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Palaeontological databases for palaeobiogeography, palaeoecology and biodiversity: a question of scale

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Abstract: Computerized databases provide an essential tool for investigating large-scale spatial and temporal palaeontological problems. Although advances in both software and hardware have made the logistics of building a database much easier, fundamental problems remain concerning the representation and qualification of the data. Data from the fossil record are highly heterogeneous. Databases must be designed to account for variations in scale (grain, resolution), inconsistency in the data, and potential errors (inaccuracy). These issues vary with the scope of the study (extent), the biological group, and the nature and scale-dependence of supplementary, non-biological datasets (e.g. climate and ocean parameters). With the application of desktop geographic information systems (GIS) to global Earth systems science, and the ability to efficiently integrate and query large, diverse datasets, the need to ensure robust qualification of data, especially scale, has become all the more essential. This chapter examines some of the issues involved, defines terminology and offers pragmatic solutions.

The fossil record is vast, despite its inherent incompleteness, and computerized databases provide the only practical means for investigating large-scale palaeobiological patterns and the processes responsible (e.g. Sepkoski 1982; Raup & Sepkoski 1986; Boulter *et al.* 1991; Benton 1993; Damuth 1993; Labandeira & Sepkoski 1993; Alroy 1995; Krebs *et al.* 1996; Markwick 1996; Lupia 1999; Lupia *et al.* 1999; Alroy *et al.* 2001). But a database is only as good as the data it contains and the questions asked of it, and palaeontological data are more complex than most. Palaeontological databases must be designed to take account of heterogeneities in scale (grain, resolution), inconsistencies in the data, and potential errors (accuracy). As more studies examine the interplay of diverse datasets (e.g. climate, soil, biodiversity), qualifying these inherent scaling differences becomes critical, as mixing of incongruent datasets may lead to erroneous results. This has become an important issue in landscape ecology (see Levin 1992) from which we draw examples, but the problems are exacerbated for palaeontologists by the addition of a temporal dimension in the data (see Kidwell & Behrensmeyer 1993). This paper reviews some of these issues, examines the potential consequences of ignoring scale, and suggests pragmatic solutions that are applicable to the design and implementation of palaeontological

databases. For many these concepts will be familiar, but in the absence of a manual for building palaeontological databases, this is aimed at helping researchers just beginning to construct their own databases.

Databases and basic database structure for palaeontological data

The earliest and most basic form of computer database is the 'flat file database' in which data are stored as a single set of records of the same kind (Fig. 1a). Conceptually this is similar to a card index system, and suffers from the same weaknesses in that data of only one kind can be queried, and each record must be edited individually (e.g. Sepkoski 1982). 'Relational databases' (Fig. 1b) can be viewed as multiple 'flat file databases' or tables (relations) linked together (related), such that complex queries can be made integrating varied and diverse data. The advantages of separating data in this way are that they only need to be entered or updated once in one table, but can be utilized by many different records in other tables of the database.

Geographic information systems (GIS) couple the power of relational databases with the visual efficiency of geographic maps (Fig. 1c). In GIS, a record can be represented by

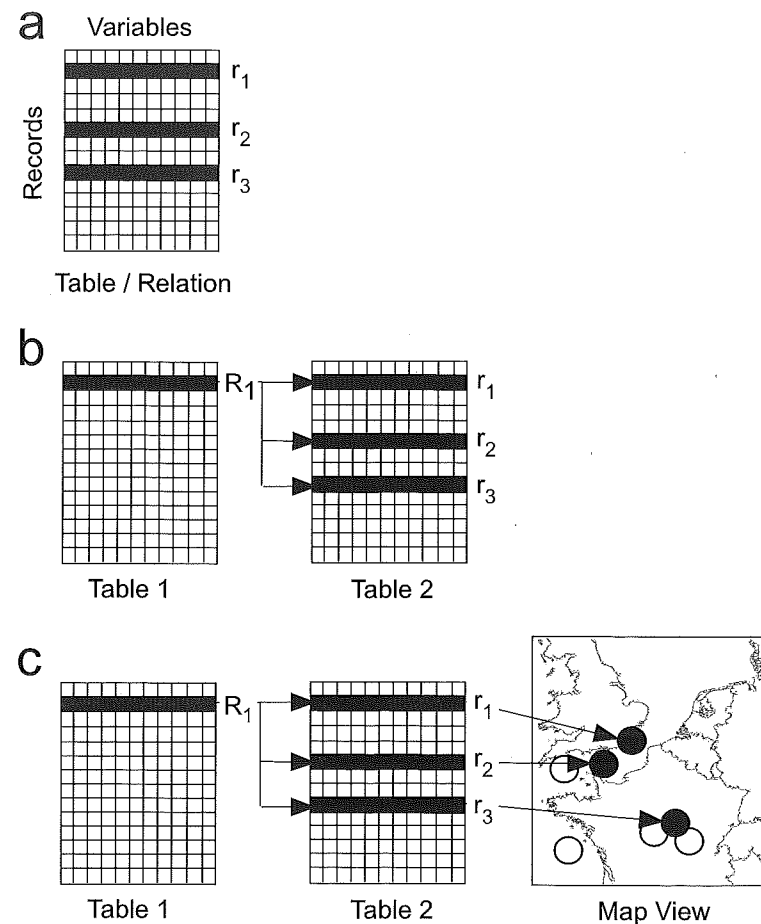


Fig. 1. Schematic representation of different database types. (a) Flat file format: r_1 , r_2 and r_3 represent three records in a single table. (b) Relational database: different kinds of data can be represented in separate tables, e.g. table 1 and table 2; data in record R_1 can be linked to relevant records in table 2, r_1 , r_2 and r_3 . (c) GIS: relational database linked and queried using map views.

a point, area (polygon), linear feature (line or 'arc') or grid (raster data). This has been particularly important to Earth scientists over the last few years investigating the complex interactions of different and diverse elements of the Earth system using different types and scales of data (e.g. points, grids). For Earth scientists geography need not be the modern geography but any reconstructed map of the world (palaeogeography).

The basic structure of most published palaeontological databases is quite similar, reflecting the nature of the fossil record (Fig. 2): an individual fossil represents a record (occurrence table) of a particular organic group (taxonomy table) at a specific time and place

(locality table). However, the inclusion of temporal and spatial information in the same table means that potentially the same geographic location might be represented by more than one record – one for each different stratigraphic level (e.g. samples from a core). A more efficient structure, which removes this duplication, is one in which the geographical and age data are placed in separate tables (space and time tables, respectively; Fig. 3), with the two linked together in what was the locality table of Figure 2. A 'locality' (in time and space) can then vary according to requirements: a chronostratigraphic interval; depth range in a well; a lithological or palaeoenvironmental associated interval; a single point (depth or time) such as a

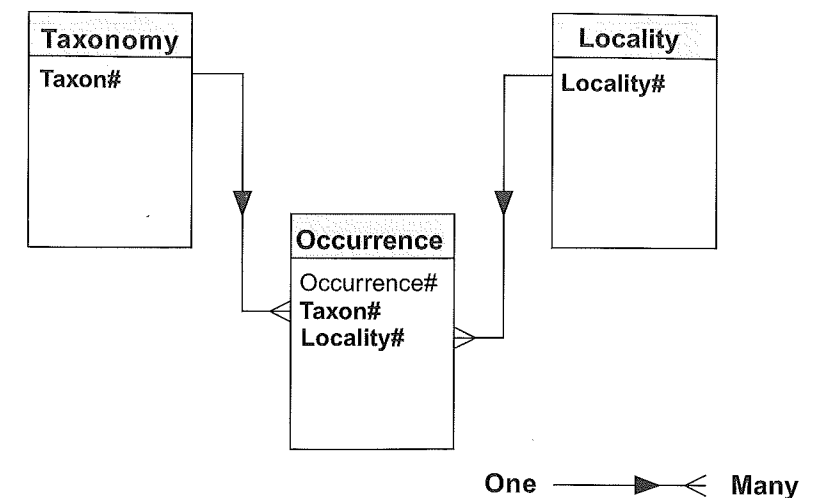


Fig. 2. Basic database structure for palaeontological databases. Fields in bold (e.g. 'Taxon#') indicate principal links between tables, although any field can be linked and queried. The 'Taxonomy' table can include any information on the individual taxon, e.g. taxonomy, ecology, habitat. The 'locality' table can comprise information such as geographic and stratigraphic data. The 'occurrence' table consists of data appropriate to that unique occurrence of the taxon at the specified time and place, such as specimen information or abundance.

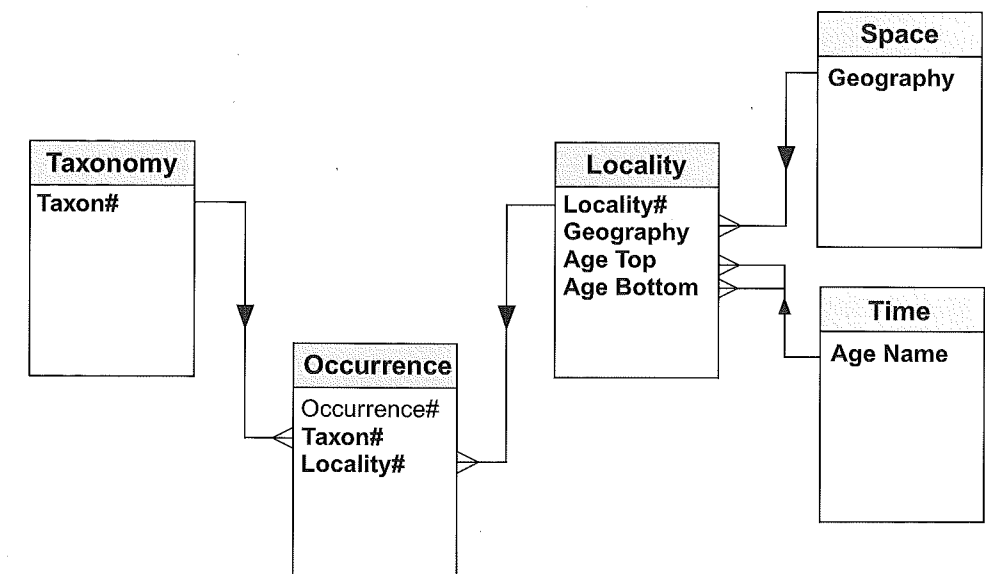


Fig. 3. Basic database structure with the locality data linked to two additional tables that store the spatial and temporal information separately.

palynological slide or geochemical sample. Additional tables can then be added as necessary for data provenance (references), higher taxonomy, timescales, etc.

Although this chapter is not concerned with a detailed description of database design (see

Peuquet (1988) for a more detailed discussion), three logistical points are worthy of mention because they directly affect the qualification of the data. First, it is advisable that all records in each database table should have a 'unique identifier'. This is a field (variable) that has a

unique value for each record and should have no other meaning (i.e. should not include an age code or taxon name that could potentially change in the future). These identifiers can then be used to link tables (e.g. in Fig. 2 linking locality and taxon records to an individual occurrence). Links can of course be made on any other fields in a table, but care must be taken in knowing the relationships of the data (one-to-one, many-to-one, one-to-many).

The second logistical consideration is data provenance. In order that the data in the database can be used with confidence it is essential to ensure that all data are referenced and audited. The provenance of information is critical to ensuring the integrity of the data, such that the issues of precision and error can be traced back to source. A distinction also should be drawn between raw data (observations) that are more or less immutable, and interpretations based on those data. If data are to be compiled from the published literature, it is also advisable to design the database to record data as it was written in the source or to record explicitly changes made to the data (e.g. correction of obvious misspellings or selected age assignment among disputed alternatives) as it is entered. For example, an author might misspell a taxon's name and this error may be amended immediately, but because some spelling variants are truly different taxonomic entities (e.g. *Cicatricosisporites*, a trilete spore, and *Cicatricosporites*, a monolete spore), any change should be noted in a comment field in case examination should verify the 'error'. In the end, original data represent facts that can be accepted or disputed (and perhaps modified) by different users of the database according to their scientific opinion. Making corrections or changes at the time of entry without annotation precludes verification without returning to the original publication.

The final logistical point is the treatment of error (inaccuracy). Errors in a database can be of three types: errors due to mistakes in data entry; errors due to mistakes in the original data; and errors due to subsequent changes to that data (e.g. new phylogenetic hypotheses or age reassignments). In general, the first of these is easily remedied by systematic checking of the data. The second and third require that the database be designed to be dynamic and allow updates as necessary.

Scale

Scale is a critical issue in ecology (Levin 1992) and palaeoecology (Kidwell & Behrensmeyer

1993), but frequently obfuscated by ambiguous terminology. In the ecological literature, scale refers to the spatial and/or temporal dimensions that describe an object (e.g. 2 cm tooth or 4 ha plot), event (e.g. 4 month rainy season) or observation (e.g. 2 year study of a 4 ha plot) (O'Neill & King 1998). This has the opposite meaning to scale in the cartographic sense, which refers to the level of detail; thus 'large-scale' to an ecologist refers to a large area or duration, but a 'large-scale map' is usually of great detail but small area. This can lead to confusion when using GIS for examining ecology and palaeoecology. To combat this we have adopted two terms from landscape ecology: grain, which is the minimum resolution/scale of an observation (the smallest spatial or temporal interval of observation); and extent, which is the total amount of space or time observed, usually defined as the maximum size of the study area (O'Neill & King 1998). Therefore, a 'large-scale map' is fine-grained but of limited extent. The important issue is to specify explicitly what the grain and extent are for each study.

In studies of the fossil record, scale can be treated in the same manner. The grain of an observation is equivalent to, for example, a rock sample, or locality, or basin (and the amount of time and space that they represent) and is determined by the size – thickness, area or volume – measured. Which grain is used depends on the questions asked of the data. A global study (global extent) might only require a summary of the fossil fauna or flora for each sedimentary basin in the world, and therefore the grain is defined by the size of each basin. Conversely, a study of a specific basin (basin extent) might require a grain based on localities, or sites, or samples within that basin. The term 'resolution' can be taken as a synonym of grain, thus 'time resolution' refers to the interval of elapsed time represented by an assemblage (see Kidwell & Behrensmeyer 1993, table 1).

Precision, strictly defined, is the ability to repeat a result, or the degree of consistency among several results, whereas accuracy is the ability to achieve the real or true value. Here we may loosen the definition of precision to refer to how easily we could return to (literally revisit) a site given the information provided in the database. To record that a site is located in 'Yorkshire' may be accurate, that is, true, but it does not get us easily to the actual site at the base of a specific cliff. Likewise, a site might really be of Eocene age, but this would not be helpful to track down the actual site. Thus precision can be construed as uncertainty in the grain or extent of a sample/analysis of the fossil record.

Table 1. Geographic precision

Code	Explanation
1	Precise location, within 1 km (equivalent to 'site/locality')
2	Within 10 km (equivalent to 'nearest town')
3	Within 100 km (equivalent to 'US county')
4	Within 500 km (equivalent to 'US state')
5	Very imprecise, not know to within 500 km (equivalent to 'country')

Grain (resolution)

Scaling issues are compounded in palaeoecology by taphonomic (i.e. preservational) processes that affect the apparent grain and extent of analyses through combining elements of assemblages that did not co-occur in space (spatial averaging; e.g. wind-blown pollen from outside the depositional area) or in time (time-averaging; e.g. reworking of shells from different depositional events), and by inaccuracies in the data. In terms of a grain represented by 'localities' these issues can be summarized into two principal questions: Where is the locality? How much 'space' and therefore time, is represented by the locality?

Accuracy. A fossil comes from a definite location, but it is not always possible to know the locality with precision, either because the details are not reported in the literature, or the location could not be known at the time due to poor maps or difficult terrain. The advent of global positioning systems (GPS) has mitigated many of these problems, but in the older literature, localities were often described with respect to a local geographic feature, e.g. a town, river confluence, etc. By using GIS to plot detailed geographic datasets (topographies, roads, rivers) at various scales, these localities usually can be placed in latitude–longitude space. Nonetheless, a simple qualifier can allow for imprecisely known localities to be distinguished from well resolved sites, if that is important in analyses (geographic precision (Markwick 1996); Table 1). It needs to be remembered that given plate motions (and the uncertainty therein), absolute spatial resolution will deteriorate the further back in geological time that the interval under investigation occurred (Fig. 4).

Locations can also be misplaced. This can be mitigated by checking locations against the coordinates given in published gazetteers and atlases, but can be performed most effectively using GIS. Again, detailed map datasets of rivers, roads, political boundaries, topography,

outcrop geology, etc. can be superimposed digitally in latitude–longitude (or x–y) space with the datapoints to be checked. This provides an immediate visual indication of error. Intentionally misplaced localities (for political or site conservation reasons) can be dealt with similarly.

Age assignments can be made incorrectly, based on incorrect radiometric ages or fossil sparsity, or subject to change based on later analysis (different timescales). Ziegler *et al.* (1985) tried to qualify confidence in age assignments by recording the provenance of the age date (Table 2). Such a scheme may be refined by distinguishing between different dating techniques within a particular category (e.g. Ar/Ar or K/Ar age dating). By keeping the absolute age data as a separate table, updates, and multiple timescales can be accommodated readily.

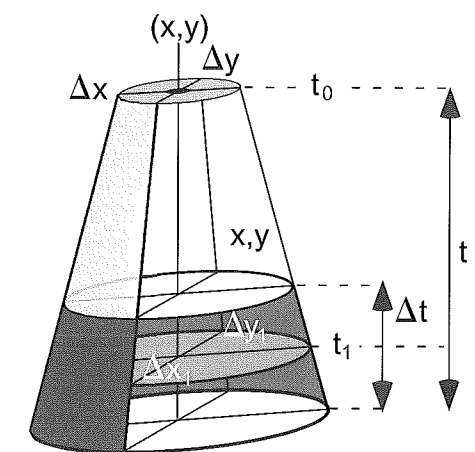


Fig. 4. A representation of the uncertainty in spatial and temporal position of a locality at point (x,y) at the present day (t_0), with present uncertainty in spatial location Δx and Δy . The past position at time t_1 is more uncertain both spatially (Δx_1 , Δy_1) and temporally (Δt) due to uncertainties in the plate reconstruction.

Table 2. Stratigraphic reliability codes (Paleogeographic Atlas Project, Chicago)

Code	Explanation
A	Complete biostratigraphic control
B	Some biostratigraphic control
C	Stratigraphic interpolation (= dating of rocks above or below)
D	Geological inference (= correlation with other site[s])
E	Radiometric dating
F	Secondary information (= methods or source unspecified)
G	Guesswork (= no age provided, or dated to Period only)

Mixing and averaging. Behrensmeyer *et al.* (2001) provide an up-to-date summary of the field and implications of taphonomic studies for palaeoecological interpretations. In short, taphonomic processes mix assemblages and the amount of space and/or time encompassed by a sample is the spatial or temporal resolution of that sample. A single 'locality' may comprise many taxa and vary spatially from a few centimetres (such as a palynological preparation) to a few tens of centimetres or metres (e.g. a bed of rock) to hundreds of kilometres (e.g. a formation within a basin). The larger the area or volume of rock encompassed, the greater the amount of time that might be represented ('analytical time averaging'); (Behrensmeyer & Hook 1992). However, biological and taphonomic processes specific to a particular group of organisms reduce generality. A series of palynological samples through a core, each very small and representing depositional instants, implies a tight temporal grain, but mixing and transport of pollen in wind and water might imply coarse spatial grain for the same samples. Furthermore, the temporal duration of a single palynological preparation from a well core may present a depositional instant if made parallel to bedding, or a few years or tens of years if made perpendicular to bedding. This will also be reflected in the interpretation of the contemporary environment, including climate.

Separate biological and taphonomic processes produce a distinctly different grain implied by most vertebrate localities. Because of the relative sparsity of specimens in most cases, a vertebrate locality might include an area that is on the order of kilometres, or even tens of kilometres, in size, and which may encompass a thickness of hundreds of metres of sediment. As such, it might represent hundreds (or thousands) of years of deposition, depending on the tectonic setting (Behrensmeyer 1982; Behrensmeyer & Chapman 1993; Rogers 1993), but if the animals are migratory, it would be

necessary to obtain a sample that adequately reflects the local fauna.

The physical mixing of earlier faunas within contemporary faunas ('taphonomic time averaging'; Behrensmeyer & Hook 1992; Behrensmeyer & Chapman 1993) further degrades resolution. The consequence of these problems is that as a palaeontological event (such as an extinction or a response to climate change) or environmental interpretation is examined over broader areas, so the temporal resolution with which it can be defined decreases. Conversely, the more finely events are resolved in time, the more difficult it is to know how large a region is affected. This is referred to as the 'paleontological uncertainty principle', analogous to the 'uncertainty principle' in quantum physics (S. Wing, pers. comm. 1991).

One solution is to use only data of a specified grain (resolution), but this can lead to loss of data, including information that, although poorly resolved, is nonetheless important. For example, if the location of a fossil is given as 'India' this may be considered spatially poorly resolved and therefore ignored, but if it is the only report of that fossil from India, then it is still useful information. However, this requires that the precision can be qualified; descriptors such as 'sample', 'composite locality', 'quarry', 'site' can be used, but each of these terms has numerous definitions, and so must be defined for every database. Landscape ecologists, faced with a similar problem, have derived numerous (mostly hierarchical) classification schemes for describing different scales of landscape system based on the areal extent considered (Huggett 1995). A similar approach might be appropriate for palaeontological databases.

An alternative solution is to include all data at the resolution at which it is reported (using a qualifier), and then to coarsen all 'localities' to some standard spatial or temporal scale by concatenating faunal and floral lists, in order to eliminate local variability. This has been used by

Markwick (2002) for present-day faunas and floras in order to examine the relationship of climate, biogeography and diversity (see also Markwick 1996). The selection of the smallest sampling unit determines the highest resolution (finest grain) possible in analysis based on information in the database. It is relatively easy to coarsen the resolution of data at a later date. It is impossible to refine it.

Taxonomy

Taxonomy influences grain, because different organisms scale with the environment differently, but this is a matter to consider when analysing the data. The major problem to be qualified in database design is taxonomic error (inaccuracy). Errors in taxonomic assignments can be due to several causes, among them the following: (i) incomplete preservation (absence of diagnostic characters); (ii) morphological uniformity (e.g. pollen of grasses); (iii) form taxa (e.g. separate genera for leaves, seed, pollen, etc.); and (iv) unreported taxonomy. Classification schemes for all biological entities are subject to change and disagreement. This is particularly true for fossil taxa, which may have no extant representatives, and which might be represented by incomplete and/or limited numbers of specimens. Different workers may adopt different taxonomic schemes depending on their own experience and opinions, and the relevant literature may incorporate a long history of taxonomic changes. The solution is partly an issue of accommodating uncertainty because assignments at a low taxonomic level may be poorly supported and disputed widely, whereas the higher level assignments can be made with considerable confidence and general agreement among professionals. Potential errors can be minimized by coarsening the data to a more 'confident' taxonomic level, and/or by recording specimen information as a guide to the characters used in the taxonomic assignment. This will vary according to the group studied, such that this method may create problems when assemblages are compared (the question of which taxonomic level to use, and whether the same level should be applied to all groups in the analysis). A species assignment based on an isolated fossil tooth will probably be of low confidence for a lizard, but significant for a mammal.

Another potential solution is to adopt a 'standard', preferably published, taxonomy and use this throughout the database. This ensures that the higher level taxonomy is at least consistent, although consistency is no guarantee of truth.

Multiple standards can be made available as separate relations in the database structure.

Synonymy

Synonymization is the method of transferring a specimen or species to its appropriate taxonomic unit (e.g. species or genus) for any of several reasons, but usually because it is identical to a previously designated taxon. This can be dealt with by adding a 'synonym table' to the database structure that is used as a look-up library for all taxon names entered into the taxonomy table. The links can be structured such that if the entered taxon is found to belong within another species according to the synonym table, the most recent synonymized form replaces it. Again, the issue of data provenance is emphasized as species nomenclature is particularly fluid and contentious.

The rules of biological nomenclature state that no two animal or plant species may have the same name, and the rules establish how to designate and name a new species. Yet different species are often encountered in the literature that have the same name given informally during a study. This is particularly so in palynology and occurs primarily in the stratigraphic literature where interest focuses on distinguishing rock units from one another by segregation of pollen types. The frequent expression of this is the designation of many species named by combining informally a genus name with 'sp. A' or 'sp.1', as in Agasie (1969) and Ravn (1995) who record '*Tricolpites* sp. 1' from their sites in Arizona and Wyoming. However, sharing the same name does not imply that these pollen types represent the same biological entity, which is implied when formally named species share the specific epithet. Indeed, '*Tricolpites* sp. 1' in the paper by Agasie (1969) does not appear similar to '*Tricolpites* sp. 1' of Ravn (1969). The simplest method to overcome this problem is to treat 'sp. 1' etc. of every author as a distinct taxonomic unit, distinguished by a unique name, for example '*Tricolpites* sp. 1 of Agasie (1969)'.

Discussion

With the ready availability of desktop computerized relational database and GIS software, the logistics of building databases to cope with the large volumes of palaeontological data is no longer a major issue. While it is useful to remember certain guidelines as to database structure (Fig. 2) and the physical amount of data to be included (a database should be 'simple enough that it can be used, but comprehensive enough

that it will be useful'; Markwick 1996, p. 921), the principal problem facing designers of palaeontological databases is how to accommodate and qualify heterogeneities within the record, specifically of scale. We have suggested here that it is always better to collect information at the finest grain (resolution) possible and to append the appropriate confidence estimate (as a qualifier that can be queried on), since higher resolution data can always be degraded to lower resolution, but the reverse is impossible. The question of how observations made at different scales can be compared has been discussed by numerous authors for both modern and fossil settings (see Signor 1978; Hatfield 1985; Levin 1992; Anderson & Marcus 1993; Brown 1995; Rosenzweig 1995). But it is important to understand why scale is so important, especially for researchers integrating datasets from different fields, which has been made so much easier through GIS.

We have already noted how the apparent grain of a fossil assemblage can be affected by physical mixing and averaging in time and space, and that this problem worsens as the extent of the study increases. Consequently, this problem is greatest for global studies. For example, Markwick (1998), using the global distribution of fossil crocodilians to reconstruct palaeoclimate, calculated that the probability that 100 Eocene fossil crocodilian localities represented the identical 30 year timespan within the Eocene (21 000 000 years) and therefore the same 'climate', was $1/700\,000^{99}$. The problem of correlating age-equivalent samples is further exacerbated when multiple lines of evidence are used (e.g. palynology, floras and vertebrates to reconstruct palaeoclimate), each subject to different taphonomic processes. Failure to recognize the mixture of biological and environmental phenomena operating at different scales can produce spurious and misleading results. Even within the same biological group, mixing data of different resolutions can have strong effects on derived interpretations, especially in quantitative analyses. Lupia *et al.* (1999) analysed palynological samples from North America to investigate the possible replacement of conifers and free-sporing plants by angiosperms. They chose to restrict analyses to individual palynological samples, from a single site and stratigraphic horizon, rather than including samples created by combining multiple samples from several sites or stratigraphic horizons. Lupia *et al.* (1999) found nearly constant within-flora diversity through the Cretaceous compared to previous results from Lidgard & Crane (1990) that showed increasing within-flora diversity from Early to

Late Cretaceous. By examining Lidgard and Crane's (1990) dataset, Lupia *et al.* (1999) concluded that the difference was attributable to the former's inclusion of combined samples, preferentially of Late Cretaceous age, in their analyses.

Likewise, the scale of biotic processes responding to abiotic conditions combined with resolution may decrease methodological power. For example, published data on using the foliar physiognomic method for reconstructing palaeoclimate suggest that the method, which seems to work well over large geographic gradients (Wolfe 1971, 1993), may break down at smaller scales probably due to the bias of local effects (Dolph & Dilcher 1979). Such problems are exacerbated when palaeontological data are compared with global climate model results, which can be of coarse spatial resolution, on the order of 4–5° of latitude and longitude (McGuffie & Henderson-Sellers 1997). Such coarseness may hide the finer scale variations in the real contemporary climate system, as experienced by the fossil organisms (climate proxies) themselves (Markwick 1998). Precipitation, for example, is very sensitive to local orography and moisture sources, and has been found to vary by 30% over a matter of a few kilometres (Linacre 1992). This may be particularly important in areas of rapid relief changes, such as the Eocene of the western United States (Sloan 1994).

The effect of error (inaccuracy) in databases also depends on the question being addressed. For North American Cambrian trilobites, Westrop & Adrain (2001) found that despite 70% of the generic records in the Sepkoski generic database being inaccurate (compiled from the published literature), when compared to their own field-based compilation, both datasets showed the same large-scale (coarse grain) patterns in Phanerozoic biodiversity (Adrain & Westrop 2000; Westrop & Adrain 2001). With finer grain, such errors become more important (Westrop & Adrain 2001).

The consequences of scale (grain) and error depend on the fossil group or assemblage investigated, the extent of the study and the questions to be asked. Palaeontological databases must therefore be designed to accommodate these issues.

Conclusions

The fossil record is the only direct evidence about the biological evolution of life on Earth. This represents a huge volume of data, and computerized databases provide the most efficient means of storing and examining the records for large-scale patterns and processes. The quantity and quality of these data are

always less than ideal. But, we suggest that it is the heterogeneities in scale (grain) in the fossil record that are potentially the major cause of problems in palaeoecology especially when different and varied datasets are mixed, as increasingly they are in studies examining the interplay of biotic and abiotic phenomena using GIS. Scale can, and should, be qualified in a database, and to facilitate this we offer the following suggestions.

- (i) Data should be collected at the finest available grain (resolution) since the finest scale of data stored in the database defines the finest grain possible in any analysis using that data. The grain in each case needs to be recorded (e.g. by a qualifier in a separate data field). In this way the database can be queried for data of a specified grain, or data of mixed resolutions can be coarsened to some common grain.
- (ii) All data in the database should have an audit trail, recording all sources and changes made to that data. To this end a distinction should be made between raw data (observations) and interpretation.
- (iii) Database structure is dictated by the nature of the fossil record, such that the most efficient structure is based around separate tables of spatial and temporal location, taxonomy and occurrence, which can also include taphonomic information (Fig. 3). The database structure should also facilitate the inclusion of multiple standards (e.g. alternative timescales and taxonomies).

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Integrating the present and past records of climate, biodiversity and biogeography: implications for palaeoecology and palaeoclimatology

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Abstract: A geographic information system (GIS) based, integrated dataset of Recent North American, European, southern African and Australian non-avian tetrapod faunas is used to examine the macroscale relationship between climate, biogeography and terrestrial taxonomic and functional species diversity (richness). The results support a modified form of the species–energy hypothesis, with the pattern of terrestrial biodiversity reflecting the manner in which species procure energy, rather than only the absolute amount of 'available energy'. Area and history are also found to be important. Ectotherms show the simplest relationship with environmental variables (and strongest latitudinal diversity gradients), and endotherms the most complex. A strong linear relationship is found between the proportion of each fauna represented by ectotherms and temperature (mean annual temperature and coldest month mean temperature). This relationship is used in an experiment to retrodict the palaeotemperature for the Middle Eocene lagerstätten fauna from Messel, Germany. Results compare well with interpretations based on other climate proxies.

Climate interpretations based on fossil data depend heavily on analogy with recent species and to this end an understanding of living groups and their distribution is crucial. Terrestrial organisms are neither randomly nor evenly distributed on the globe, and natural historians have long postulated that this is due, at least in part, to climate and other environmental factors (Humboldt & Bonpland 1807; Wallace 1876; Matthew 1915; Darlington 1948). Some taxa, such as crocodilians, are demonstrably limited by temperature and have been used by geologists since the early nineteenth century as tools for reconstructing palaeoclimate (Lyell 1830; Colbert *et al.* 1946; Hibbard 1960; Markwick 1994, 1998a). A climate origin has also been postulated to explain observed 'latitudinal' species diversity (or richness) gradients in many Recent terrestrial organic groups (Pianka 1966; Stevens 1989; Currie 1991; Rohde 1992; Wright *et al.* 1993). Ostrom (1970) has suggested that such gradients might provide a better tool for retrodicting palaeoclimate than comparison of an individual fossil with the climate of its living relative (see also Fischer 1961, p. 50).

Many theories have been proposed to account for observed latitudinal diversity gradients in the Recent (see Rohde (1992) for review), of which area–history and species–energy have perhaps received the most attention. Arguments based on area (Rosenzweig 1995) derive from the observation that island habitats tend to have

fewer species than non-isolated habitats of the same area. This is embodied in the island biogeography theory of MacArthur & Wilson (1967), in which standing diversity reflects the balance between immigration and extinction rates, as dictated by island area (smaller areas hold smaller populations that are therefore assumed to be more susceptible to extinction) and the proximity in time (history) and space to the dispersal source. Historical changes in insularity, for example the repeated fragmentation and coalescence of 'islands' during Pleistocene interglacial–glacial changes, are envisaged to increase the opportunity for allopatric speciation, and have been used to account for the high species diversities in SE Asia (Qian & Ricklefs 2000). Similar arguments have been used to explain patterns in the pre-Pleistocene marine invertebrate fossil record (Flessa 1975; Sepkoski 1976; Flessa & Sepkoski 1978; Crame 2001). But the relationship between area and diversity is not unequivocal, even for well documented examples such as SE Asia (Harrison *et al.* 2001), and the use of area *per se* must be viewed with caution. As Rohde (1997) has pointed out in regard to latitudinal diversity gradients, the low latitudes today do not necessarily contain the largest areas, despite being the location of the greatest species richness. However, islands need not be geographic entities (ocean islands), but may include other isolated physiological features (mountains, lakes) or distinct habitats