d*) An altered Linnaean-ranked classification designed to reflect the phylogeny. This incorporates intermediate ranks such as grandorder and magnaorder (ranks after McKenna 1975) as well as changing the rank of already-established names. (*e*) An alternative method using the annotated Linnaean system where the phylogeny is read from the classification as the sequence of branching is given by the order of listing, with the inclusion of the rankless category plesion for the fossils as meaning plesiomorphic sistergroup. (*f*) An alternative using the PhyloCode system whereby taxa are defined relative to a particular phylogeny. Here, the fossils can be incorporated by using a stem-based definition: for example, Osteoglossomorpha could be defined as all those taxa more closely related to *Hiodon alosoides* (Hiodontiformes) than to *Elops saurus* (Elopocephala). In the annotated Linnaean system the traditional Linnaean ranks need have no hierarchical relationship to one another. Under PhyloCode nomenclature the ranks are meaningless and could be eliminated. Indeed, this is recommended if the name is to be used in a PhyloCode sense. [L] and [P] refer to a notation to indicate under which system (Linnaean or PhyloCode) the name is to be used.

with a specific phylogenetic definition tied to a particular phylogenetic hypothesis. This last is the method suggested by the PhyloCode (Cantino & de Queiroz 2000) and has been much discussed in general (de Queiroz & Gauthier 1994; Bryant & Cantino 2002) and from a palaeontological perspective (Benton 2000; Brochu & Sumrall 2001; Dyke 2002). A rank-free classification does not overcome the problem of competing classifications of the same hierarchy. In either rank-free or rank-order usage a taxonomic name cannot therefore stand unambiguously alone. It needs to be accompanied by reference to a particular classification. Figure 7 provides an example of the inclusion of fossil taxa with Recent organisms and the

classificatory consequences of following some of the different strategies.

6. THE WAY FORWARD

In the preceding text we have highlighted many of the problems in naming and classifying fossil taxa. In this concluding section we offer some suggestions as to how we may proceed. We do so in the context that fossil and Recent taxa need to be classified together in a common hierarchy that contains information about past as well as Recent biodiversity (we therefore distance ourselves from

those who have suggested fossils be classified quite separately from Recent organisms; e.g. Crowson (1970)).

(a) *The species*

We have highlighted problems faced by palaeontologists in trying to identify and name species. Many of these problems, such as morphotaxa, different species representing parts of the same organism or stages of life histories will be difficult to overcome. One possibility is to make the nature of these taxa more explicit at their point of use (Collinson 1986). One could, for example, always indicate the organ type or life cycle part along with the binomial and its author on the first citation (e.g. *Genus species* author [seed], *Genus species* author [larva]). For chronospecies and stratigraphic species we suggest that their use be discouraged and that species be established on unique combinations of characters as advocated by Wheeler & Platnick (2000). This will allow closer comparison with Recent species. We also recommend that original descriptions should contain specific designation of paratypes (recommended by the codes) along with the holotype (demanded by the codes). This is because individual fossils rarely display all of the features regarded as diagnostic by the original author.

(b) *Higher taxa*

Most of the compendia on fossil taxa do contain some form of higher classification to at least family level (often more inclusive). Rarely, however, is there any indication of whether the author(s) consider individual taxa to be monospecific, monophyletic, paraphyletic or polyphyletic, or indeed unknown. We recommend this information be included as standard practice as this will avoid the many deductions about diversity through time being based on disparate and sometimes misleading data. To address the problem of competing classifications of the same or similar hierarchical structures, we recommend that the name of a higher taxon always be accompanied on first citation by reference to a classification. However, we stop short of recommending adoption of the PhyloCode.

There is also a compelling case to be made for suggesting that palaeontologists concentrate on compiling annotated lists of genera rather than species (see below). Genera are easier to recognize and free from many of the species problems outlined above (§ 4a). This, of course, means that we support the maintenance of the binomial (cf. Cantino *et al.* 1999).

(c) *The case for Web-based data*

Like many of our neontological colleagues we would like to see the World Wide Web playing an increasingly important role for the dissemination of taxonomic data on fossils. Palaeontology would benefit from having a Web-based taxonomy for exactly the same reasons that are cited by neontological taxonomists (Scoble 2004), namely: Web-based taxonomic databases can significantly reduce the time lag between the acquisition and dissemination of knowledge. For example, in the decade after Sepkoski first published his family-level compilation of marine animals, 45% of the stratigraphic records alone were altered (owing to reassignment, more refinement and addition of new stratigraphic units; Sepkoski 1993). Thus, some of that newly identified data were already up to 10 years out of date when published in 1992. The ability to constantly update taxonomic data is an obvious advantage of the Web, but of course this assumes that there are dedicated experts willing and able to undertake this task.

The pertinent primary literature for fossil species is scattered through a multitude of books and journals, many of them restricted to specialist libraries. If basic taxonomic information can be placed on the Web it will help standardize the use of names by allowing easier access to critical data by many more people. Web-based lists make it potentially easier to collate information (i.e. numbers of genera/species from named horizons, etc.) with the possibility of calculating rates of origination and extinctions (e.g. the Web-based *Fossil record 2*, http://palaeo.gly. bris.ac.uk/frwhole/FR2.html).

The description of fossil taxa can often involve reference to many different partial specimens so as to capture the complete morphology or the variation encompassed by different preservation styles (see § 4a). The unlimited space for illustration on the Web is clearly an advantage.

There are, of course, some potential disadvantages of a Web-based taxonomy but none is unique to palaeontology. The host server has to be secure (Kaesler *et al.* 2001) and prepared to support the taxonomic site as a long-term commitment, and Web sites need to be actively maintained if they are to meet the aspirations of the scientific community. The relative ease, flexibility and timeliness of setting up Web sites encourages their birth. But, this needs to be followed by nurture—a continued investment in building, maintaining and updating. The cost both in terms of commitment from individuals and finance should not be underestimated. For example, the Plant Fossil Record database (http://ibs.uel.ac.uk/ibs) was established in 1992 with the aims of making available formal descriptions of plant fossil genera and additional details on their publication, their stratigraphic and geographical distributions and their classification. Unfortunately, 10 years later this ambitious project appears to have stalled, and there are still a great many gaps in the data such that the aims of the database are by no means fully met.

A related issue concerns archiving the data submitted to Web sites. One of the advantages of 'hard paper copy' is the relative permanence of such a medium. We have a continuous trail of taxonomic literature dating from before Linnaeus. Improved techniques of paper conservation are being developed with as much enthusiasm as there is willingness to preserve paper records. We are less confident about electronic copy, although the medium is too young to be able to assess this critically. Archiving may be an issue when the site is used as a repository for taxon distributions. Different iterations of data applied to a species or genus, etc. may vary (e.g. geographical and stratigraphic data). It may be important to retain such data (with dates) in a manner similar to the revisions of monographic treatments. There is, as far as we know, no standardized protocol for archiving electronic data.

The major outstanding administrative problem to be solved is how Web-based taxonomy is to gain validation. Taxonomic data can be posted on the Web without passing through any review process. To avoid a flood of poorly construed taxa, it might be necessary to establish accredited host sites and/or panels of experts who could

ensure quality control. None currently exists. In the immediate future, the best way forward is to concentrate on developing the Web for disseminating information about established species rather than as an outlet for new taxa. The best taxonomy has always come from individuals with the experience and breadth of knowledge to provide an authoritative overview, and it is our belief that data-rich and scientifically useful sites will become self-evident to the wider community.

From our own experience the process of assembling a database of images and accompanying text is really very straightforward, but more than this is needed for a taxonomic site to aid and direct the non-specialist. However, all this requires care and attention to keys and cross-referencing, and the design and construction of a user-friendly framework to a taxonomic site takes considerably longer.

An important consideration of Web-based reference taxonomy is therefore the feasibility of its goals. In our experience taxonomic problems associated with defining species are manifestly more complex and difficult than those associated with monophyletic clades. Species-level taxonomy usually requires data on large numbers of individuals to encompass ontogenetic, preservational, stratigraphic and geographical variability, and is often based on very subtle character assessments (see § 4 for inherent problems for species assessment). Consequently, species boundaries are rarely unambiguous and obvious. By contrast, generic and higher taxonomic levels are usually established on the basis of more major character traits that are easier to define and illustrate (see also Boulter 2003). Whereas we see a Web-based taxonomy at genus level and above being relatively easily achieved, the goal of placing all species on the Web seems massively over-ambitious given present resources devoted to taxonomy.

(d) *The need for specimen care*

In general, fossil species are based upon type material in recognized collections, and it is a stipulation for most publications that material typifying a new species is deposited in such a collection. We do not envisage a change in this procedure—for example, to Web-based typification. Fossil material is generally stable and permanent, and frequently has a uniqueness that distinguishes it from that forming the basis of Recent species. Re-collection of material from type localities is something that cannot be taken for granted. Nor are synonymies produced by revisions of fossil taxa ever objectively 'final'. The material needs to be available as the 'ground truth' in perpetuity. Some of the greatest biologists of the nineteenth century left their legacy not merely in names, but in great collections which have been consulted periodically ever since (Darwin on barnacles; Barrande on trilobites; Davidson on brachiopods).

It is important that palaeontological collections are safeguarded for future revision. In some cases, taxonomic research collections made by individuals and deposited in university collections may be endangered when different aspects of science rise to prominence in the same institution, and they are forgotten. The same applies to small museums that do not know quite what they have. It would be an advantage to gather such collections together under a national umbrella where their future is guaranteed.

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