Aspects of the Genesis and Maintenance of Biological Diversity

Edited by

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Diversity in the past: comparing cladistic phylogenies and stratigraphy

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Introduction

The study of biodiversity involves the dimension of time, whether short- or long-term. Most research in biodiversity is based on observations on human time scales, either experimental protocols lasting for one or two years, or data collation from historical records spanning back a few hundred years. The scale of regional or global diversity change at present is great enough, however, to require comparison with information based on geological time scales of thousands or millions of years. There are many problems in bridging the gap from experimental and field-based studies to the palaeontological work which extends into the depths of the geological past. Many of these problems, often gathered together under the heading 'the incompleteness of the fossil record', are geological, and they will be outlined briefly. Other issues are, however, more biological, and are concerned with phylogenetic reconstruction; these may offer insights into understanding the past history of life.

The value of the fossil record in giving a clear account of evolutionary history has been questioned. Charles Darwin hoped that, over time, more and more fossils would be found which would fill in all the 'missing links' and give a full picture of the history of life. By 1866, some of the first phylogenetic trees based explicitly in evolution were published (Haeckel 1866). Until recently, phylogenetic trees were composed by taking account not only of the morphology of organisms, but also their place in geological time, and hence it was not possible to test the nature of phylogenies and the fossil record directly. However, the development of cladistic techniques has opened up the possibility of testing the pattern of evolution. Cladograms based on morphological and/or molecular data involve no direct measure of the age of fossils: fossils are included as terminal taxa, side by side with living taxa. The divorce of phylogeny reconstruction from stratigraphic evidence opens up exciting possibilities for testing the two sets of evidence against each other, and for moving to fill some of the inevitable gaps in the fossil record.

The quality of the fossil record

It has been asserted that the fossil record is too incomplete for it to yield any useful macroevolutionary results. A lesser claim is that cladistic analyses should be based solely on living forms, since the fossils are both incomplete morphologically and they represent an incomplete sample of all the fossils that ever lived (e.g. Goodman 1989; Hennig 1981; Løvtrup 1977; Nelson 1969; Patterson 1981). This attitude has been opposed by palaeontologists and by many biologists (Gauthier et al. 1988a; Hecht 1976; Norell and Novacek 1992a; Schaeffer et al. 1972; Schoch 1986; Smith 1994) on the grounds that

(1) some evidence is better than none;

(2) fossils include a sample of the majority of species that have ever lived;

(3) most fossils represent morphologies that are quite unknown today, and they greatly enrich the content of a phylogeny;

(4) fossils may be placed more or less precisely in time, which provides good cross-evidence for the order and age of branching points; and

(5) for many groups, fossils in practice offer as much morphological data as do museum specimens of modern representatives.

The incompleteness of the fossil record may be ascribed to many factors of the organisms themselves, of their habitats, of later changes within the lithifying rocks, and of the ways in which palaeontologists work (Paul 1990; Raup 1972; Sheehan 1977; Signor 1990). Soft-bodied organisms are less likely to be preserved than those with hard parts. Long-living, rare, organisms are less likely to die and be preserved than short-lived common organisms. However, large organisms have a greater preservation potential than small ones, because they can survive incarceration in fine- and coarse-grained sediments and because they are easier to find. As for habitats, organisms that fly, or live in trees, are less often preserved than those that lurk around ponds and rivers, or live on the sea bed. Subsequent geological history is also important: organisms preserved in ancient rocks are more liable to have been subducted, metamorphosed, or eroded out of existence, than are those in more recent sediments. Human factors are also very important: our knowledge of the fossil record depends critically on the interest people have in particular groups, their geographic location, and their ease of study; these variables have been quantified as 'paleontologic interest units' (Sheehan 1977).

The quality of the fossil record, or parts of it, may be tested by relative and absolute measures. Measures of the relative quality of the fossil record are frequently obtained by palaeontologists (Paul 1982; Benton 1987, 1994), and some approaches to measuring absolute quality have been proposed (Meehl 1983; Maxwell and Benton 1990; Benton and Storrs 1994). Both sets of

techniques offer the possibility of enhancing existing palaeontological data and of achieving better estimates of phylogenetic patterns and of past diversities. There is a three-step process: (1) filling the Lazarus gaps; (2) estimating range extensions, based on calculations of confidence intervals; and (3) searching for ghost ranges (cladistically defined minimum-implied gaps).

Filling the gaps

Lazarus gaps

A standard graphical approach in palaeontology is the use of range charts. These show by means of solid vertical lines the known distributions in time of particular fossil species or other taxa. A solid vertical line spanning a time interval of 5 myr might represent a succession of rocks containing densely packed fossils all the way through the sequence, or it might represent simply two point occurrences, each of a single fossil, spaced 5 myr apart in the rock column. Knowledge of the density of packing of the fossils along the range bar can provide useful statistical and predictive information (Paul 1982, 1990).

A first approach is to construct a grid of taxa versus time units, and to record presences and absences (Fig. 1.1(a)). Certain absences can then be determined as apparent rather than real; that is, gaps in the range which have resulted from non-preservation rather than non-existence of the taxon. These are the 'Lazarus taxa' (Jablonski 1986), those which apparently go extinct and then reappear higher up in the rock record. The ratio of known taxa to total known plus assumed taxa gives a minimal measure of relative completeness, the Simple Completeness Metric (SCM) (Benton 1987, 1994). This measure allows one to assess the relative quality of the fossil record either of groups or of time intervals (Fig. 1.1(b)).

Confidence intervals and range extensions

It is impossible to say whether a taxon arose before its first known fossil record, or whether it survived its last. Strauss and Sadler (1989) presented a technique of calculating confidence intervals for the ends of stratigraphic ranges. This was based on the intuitive assumption that recorded total ranges will tend to be more accurate the more closely packed fossils are within the known range. In other words, confidence intervals on both end-points of a range should be very small when fossils are closely packed, but huge when fossils are sparse. The confidence intervals on end-points of a range, expressed as a fraction of that range a, are calculated according to (Strauss and Sadler 1989; Marshall 1990):

$$a = (1 - C_1)^{-1/(H-1)} - 1,$$

where C_1 is the confidence level and H is the number of known fossiliferous horizons (smallest identifiable unit levels in the rocks at which fossils occur).

(a)

(b)

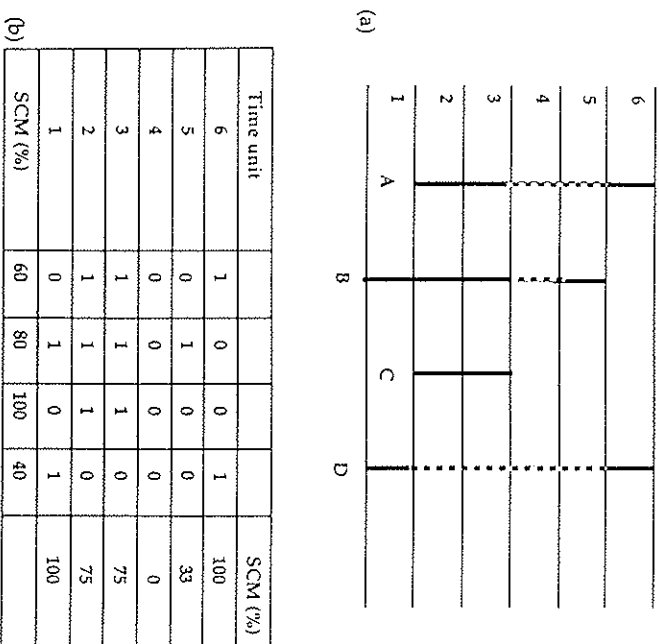| Time unit	A	B	C	D	SCM (%)
6	1	0	0	1	100
5	0	1	0	1	33
4	0	0	0	0	0
3	1	1	1	0	75
2	1	1	1	0	75
1	1	0	1	0	100
SCM (%)	60	80	100	40	100

Fig. 1.1 Calculating the effect of Lazarus taxa. (a) A hypothetical range chart of four fossil taxa (A–D) plotted across six time units (1–6); solid lines indicate known stratigraphic ranges, checked lines represent Lazarus ranges, or known intrarange gaps. (b) Calculation of the Simple Completeness Metric (SCM) for the range chart in (a), where the SCM is the ratio of Lazarus gaps to known fossil ranges, calculated by time interval (rows) or by taxon (columns).

At the extreme, where only the terminal points of a range are represented (i.e. $H = 2$), the 95% confidence intervals are more than ten times the observed range ($a = 19$). Even with six point occurrences of fossils through the range, the predicted range extensions must equal the observed range at the 95% confidence level (Fig. 1.2). With more than six records, the error bars diminish, but never quite disappear, reaching negligible values for intensely sampled ranges (e.g., $a = 0.03$ when $H = 100$).

Adding ghost ranges

The ghost range (Norell and Novacek 1992b; Norell 1993), or Minimum Implied Gap (MIG) (Benton 1994; Benton and Storrs 1994; Storrs 1994), or Minimal Divergence Time (MDT) (Weishampel and Heinrich 1992), is the difference between the age of the first representative of a lineage and that of its phylogenetic sister. Postulated sister groups in a cladogram arose, by definition, from a single node representing a point in time and hence both

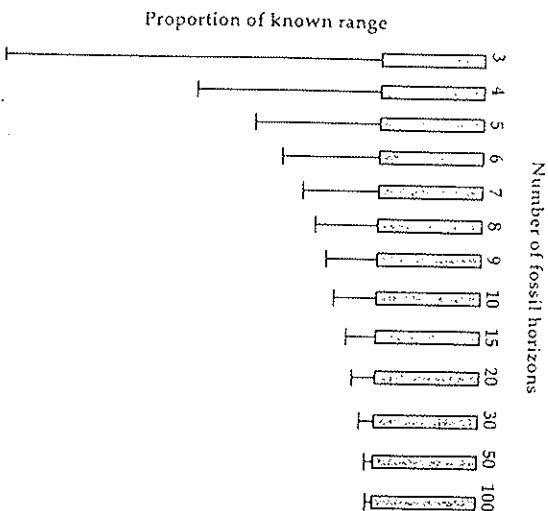Number of fossil horizons

Proportion of known range

Fig. 1.2 Estimates of true range lengths based on known stratigraphic ranges; 95% confidence intervals are shown. The more densely packed the fossil horizons are within the known range, the shorter is the confidence interval. (Based on information in Marshall 1990.)
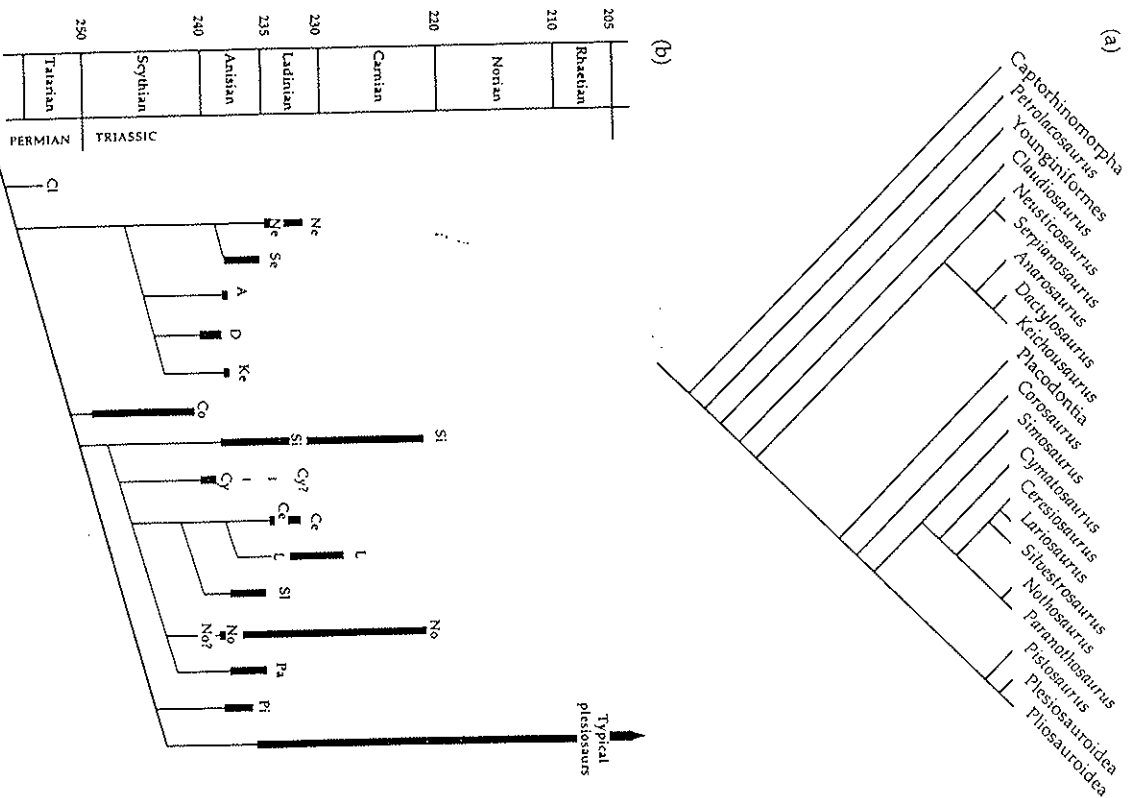
taxa should have oldest fossil representatives of the same age. In practice it is rarely the case that known fossil sisters are of the same geological age and the ghost range is a predictable range extension for one of the sister taxa. This depends on the assumptions that (1) the cladogram is a correct representation of relationships, and (2) both sister taxa are correctly assigned stratigraphically.

The fossil record of Triassic sauropterygians (Storrs 1991, 1994), long-necked marine reptiles, is chosen as an example (Fig. 1.3). Individual skeletons are well preserved and rich in osteological characters, which has permitted the production of a cladogram at genus level (Fig. 1.3(a)). When the cladogram is converted into a phylogram, by the addition of stratigraphic information (Fig. 1.3(b)), it can be seen that most genera are point occurrences, known from single geological horizons. Additionally, there are many ghost-range additions: MIGs represent a total of 65 myr, compared to 41.5 myr of known range, giving a value of only 39% completeness (41.5/(41.5 + 65)).

Estimating the absolute quality of the fossil record

How do revisions of data bases affect macroevolutionary conclusions?
The absolute quality of the fossil record has been tested by comparing changes in palaeontological knowledge over research time. The basic

(a)

Captorhinomorpha
Petrolacosaurus
Younginiformes
Claudiosaurus
Neusticosaurus
Serpianosaurus
Anarosaurus
Dactylosaurus
Keichousaurus
Placodontia
Corosaurus
Simosaurus
Cymatosaurus
Ceresiosaurus
Lariosaurus
Silvestrosaurus
Nothosaurus
Paranothosaurus
Pistosaurus
Plesiosauroidea
Pliosauroidea

(b)

205 Rhaetian
210 Norian
220 Carnian
230 Ladinian
235 Anisian
240 Scythian
250 Tatarian

PERMIAN | TRIASSIC

Cl   Ne   Se   A   D   Ke   Co   Si   Cy   Ce   L   Sl   No   Pa   Pi

No?   No?

Typical plesiosaurs

assumption behind these studies is that the cumulative sum of palaeontological research activity will tend to fill gaps and increase knowledge, and theoretically at some time in the future everything that can be known will be known. The absolute quality of the fossil record has been tested in two ways: (1) tests of how changes in palaeontological knowledge affect our perceptions of macroevolutionary patterns and (2) tests of the goodness of fit of cladograms to different stages of palaeontological knowledge.

The first set of tests demonstrate substantial changes in the documented fossil record through research time. For example, palaeontological knowledge of the fossil record of tetrapods has increased most over the past 100 years (Maxwell and Benton 1990), but although the gross number of taxa increased as a result of new finds (Fig. 1.4(a)), other aspects of the taxon lists changed in non-systematic and unpredictable ways. Revisions of stratigraphy, revisions of taxonomy at the alpha level, and broad-scale cladistic revisions of larger groups all affected the taxon range lists, but some ranges were shortened, some increased, and some remained unaltered. Some families and genera disappeared as a result of taxonomic revision, while others appeared, so that there was no overall shift in the results. The main change detected in a comparison of a 1967 data base (Harland et al. 1967) with one compiled 20 years later (Benton 1987) was that familial durations of tetrapods had increased marginally (29.1% of families with unchanged range lengths, 44.8% with increased range lengths, 26.1% with decreased range lengths). Increased range lengths would be predicted by the simple rallying cry that 'more palaeontological research means collecting more fossils', but the fact that more than one-quarter of the 515 families analysed showed decreased range lengths was more of a surprise. This was the result of cladistic redefinitions of families and the removal of suspect ancestral taxa from the bottoms of ranges, the latter of which lacked autapomorphies of the family.

A surprising conclusion of this study (Maxwell and Benton 1990) was, however, that although stratigraphic ranges of 70.9% of the tetrapod families had changed in a span of 20 years of research, the macroevolutionary conclusions derived from the data bases altered little. In fact, the phases of diversification and of extinction remained the same (Fig. 1.4(a)). Rates of origination and extinction at particular times also remained in proportion.

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Fig. 1.3 Calculation of relative completeness of the fossil record of Triassic sauropterygians, marine long-necked reptiles. (a) Cladogram of the genera of Triassic sauropterygians, as well as outgroups, placodonts, and the later clades Plesiosauroidea and Pliosauroidea. (b) Phylogenetic tree of the same sauropterygian genera plotted against a Triassic time scale, with ages in millions of years indicated. Higher taxa and most outgroups excluded. Known ranges are indicated in black, and assumed additional ranges are shown cross-hatched (these are based on cladistic patterns of pairing; see Fig. 1.6). Abbreviations of genera correspond to names given in full shown in (a). (Based on information in Storrs 1991, 1994.)

(a) Tetrapods

Geological time (myr)

Family diversity

(b) Marine animals

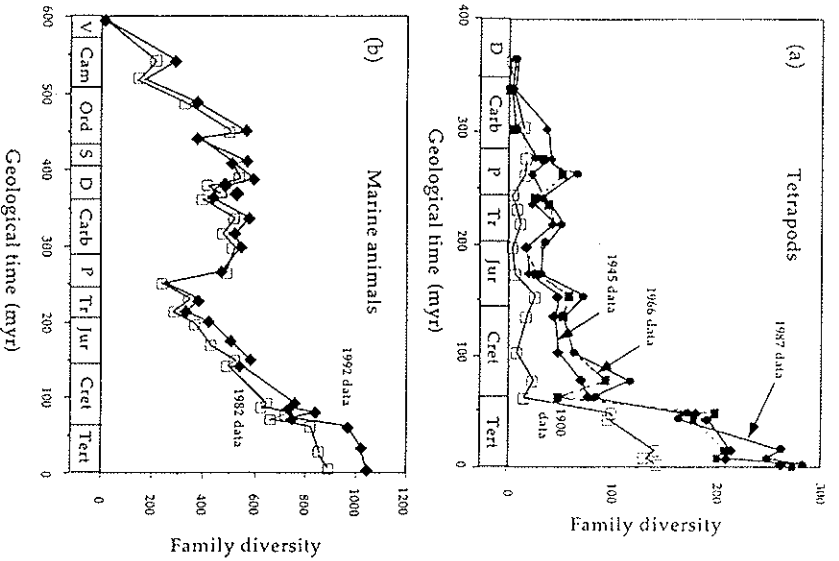Geological time (myr)

Family diversity

Fig. 1.4 Revisions of data bases have not affected macroevolutionary patterns. Diversity change through geological time for families of tetrapods (a) and marine animals (b), based on data bases published at different times. (Based on data in Maxwell and Benton 1990 and Sepkoski 1993.)

The main effects to be seen were an increase in overall diversity through much of the past 400 million years of tetrapod evolution and a slight sharpening of extinction events.

A similar study (Sepkoski 1993) of the past ten years of change in the standard marine animals data base (Sepkoski 1982, 1992) found turnover in 50% of the data—families had been added and deleted, low-resolution stratigraphic data had been improved, and dates of apparent origination and extinction of families had been altered. However, despite these changes, plots of diversification remained nearly identical but for the fact that the 1992 curve lies 13% higher than the older one (Fig. 1.4(b)). Further, the identity and magnitudes of extinction events remained the same. The main changes

were that family range lengths tended to increase (with an approximately equal distribution of earlier originations and later extinctions) and mass extinctions became slightly sharper, with extinctions shifting closer to chronostratigraphic boundaries. Hence, these tests have indicated two facts: (1) palaeontological knowledge is changing (advancing, one hopes) rapidly; (2) despite this, broad-scale macroevolutionary patterns have remained stable. If the fossil record were hopelessly incomplete, the patterns derived therefrom might change wildly as a result of new discoveries.

Has palaeontological knowledge improved?

The second test of the absolute quality of the fossil record compares the quality of different stages in palaeontological research in a quantitative way. Benton and Storrs (1994) compared a sample of 74 tetrapod cladograms (Table 1.1) against two recognised landmark data bases, the *Fossil Record* (Harland *et al.* 1967) and the *Fossil Record 2* (Benton 1993), using two measures of fossil record quality: (1) the correlation of clade rank and age rank, measured using the Spearman Rank Correlation statistic (SRC, with quality of correlation assessed at confidence levels of $P < 0.05$ and $P < 0.01$); and (2) the Relative Completeness Index (RCI) of all test cladograms when plotted as phylogenies against a geological time scale (measured as the proportion of Minimum Implied Gaps (MIGs), indicated by branching points of sister group pairs, to Simple Range Lengths (SRLs), based on total range lengths represented by fossils).

The results (Fig. 1.5) were mixed: the comparisons of age and clade rank showed no change from 1967 to 1993; but the more precise test of completeness showed a clear improvement. The first test showed no change in the degree of correlation of clade rank and age rank data when the 1967 and 1993 data sets were compared for all 71 comparable cladograms (Fig. 1.5(a),(b)): 43 of the 71 comparisons (61%) showed no change of state, while 28 (39%) changed, but the changes were equally balanced, with 14 'improvements' (i.e. negative to positive correlation; insignificant to significant correlation, at values of $P < 0.05$ or 0.01; correlation at $P < 0.05$ to correlation at $P > 0.01$) and 14 deteriorations. When the RCI values were compared as a whole (Fig. 1.5(c)), however, the means for 1967 and 1993 (67.856, 72.289) show a significant ($P < 0.05$) improvement whether tested parametrically (*t*-test) or non-parametrically (sign test; Wilcoxon signed ranks test).

Hence, the two tests just outlined have shown that knowledge of the fossil record is changing substantially, but that most of the macroevolutionary conclusions based on that record are relatively stable to these statistically non-systematic changes, and the relative completeness of the fossil record is increasing through research time. This may be the first time a quantitative demonstration has been made of improvement in knowledge in palaeon-tology.

Table 1.1 Seventy-four test-case cladograms used by Benton and Storrs (1994) to test the quality of knowledge of the fossil record in 1967 (data from Harland et al. 1967) and 1993 (data from Benton 1993). The match of cladistic node order and stratigraphic position was measured using the Spearman Rank Correlation (SRC) statistic. The quality of the fossil records implied by each phylogeny, for 1967 and 1993 data, was calculated as the Relative Completeness Index (RCI), which is the proportion of the cladistic Minimum Implied Gaps (MIGs) to the known Simple Range Lengths (SRLs) for all taxa in the phylogeny.

TAXON	1967			1993			
	RCI	SRC	n	RCI	SRC	n	
Actinoptergyii	−194.7	0.346	9	71.9	0.139	9	(Lauder and Liem 1983)
Amniota 1	84.5	0.928*	6	90.1	0.642	6	(Gardiner 1982)
Amniota 2	75.3	0.957**	10	82.6	0.982**	10	(Gardiner 1982)
Amniota	83.1	0.641*	11	75.3	0.493	11	(Gauthier et al. 1988b)
Amphibia	69.3	0.899**	12	80.5	0.860**	12	(Gardiner 1983)
Amphibia	41.1	0.655*	8	66.7	0.673*	10	(Milner 1988)
Amphibia 1	89.1	0.947*	5	95.0	0.772	6	(Panchen and Smithson 1988)
Amphibia 2	84.9	0.418	6	89.8	0.508	6	(Panchen and Smithson 1988)
Amphibia	48.0	0.682	11‡	74.3	0.276	11	(Trueb and Cloutier 1991)
Archosauria	94.7	0.791*	8	95.2	0.657*	9	(Benton and Clark 1988)
Archosauromorpha	84.2	0.151	8	85.4	0.108	8	(Benton 1985)
Archosauromorpha	73.4	−0.620	9	68.1	−0.253	15	(Evans 1988)
Artiodactyla	86.3	0.677*	10§	89.3	0.428	10	(Gentry and Hooker 1988)
Aves	48.5	0.609*	11	77.2	0.720*	11	(Cracraft 1988)
Brontotheriidae	56.1	0.969**	8§	67.7	0.975**	10	(Mader 1989)
Chalicotheriinae	—	—	—	59.3	0.903**	8	(Coombs 1989)
Chalicotherioidea	54.7	0.938*	6§	54.3	0.962**	7	(Coombs 1989)
Crocodylomorpha 1	17.7	0.556**	18§	5.3	0.801**	22	(Benton and Clark 1988)
Crocodylomorpha 2	4.6	0.569*	17§	0.1	0.815**	19	(Benton and Clark 1988)
Diapsida	82.3	0.927**	7	71.0	0.849*	8	(Laurin 1991)
Equidae	58.3	0.975**	12§	59.8	0.942**	12	(Evander 1989)
Eutheria	55.2	0.904**	9	75.6	0.781*	9	(Gregory 1910)
Eutheria	64.1	0.809**	10	81.1	0.590*	10	(Simpson 1945)
Eutheria	44.6	0.646*	12	81.6	0.795**	12	(McKenna 1975)
Eutheria	46.3	0.723**	14	73.1	0.650**	14	(Novacek 1982)
Eutheria	27.4	0.078	9	74.7	−0.211	9	(Miyamoto and Goodman 1986)
Eutheria	53.7	0.857**	12	72.5	0.590*	12	(Novacek and Wyss 1986)
Eutheria	90.6	−0.159	10	74.0	−0.093	10	(Shoshani 1986)
Eutheria	39.7	0.063	13	60.5	−0.031	13	(Novacek et al. 1988)
Eutheria	71.3	0.915**	10	82.0	0.883**	10	(Novacek 1989)
Gnathostomata	96.4	−0.185	7	93.8	−0.286	7	(Rosen et al. 1981)
Gnathostomata	92.6	0.273	8	92.6	0.232	8	(Lauder and Liem 1983)
Hadrosauridae	100.0	—	7§	63.8	0.549	8¶	(Weishampel and Horner 1990)
Hadrosaurinae	100.0	—	5§	73.1	0.803	5¶	(Weishampel and Horner 1990)
Hystricomorpha	67.9	0.288	6	69.1	0.626*	9	(Jaeger 1988)
Lepidosauromorpha	74.1	0.973**	7‡	77.6	0.988**	8	(Benton 1985)
Lepidosauromorpha	63.3	0.876**	12‡	72.5	0.895**	16	(Evans 1988)
Lepidosauromorpha	92.4	0.734*	7	76.6	0.821*	7	(Gauthier et al. 1988a)
Lissamphibia	38.1	0.718	5	71.4	0.754	6	(Bolt 1991)
Mammalia	31.1	−0.012	15	66.7	0.368	15	(Novacek et al. 1988)
Mammalia	56.1	0.460	12	83.9	0.935**	12	(Novacek 1989)
Ornithischia	68.7	0.809	6	68.9	0.927**	7	(Sereno 1984)
Ornithischia	60.1	0.455	8	64.9	0.725*	9	(Sereno 1986)
Ornithischia	60.1	0.455	8	64.9	0.725*	9	(Benton 1990)
Ornithopoda	79.2	−0.487	5	56.6	0.603	6	(Norman 1984)
Perissodactyla	76.9	0.214	12§	97.6	0.428	130	(Hooker 1989)
Primates	49.0	0.376	11§	50.0	0.442	11	(Andrews 1988)
Proboscidea	53.8	0.882**	15§	51.1	0.935**	18	(Tassy and Shoshani 1988)
Ruminantia	59.9	0.582*	16§	67.4	0.606**	17	(Janis and Scott 1988)
Sarcopterygii	94.1	0.588	6	95.0	0.662	7	(Schultze 1987)
Sarcopterygii	95.9	−1.000	5	93.2	−0.973	5	(Chang 1991)

Table 1.1 *Continued*

TAXON	1967			1993			
	RCI	SRC	*n*	RCI	SRC	*n*	
Sarcopterygii	94.1	−0.221	6	92.2	−0.387	7	(Forey *et al.* 1991)
Sauropodomorpha	92.0	0.924**	6	61.3	0.376	9	(Benton 1990)
Sauropterygia	73.1	0.031	6§	94.4	0.651	7	(Storrs 1991)
Squamata 1	41.3	0.291	7	73.4	0.164	7	(Estes *et al.* 1988)
Squamata 2	82.0	0.782*	8	81.7	0.264	8	(Estes *et al.* 1988)
Squamata	77.3	0.718	6	64.6	0.638	6	(Rieppel 1988)
Squamata	79.5	0.895**	7‡	64.6	0.749*	8	(Schwenk 1988)
Synapsida	75.2	0.983**	17	73.1	0.986**	17	(Kemp 1982)
Synapsida	69.4	0.958**	16	76.2	0.950**	16	(Gauthier *et al.* 1988*b*)
Synapsida	35.4	0.965**	19	64.5	0.967**	19	(Rowe 1988)
Synapsida	71.0	0.957**	20	77.4	0.942**	21	(Hopson 1991)
'tapiroids'	76.0	0.817**	9§	81.1	0.673*	10	(Schoch 1989)
Teleostei	70.6	0.883**	15	75.7	0.827**	16	(Lauder and Liem 1983)
Testudines	79.9	0.250	6	61.4	0.563	6	(Gaffney 1975)
Testudines	53.4	0.236	9‡	58.0	0.748**	11	(Gaffney 1984)
Testudines	83.9	0.388	6	62.0	0.716	6	(Moody 1984)
Testudines	54.7	0.594*	11‡	59.6	0.910**	14	(Gaffney and Meylan 1988)
Tetrapoda	89.7	0.873*	7	89.0	0.883*	7	(Gaffney 1979)
Therapsida	80.2	0.950**	14	91.6	0.905**	14	(Hopson and Barghusen 1986)
Theropoda	84.6	0.730	5	61.1	0.782*	7	(Gauthier 1986)
Theropoda	84.6	0.730	5	40.4	0.476	9	(Benton 1990)
Ungulata	87.4	0.548*	12	85.8	0.553*	14	(Prothero *et al.* 1988)

n = sample size. ‡ = data from Harland (1967) and Romer (1966), § = data from Romer (1966), ¶ = data from Weishampel *et al.* (1990), † = data from Prothero and Schoch (1989). * = significant correlation at *P* < 0.05. ** = significant correlation at *P* < 0.01.
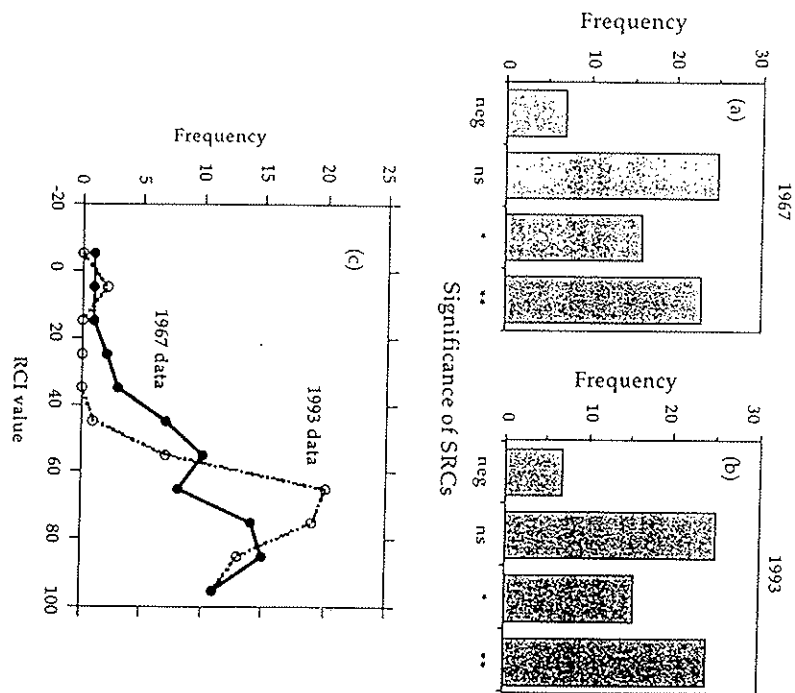

Fig. 1.5 Palaeontological knowledge has improved since 1967. Comparison of a 1967 and a 1993 data base on the fossil record of vertebrates shows no change in the patterns of matching between ordering of branching points based on cladistic and stratigraphic data (a,b), but the relative completeness of phylogenetic trees has improved significantly (c). The first test is Spearman Rank Correlation (SRC) of matching of rank order of origin of taxa, based on cladistic and stratigraphic data, in 71 cladograms of vertebrates. The second test is a comparison of measures of relative completeness of 73 phylogenies, based on comparisons of known Simple Range Lengths (SLRs) and interpreted Minimum Implied Gaps (MIGs) from sister-group comparisons. The first test assesses rank order only, recording simply correlation (* at 95% and ** at 99% significance levels), non-correlation (ns), or negative correlation (neg), and takes no account of the *amount* of difference that exists. The second test is based on a continuous numerical summation of SRLs and MIGs, and offers clear evidence for a significant reduction in the relative *amount* of mismatch between the known fossil dates of origin of sister groups.

Comparing cladograms and stratigraphy

Cladograms are composed essentially independently of geological input. This was not always the case in pre-cladistic days: classically, systematists would use the first known date of occurrence as a measure of the 'primitiveness' of a species or larger group, or of a character. Phylogenies were frequently compiled by stringing together the known fossil and living taxa in sequence of occurrence, in a kind of joining-the-dots procedure. Cladists have shown (Ax 1987; Eldredge and Cracraft 1980; Hennig 1966; Wiley 1981) that geological sequence is a poor guide to the polarity of characters and the order of occurrence in time need not match the order of nodes in a cladogram. Only in cases of superbly good fossil records and poor morphological differentiation may the stratophenetic approach (Gingerich 1985) be appropriate, *faute de mieux*.

Thus, cladograms, whether based upon morphological or molecular data, are largely, or entirely, independent of geological input. One view (Patterson 1981; Platnick 1979) holds that the procedure is wholly divorced from evolutionary and stratigraphic assumptions, while another (Gauthier *et al.* 1988*a*; Norell and Novacek 1992*b*; Novacek 1992) states that the coding of characters and determination of polarity depend to some extent on broad evolutionary assumptions. For example, the members of the outgroup are not selected blindly—they are chosen by a systematist who clearly cannot ignore currently postulated phylogenies. In testing the relationships of mammalian orders, a systematist would typically choose a number of non-mammalian vertebrates to form the outgroup, based on previously established clades such as Chordata, Vertebrata, and Amniota. In this case, the outgroup could legitimately consist of a slug, a virus, an oak tree, and a cabbage, but the determination of character polarities would then be nonsensical.

If they are wholly (or largely) independent, then cladograms and stratigraphic data, information relating to geological time and sequence, may be tested against each other. Recent tests of the match between cladograms and stratigraphic data have suggested that there is strong correspondence. The stratigraphic sequence of first occurrences of fossil vertebrate groups frequently matches the order of branching of cladograms based upon character analysis alone (Gauthier *et al.* 1988*a*; Norell and Novacek 1992*a,b*; Benton and Storrs 1994).

The technique for comparing clade-rank data with age-rank data (Fig. 1.6) involves certain simplifications. Cladistic rank is determined by counting the sequence of primary nodes in a cladogram; nodes are numbered from 1 (basal node) upwards to the ultimate node. As this method cannot cope objectively with complex cladograms comprising several subclades, such cladograms are converted to a hierarchy of nodes along a single branch (Fig. 1.6(a)). This is accomplished (Fig. 1.6(b)) by collapsing each subordinate clade to a single polytomous node originating at the main stem; each polytomous lineage is assessed equally and given equal cladistic rank. Yet, in practice, the oldest
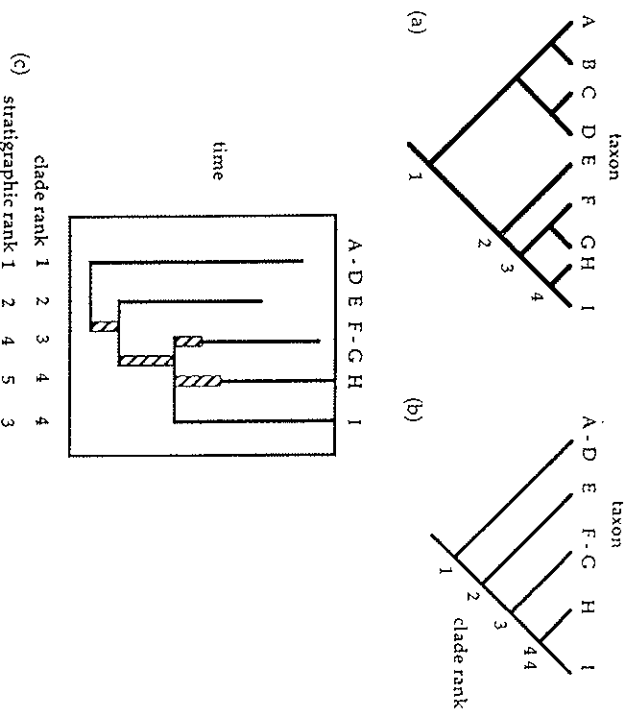

Fig. 1.6 Method for comparison of cladistic and stratigraphic data. A cladogram (a) is reduced to a single stem lineage, or 'Hennigian comb' type of cladogram (b), in order to allow the clade rank to be assessed unequivocally. The polytomes representing collapsed parts of the original cladogram (here numbered 1, 3) are counted as single lineages: to include each separate branch collectively could introduce large amounts of implied gap where information actually exists. The stratigraphic rank is assessed (c) independently by recording the known order of appearance of the taxa. Because of missing early ranges (shown cross-hatched), clade rank does not always match stratigraphic rank.

representative branch is the one chosen for the analysis. In cases where subordinate clades are large, we adopted the convention that the source cladogram is collapsed so as to maximize node number (using the principle of free rotation). The stratigraphic sequence of clade appearance is assessed from the earliest known fossil representative of sister groups. The Minimum Implied Gap (MIG, indicated by cross-hatching in Fig. 1.6(c)) is the difference between the age of the first representative of a lineage and that of its sister, since the oldest known fossils of sister groups are infrequently of the same age. The MIG is a minimum estimate of stratigraphic gap, as the true age of lineage divergence may lie well before the oldest known fossil.

In their small-scale study, Gauthier *et al.* (1988*a*) found that clade rank and age rank are correlated. Using a larger sample, Norell and Novacek (1992*a*) found that 18 of their 24 test cases (75%) gave statistically significant

($P < 0.05$) correlations of cladistic branching order and stratigraphic order. Best values were found for mammalian ungulate groups, which are believed qualitatively to have 'good' fossil records and relatively stable, well-resolved cladograms. The six cases that failed (amniotes, Squamata, hadrosaurs 1, hadrosaurs 2, higher primates, artiodactyls) could not be simply explained.

Benton and Storrs (1994) found less convincing results from their study of 74 cladograms of vertebrates, only 41 (55%) of which showed statistically significant correlations of clade order and age order at $P < 0.05$, and 25 (35%) at $P < 0.01$. The greater proportion of mismatches between clade rank and age rank in this latter study may be the result of including a wider range of cladograms in the test, some of which might not be so well resolved as those chosen by other authors. Nonetheless, all studies to date show that the majority of fossil records correspond to relevant cladograms in terms of their predictions of the order of appearance of groups: if the fossil record were hopelessly bad, the dates of origin of groups based on fossil evidence would show no match to clade ranks at all.

Conclusions

The long-term temporal aspect of biological diversity can be assessed only from phylogenies. Opinions vary about the value of the fossil record in establishing and testing phylogenies and in presenting information about species richness in the past; at one extreme, the historical record is accorded little value because of its supposed incompleteness, and at the other, the palaeontological data are read literally, and with no consideration of how information may have been lost.

There is no doubt that the information content of the fossil record diminishes backwards in time and that no instant in geological time has the potential to be as well understood as the present. However, evidence about phylogeny is available from various independent sources: cladistic reconstruction of phylogeny from morphological characters, stratigraphic information, and molecular phylogeny reconstruction. Statistical methods are available for applying correction factors to particular parts of the fossil record by filling interpolated gaps, estimating terminal confidence intervals, and adding ghost ranges predicted from cladistic phylogenies.

Broad-scale studies of the fossil record have shown that the documented data base has changed substantially during the past 25 years, but that major events appear to be robust enough to be unaffected by the statistical noise produced by the unpredictable vagaries of research. Palaeontological knowledge has improved in the past 25 years, when tested against a constant of cladistic information. The availability of several sets of independent information about the history of life suggests that it will be possible to give quantitative measures of confidence in estimates of diversities in the past.

Note added in proof

Since this manuscript was completed, a number of relevant papers have been published. Marshall (1994) has developed a modified approach to the calculation of range extensions (Fig. 1.2). The simple technique shown here is based on an assumption of randomly distributed fossil finds, and hence classical confidence intervals are applicable. His new technique relaxes the assumption of randomness of distribution of fossil horizons, but it is less universally applicable, and there are uncertainties associated with the sizes of the confidence intervals. Huelsenbeck (1994) has presented a test of the fit of cladograms to the stratigraphic record, a stratigraphic consistency index. This technique uses the same approach as has been applied in the present paper, but turns the focus on testing the quality of cladograms instead of the quality of stratigraphic records of fossil occurrences. Finally, Benton and Simms (1995) have shown that the fossil records of continental vertebrates and echinoderms are equivalent in quality when compared to a large sample of available cladograms and molecular trees. This finding validates the use of different kinds of fossil data (continental vs. marine; vertebrate vs. invertebrate) in broad-scale phylogenetic studies.

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