Paleobiology, 34(4), 2008, pp. 516–533

How to find a dinosaur, and the role of synonymy in biodiversity studies

Michael J. Benton

Abstract.—Taxon discovery underlies many studies in evolutionary biology, including biodiversity and conservation biology. Synonymy has been recognized as an issue, and as many as 30–60% of named species later turn out to be invalid as a result of synonymy or other errors in taxonomic practice. This error level cannot be ignored, because users of taxon lists do not know whether their data sets are clean or riddled with erroneous taxa. A year-by-year study of a large clade, Dinosauria, comprising over 1000 taxa, reveals how systematists have worked. The group has been subject to heavy review and revision over the decades, and the error rate is about 40% at generic level and 50% at species level. The naming of new species and genera of dinosaurs is proportional to the number of people at work in the field. But the number of *valid* new dinosaurian taxa depends mainly on the discovery of new territory, particularly new sedimentary basins, as well as the number of paleontologists. Error rates are highest (>50%) for dinosaurs from Europe; less well studied continents show lower totals of taxa, exponential discovery curves, and lower synonymy rates. The most prolific author of new dinosaur names was Othniel Marsh, who named 80 species, closely followed by Friedrich von Huene (71) and Edward Cope (64), but the ''success rate'' (proportion of dinosaurs named that are still regarded as valid) was low (0.14–0.29) for these earlier authors, and it appears to improve through time, partly a reflection of reduction in revision time, but mainly because modern workers base their new taxa on more complete specimens. If only 50% of species are valid, evolutionary biologists and conservationists must exercise care in their use of unrevised taxon lists.

Michael J. Benton. Department of Earth Sciences, University of Bristol, Bristol, BS8 1RJ, United Kingdom. E-mail: mike.benton@bristol.ac.uk

Accepted: 21 May 2008

Introduction

A key question for evolutionary biologists and paleontologists is whether they have reasonably complete species lists or not. Completeness of a species list depends on sampling and error. It is commonly assumed that some clades, such as mammals, birds, or flowering plants, are well sampled: new species are reported at the rate of only one or two a year, and sampling is presumably rather complete (Wilson 1992; Magurran and May 1999; Purvis and Hector 2000). Other groups, such as insects, meiofauna, and microbes, appear to be less well sampled: new species are reported from every collecting trip, and the limiting factor on discovery is the number of working systematists (May 2004).

Error is equally important. Wilson (1992) assumed a global synonymy rate of 22% for extant taxa, reducing the tally of named species from 1.8 to 1.4 million. May and Nee (1995) confirmed this figure, stating that ''one-fifth of the names are ''aliases'.'' These estimates, however, may be too low and they may imply too much uniformity in the behavior of systematists. Synonymy rates range from 7% to 80% (mean 31%) among certain insect groups (Gaston and Mound 1993), from 5% to 93% among Mediterranean freshwater mollusks (Altaba 1996), and from 33% to 88% (mean 66%) among seed plants (Wortley and Scotland 2004). Further, rates such as these are based on the current list of recognized species names. They take no account of the fact that many years may pass before synonyms and other errors are identified, and recently named species have not yet been revised; if the current estimate of a synonymy rate is 20%, this is almost certainly an underestimate because at least 20% of recently named taxa are also likely to be invalid, and they are not included in the error estimate.

With this in mind, Solow et al. (1995) presented a modeling approach to identify the true error rate. They found that the empirical error rate for thysanopteran insects is 22%, based on a survey of all 6112 named species.

0094-8373/08/3404-0006/$1.00

They then fitted a probability distribution to the year-by-year count of synonym and error discovery to reach an estimated actual error rate of 39%, roughly twice the static estimate. Alroy (2002) applied a modified approach to his data set of North American fossil mammals, and found error rates of 24–31%.

The purpose of this study is to explore a comprehensive database of a single clade, the Dinosauria, to determine the taxon discovery pattern and how synonymy rates change through study time. Hypotheses to be tested are whether (1) the overall synonymy rate for dinosaurs is higher than for extant groups because of inadequacies of the fossil material; (2) the discovery rate of new dinosaurian species depends on the availability of new material or sufficient systematists; (3) the taxon list is dominated by a small number of systematists; (4) patterns and practices of naming and revision of species differ from continent to continent; (5) taxonomic error rates reflect the intensity or ''maturity'' of study.

Definitions

The pattern of accumulation of knowledge about any clade through research time may be documented by means of a collector curve (Cain 1938), also called a species accumulation curve (Gaidet et al. 2005) or a discovery curve (Wickström and Donoghue 2005; Bebber et al. 2007). We prefer the last term for studies such as this where global species counts are being assessed. The collector/discovery curve is a plot of numbers of new taxa discovered against some measure of effort, perhaps the number of days or years of study (Preston 1948). Such curves can be plotted for ecological sampling within a restricted area (Colwell and Coddington 1995; Mao et al. 2005; Olszewski 2004), or at global scale for assessing the rate of discovery of taxa within a major clade in large-scale biodiversity studies (May 1990; Tarver et al. 2007). A complete discovery curve might plot as a logistic, or S-shaped, curve, with a slow rate of discovery at the start, then a rapid rate of discovery, followed by an asymptote as sampling has recovered nearly all taxa. In estimating modern biodiversity, it is assumed that some groups, such as birds and mammals, are rather well collected, and so lie on the asymptote on a discovery curve (May 1990; Bebber et al. 2007). Other groups, such as insects, microbes, or meiofauna, where new taxa are discovered at a high rate, are presumably located somewhere on the rising part of the discovery curve.

Estimates of synonymy rates noted above (Wilson 1992; Gaston and Mound 1993; Solow et al. 1995; Altaba 1996; Wortley and Scotland 2004) indicate the need to document year by year the decisions of systematists. Rather than a static estimate of the ratio of synonyms to valid species names, Alroy (2002) recommended the use of a ''flux ratio'' approach that considers historical patterns of species discovery, validation, invalidation, and revalidation. In the normal run of things, a species is named and is then subject to scrutiny and revision by other systematists at a later date; these later revisers may choose to validate the species or invalidate it. Later revisers of course sometimes revalidate species that others had invalidated. The flux ratio approach attempts to take all these systematic actions into account in allowing a prediction of the true taxonomic error rate for a group.

Hitherto, most commentators have concentrated on only one of the several reasons for rejecting a taxon name. A species may indeed be declared invalid because it has been named before (it is a synonym), but there are other reasons for rejection. A species may have been named without definition of type material (nomen nudum), the name was an unnecessary invention to correct an earlier supposed error (nomen vanum), the name has been forgotten/never used (nomen oblitum), or the status of the name is equivocal (nomen dubium). Further, the species may be based on material belonging to a different clade. Dodson (1990) reported that 9% of dinosaurian generic names were replaced because they were preoccupied, that is, they had been used for another taxon altogether at an earlier date (e.g., the theropod name *Laelaps*, given by Cope in 1866, was found to have been published by Koch in 1836 for a new genus of mites that infest rodents).

All these aspects of the normal behavior of taxonomists (Alroy 2002) ought to be summed together. Commentators (e.g., Wilson 1992; May and Nee 1995; May 2004) have tended to focus on the issue of synonymy, or alias names, and yet in practice taxonomists are just as likely to name a taxon, especially a fossil taxon, on inadequate material as to rename something that has already been named. Summing all forms of error together, we refer to the *taxonomic error rate* as encompassing synonyms, nomina dubia, nomina nuda, nomina vana, nomina oblita, and preoccupied names.

Issues concerning the quality of species lists are comparable for extant and extinct groups. Systematists work in the same way, although material of fossil taxa is generally less complete than for extant taxa. Comprehensive taxon lists are important for paleobiologists in debates about origination, diversification, turnover, decline, and extinction of a group. If a particular fossil record is substantially incomplete, then any pattern of decline or expansion will be biologically meaningless (Peters and Foote 2002). If, on the other hand, the fossil record is believed to be complete, or at least complete enough at certain taxonomic and stratigraphic levels of scrutiny (Benton et al. 2000), then the patterns may have some biological validity.

Materials and Methods

The analyses are based on a database listing all taxa I have found that have ever been considered to represent valid dinosaurian genera. This compilation may be more comprehensive than is generally possible for other groups, because there are so many precursor lists of ''all dinosaurs'' in print and on the web. Genera, rather than species, were chosen for this study for two reasons: (1) most dinosaurian genera contain only one species, and (2) the status of dinosaurian species is less clear than that of genera; whereas dinosaurian genera have been subject to repeated review and comparison (e.g., Weishampel et al. 1990, 2004), and the species-level taxonomy of some dinosaurian taxa that once contained many species has been revised thoroughly (e.g., *Triceratops*, Ostrom and Wellnhofer 1986), other multispecies dinosaurian genera have not been revised. Nonetheless, species data were collected and analyzed, but the results were indistinguishable from those at generic level, and they are not shown here.

A further problem that may be particular to dinosaurs, and some other pre-Cenozoic vertebrate taxa, is that most species are based on incomplete specimens. Dodson (1990) estimated that only 20% of dinosaurian species and genera are based on more or less complete skeletons; in many cases, apparently closely related genera or species might be based on different body parts—a jawbone, a tail, or a limb element—and so it is hard to establish whether there truly were three species, or one. Recent synoptic revisions (e.g., Weishampel et al. 1990, 2004) have taken a highly critical view of such issues, and have determined as nomina dubia many such incomplete specimens that lack apomorphies.

A comprehensive survey of the quality of all dinosaur type specimens is beyond the bounds of this study, but sampling by cohort provides some information. Six five-year cohorts (1840–44, 1870–74, 1900–04, 1925–29, 1950–54, 1975–79) of genera and species of dinosaurs were tracked through study time to observe the pattern of validation and invalidation of taxa. The 122 genera and 188 species in all that were named during these sample periods represent just over one-tenth of the total counts. The nature of the type specimens used for those taxa was also coded, as follows: 1 (isolated teeth or bones); 2 (one complete or near-complete skull; 3 (several skulls); 4 (one complete or near-complete skeleton; 5 (several skeletons). These quantitative codings provide a basis for testing whether dinosaur systematists use more or less complete materials for their diagnoses today than in the past.

The database used in these studies documents year by year the status of each genus according to then-current publications, from 1824 (when the first dinosaurian genus, *Megalosaurus*, was named) to 2004. The genus list was compiled from Weishampel et al. (2004), together with original papers through 2003 and 2004 to bring the list to the end of 2004, for a total of 1036 named dinosaurian genera. Mesozoic birds were included in the listing, so that the clade Dinosauria is complete when viewed from the point of extinction of the nonavian dinosaurs at the end of the Cretaceous

Period, 65 million years ago. The birds comprise 100 of the 1036 genera.

Then, an exhaustive search was made of previous publications on dinosaurian systematics, especially monographic reviews and synoptic works, in order to establish a moving total of then-valid dinosaurian taxa. Year by year, new genera were named from all over the world, and the cumulative total of named taxa increased. Equally, from time to time, taxonomists pointed out errors in previous determinations, as noted above.

At times, all sorts of non-dinosaurian material has been ascribed to Dinosauria—remains later assigned to other fossil reptile groups, such as crocodilians, basal archosaurs, synapsids, or marine reptiles. Some forms even turned out to be mammals or inorganic remains. The dividing line between birds and dinosaurs has been hard to establish, especially with incomplete theropod specimens, but that does not affect the current study because Mesozoic birds are included in Dinosauria. Further, some taxa that were originally assigned to other groups were later identified as dinosaurian and added to the list long after they had been named.

For Dinosauria, invalidations and revalidations sometimes happened promptly, within a year or two of the naming of the genus; at other times it took decades or centuries for such decisions to be published. Revalidations and discoveries of dinosaurian taxa previously assigned to other groups are uncommon events in comparison to the numbers of invalidations of taxa, so this last factor tends to damp the rising curve of new dinosaurian taxa. The movement in current numbers of taxa considered valid is not smooth, however, and depends on the publication of major review monographs. There may be several years, or even a decade, during which little revision is carried out, and the curve of accepted taxa keeps rising as new taxa are named. Then, a synoptic review, such as *The Dinosauria* and *The Dinosauria 2* (Weishampel et al. 1990, 2004) may be published, and this produces a dramatic reduction in accepted taxa at a stroke.

In summarizing the totals of valid genera through time, it is important to distinguish between ''then valid'' and ''now valid'' totals. The ''then valid'' total documents opinions at the time, and is suitable for a study of changing opinion through time (Alroy 2002). This approach has further merit in answering concerns about how knowledge accumulates and whether the accumulation of knowledge changes our big-picture view of evolution. The ''now valid'' total maps today's opinion back in time, and this gives a clearer picture of how current knowledge accumulated. In the future, the ''then valid'' curve will be correct up to 2005, and will be augmented by addition of post-2005 data. The ''now valid'' curve is constantly subject to revision as current opinions on taxon validity change.

Factors that might determine the number of known taxa include areas explored and numbers of authors. The areas explored are represented by cumulative totals of basins and countries. I use the term ''basin'' here, somewhat informally, to refer to named fossiliferous geological units, such as the Solnhofen Limestone of southern Bavaria or the Tendaguru area; widespread units, such as the Wealden of southern England, or the Morrison Formation of the American Western Interior, are divided into major geographic units, by counties or states. Countries are identified according to the modern political map. For comparisons of subsets of the data, modern continents are used.

Numbers of authors are based on counts of paleontologists who were active in naming new dinosaurs, or in reviewing dinosaurian systematics: a time span was established for each author from their first to last publications, and totals were established for each year. This became harder to do after 1990 because of sheer numbers, and the ''total authors active in any year'' is taken from *Web of Knowledge*© from 1990 to 2005, based on the number of people writing papers each year with ''dinosaur'' in the title or abstract. Note that these totals of ''active workers'' include all authors named on publications, whether they are first or subsequent authors.

The taxonomic error rate is the ratio of numbers of synonyms and other erroneous taxa divided by the total numbers of named taxa at any time. The taxonomic error rate could also be calculated as the ratio between invalid names and valid names, but this measure is less stable, being more subject to vicissitudes in the numbers of both invalid names and valid taxa.

Numbers of Taxa

The database (to the end of 2004) lists 1401 species, of which 675 (48.2%) are regarded as invalid, and 1036 genera, of which 388 (37.4%) are deemed to be invalid. There are more species than genera of course, and the taxonomic error rate is considerably lower for genera than species. This is partly because most dinosaurian genera are monospecific, and where multiple species have been established within a genus, systematists have debated these endlessly. The minor anatomical differences used to establish species of dinosaurs are easier to reject than the more substantial characters used to diagnose genera.

How many of the erroneous taxa are synonyms? It is meaningful to look at patterns of invalidity among species, rather than genera, of dinosaurs, because the determinations were made at species level. In the present species list of dinosaurs, 230 of the 1401 names (16.4%) are currently regarded as synonyms, 340 (24.3%) are designated nomen dubium, 47 (3.4%) are designated nomen nudum, and 58 (4.1%) are not dinosaurs. So, of invalid dinosaurian species, twice as many have been invalidated for reasons other than synonymy (16.4% of the total are synonyms; 31.8% are invalid for other reasons).

This unexpected finding, that synonyms are outnumbered substantially by other taxonomic errors, may apply only to fossils, where the temptation to name new taxa on the basis of inadequate type material (e.g., an isolated tooth or single bone) is higher than for most living taxa. Among extant taxa, high invalidity for reasons other than synonymy would presumably be found only in groups where it is hard to collect and preserve complete specimens, or where there has been a major shift in practice (e.g., earlier workers named taxa on the basis of external ornament, whereas modern workers exclusively use internal organ characters).

Note the proportions of species to genera: with 649 valid genera and 726 valid species in the current listing, this works out as 1.12 species per genus. The number seems to be stable. Dodson (1990) recognized 285 genera and 336 species, or 1.18 species per genus. This is a key reason (noted above) that dinosaurian paleontologists tend to use genera as a reasonable proxy for species.

The Balance between Naming and Revision

Tracking through research time, new dinosaurs were named at a rate of 0–5 per year through much of the nineteenth and early twentieth centuries (0–2 per year from 1824 to 1850, 3–4 per year from 1851 to 1900, 3–4 per year from 1901 to 1980, 20–30 per year from 1980), with highs of 10–20 in 1876 and 1877, corresponding to intense activity by Cope and Marsh, and 1914, 1932, and 1933, mainly from publications by Friedrich von Huene. Current annual totals are the highest ever, with some 20–30 new genera being named per year, which might suggest a still largely untapped potential for new finds, or could be inflated by soon-to-be identified synonyms and nomina dubia.

The discovery curve for dinosaurian genera shows a drawn-out somewhat exponential pattern, when all genera are considered (Fig. 1A; total genera). However, when only valid dinosaurian genera are considered (Fig. 1A; now valid/then valid genera), the pattern is substantially damped. The current global totals fall from 1036 named dinosaurian genera to 649 valid dinosaurian genera (suggesting that, at the end of 2004, 63% of named dinosaurian genera are valid, and 37% are synonyms or otherwise erroneous). The numbers of ''then valid'' genera show large drops in 1973, 1990, and 2004 that coincide with the publication of major reviews (White 1973; Weishampel et al. 1990, 2004) that identified many synonyms and erroneous taxa. The ''now valid'' curve (Fig. 1A) is lowest, showing only the genera currently regarded as valid. The substantial revisions in Weishampel et al. (1990), representing the collective view of dinosaurologists worldwide, have dominated the latest opinions on validity, and the then and now curves have differed little since 1990.

Patterns of contemporary taxonomic error determination vary dramatically through time, whether considered as totals (Fig. 1B) or as proportions of named genera (Fig. 1C). Allowing for some early high figures from 1824 to 1860, when cumulative total numbers of genera were low, the taxonomic error rate, assessed from the ''then valid'' data, remained at 20% from 1860 to 1960. Then, with a new phase of revisions of older work, the taxonomic error rate rose steadily to 30% by the early 1970s. Then, following a series of synoptic overviews (Steel 1969, 1970; White 1973; Weishampel et al. 1990, 2004), and intense scrutiny and revision of older work, the rate climbed to a mean of 40% from the late 1970s to the present day. The taxonomic error rates are much higher, currently some 70–80%, if the ratio of invalid taxa to currently accepted valid genera is calculated (Fig. 1C).

The revisers, the paleontologists who have reexamined earlier work and invalidated many names (identifying synonyms or incorrectly established taxa), have operated in three modes that reflect normal working practices: background, monographic, and catalog. These correspond to rising levels of invalidation as the systematist is obliged to make increasingly comprehensive and clear-cut decisions.

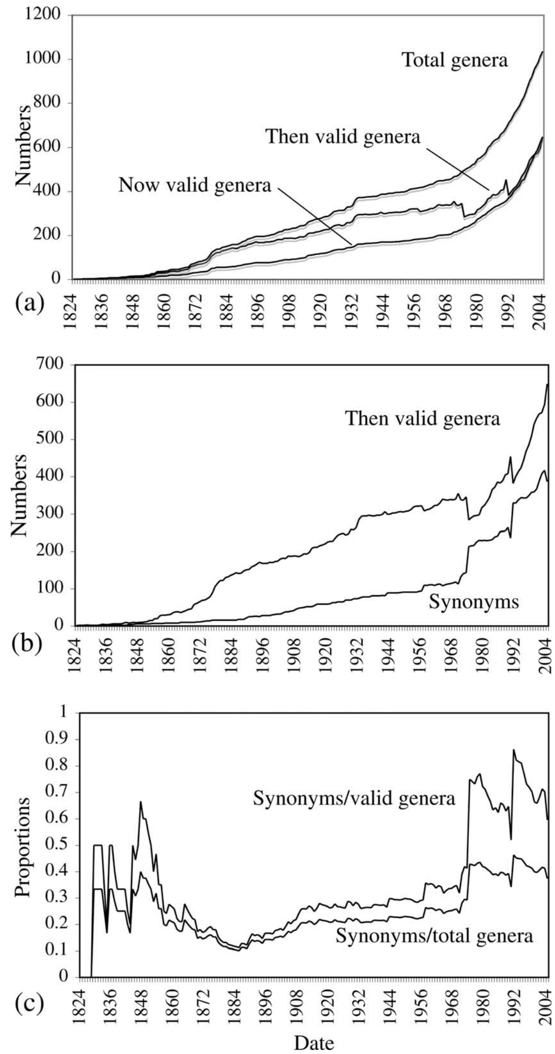


FIGURE 1. Global discovery and synonymy curves for dinosaur genera. A, The total number of new genera, compared to ''then valid'' and ''now valid'' totals, the global diversity of dinosaur genera accepted at the time (then) as valid, or those established that are now regarded as valid. B, The number of synonyms and other incorrect taxa, and number of valid genera (total minus errors) calculated year by year through research time (1824–2004). (c) Two metrics of taxonomic error rates through research time for dinosaurs: the usual measure, which is the proportion of then invalid to total genera, hovering at about 40% over the last 25 years, and the ratio of then invalid to valid genera, which is much more variable, and has sometimes exceeded 70% recently.

1. *Background mode* covers normal publications in which occasional comments are made about earlier work. In describing a new dinosaur or reviewing a fauna, a paleontologist may cast doubt on some former names, or make modest revisions. Difficult decisions about the validity of earlier taxa may be avoided.
2. In *monographic mode*, a systematist undertakes to review a clade, perhaps a family, of dinosaurs, and is obliged then to make decisions that might otherwise be avoided when in background mode. In a monographic overview, the systematist has to consider all previously established names for members of the clade of interest and make decisions about the validity of each.
3. In *catalog mode*, the systematist is committed to reviewing a substantial clade, here the whole of Dinosauria. Earlier catalogers (e.g., Zittel 1890; Lapparent and Lavocat 1955; Huene 1956; Kuhn 1961; Rozhdestvesnky and Tatarinov 1964; Romer 1966; Steel 1969, 1970; White 1973) often did not examine original material and listed everything without comment, relying on the authority of previous workers. More recent catalogers (e.g., authors in Weishampel et al. 1990, 2004) have looked at everything, or

> nearly everything, and have made clear decisions about each taxon. Indeed, in the last two volumes, the standard view was to accept most previously published proposals of synonymy, and to shift large numbers of taxa to the nomen nudum and nomen dubium lists following simple rules of thumb (''if it's based on a single tooth, it's a nomen dubium''). The approach is firm, but acceptable to most workers in the field; had the catalogs not been produced, however, many of these decisions would have been avoided and dubious taxa might still remain on the lists of valid taxa.

It is no surprise then that the three most recent catalogs of all dinosaurian genera (White 1973; Weishampel et al. 1990, 2004) correspond to substantial dips in numbers and proportions of valid taxa (Fig. 1B,C). The question is whether these efforts have corrected the totals to something approaching reality, or whether they have been overly harsh in rejecting potentially valid taxa. Doubtless, a number of the rejected tooth taxa are actually valid, unique, and otherwise unnamed dinosaurs, but we shall not know until more complete fossils come to light. There are cases of revisions occurring in both directions. In Weishampel et al. (1990) *Gorgosaurus* is listed as a synonym of *Albertosaurus*, whereas in Weishampel et al. (2004), *Gorgosaurus* is regarded again as a valid and distinctive genus.

What has been happening in the last 15 years? Total numbers of valid genera have been rising in line with total named genera since 1990 (Fig. 1A), and this is matched by a drop-off in taxonomic error rates (Fig. 1B,C). This upkick in discoveries after 1990 could be real, indicating that more of the recently named dinosaurian genera are valid, and that dinosaur systematists are exercising more care in their practices than was formerly the case (avoiding synonymy, not basing new taxa on inadequate material). In order to test this, the records of validity of names through time were divided into five-year cohorts, and six of these are shown (Fig. 2). Each cohort consists of 4–48 new genera (mean, 20).

The behavior of each generic cohort is somewhat erratic (Fig. 2A). The 1840 cohort shows a rapid drop and remains constant, with a few variations, to the present, but this cohort consisted initially of only four genera. The other cohorts show an immediate, but more modest, drop in accepted taxa, as several new genera were quickly rejected by contemporary authors, followed by a longer-term, but relatively steady, reduction. Each of the other nineteenth century cohorts took some 70–80 years to reach half its original size (rejection of half the original named genera), but the 1950 cohort was cut in half within 30 years, and the 1975 cohort appears to have undergone some rapid, early revisions. The speed of early revision is a little surprising, and this phenomenon was as true in the 1840s as in the 1970s. However,

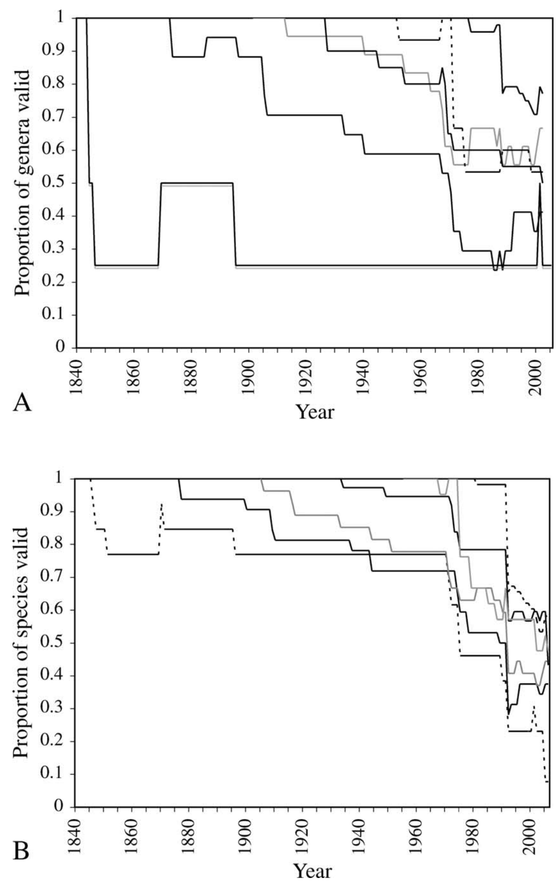


FIGURE 2. Survivorship curves for five-year cohorts of genera (A) and species (B) of dinosaurs. The curves show changes in the proportion of species of a certain historical age that are regarded as valid now. Data are subdivided into cohorts (e.g., the 1840 cohort includes all species named from 1840 to 1844, inclusive), and only six cohorts, scattered through the total range, are shown.

there may be hope that current naming practices have improved in that the proportions of currently valid taxa in each are higher for the more recent cohorts: current levels are as follows: 1840 (0.25), 1870 (0.41), 1900 (0.67), 1925 (0.5), 1950 (0.53), 1975 (0.77). Providing some comparability, one can examine the equivalent levels after 50 years in each case: 1840 (0.5), 1870 (0.71), 1900 (0.89), 1925 (0.6), 1950 (0.6), 1975 (currently 0.77).

As noted earlier, studies of dinosaurian species show little difference from genera, and so are not shown, but in the case of cohorts of named taxa, the behavior is somewhat different (Fig. 2B). Here, the cohort sizes range from 13 to 58 (mean, 31). The species cohorts show more uniform patterns of decline than the genus cohorts, partly because of larger sample sizes, but mainly because it seems to have taken longer for revisers to tackle species than genera. Dinosaur paleontologists have always perhaps focused on genera, and have felt more confident in accepting or rejecting them. For all species cohorts, there is an initial lag period of some 50 years during which few revisions are made and the proportions of valid taxa fall to 0.8, and then the fall continues to a valid proportion of less than 0.1 for the 1840 cohort, and 0.4 or so for the other cohorts. The main characteristic is bunching of the curves at the right-hand side of the plot, and all cohorts show dramatic drops in proportions of valid taxa in 1973, 1990, and 2004, reflecting the dominant role of the revision catalogs. The particularly rapid falloff of the last, 1975, cohort could suggest that current naming practice is no better than it was 150 years earlier, although the long lags in revising nineteenth century names may reflect smaller numbers of active researchers and a slower pace of research. Note, however, that the ultimate totals for the cohorts show apparent improvement in the current acceptance of specific names: 1840 (0.08), 1870 (0.38), 1900 (0.44), 1925 (0.43), 1950 (0.48), 1975 (0.57). The equivalent levels after 50 years in each case are as follows: 1840 (0.85), 1870 (0.81), 1900 (0.78), 1925 (0.78), 1950 (0.57), 1975 (currently 0.57), suggesting remarkable constancy for 50 years of revision and restudy of the first four cohorts, but then rather rapid and continuing removal of invalid taxa thereafter.

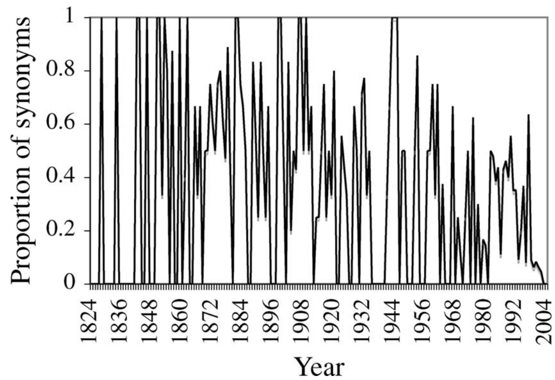


FIGURE 3. Proportion of dinosaur genus names that are now regarded as synonyms, or otherwise erroneous, plotted year by year. Values range from 0 (meaning that all genera named in a year are still regarded as valid, or that nothing was named that year) to 1 (meaning that all names given that year have subsequently been invalidated).

These patterns of decay in cohorts of valid generic and specific names differ from the patterns for fossil mammal species in North America. Alroy's (2002: Fig. 5) plot showed continuous rapid declines in accepted taxa for cohorts from 1880 to 1980. There were some correlated effects, such as a slow-down during World War II, but there were no major shifts imposed by single monographic revisions, as here. Both studies share the finding that naming practice might be no better now than it was 150 years ago. It is likely then that the explosive rise in new dinosaur names reflects the well-known lag time between the naming of a taxon and its subsequent revision and possible invalidation (Solow et al. 1995; Alroy 2002).

A simpler question might be, How likely are current dinosaur names to survive later scrutiny? Is a name given in 1870 more or less likely to have been valid than one given in 1970? Annual synonymy ratios (number of ''now'' synonyms/totals named) vary, of course, from 0 to 1 (Fig. 3), depending on whether all names given in a year have survived subsequent scrutiny, or whether all have been synonymized. During the nineteenth century, there were 14 years in which all dinosaurian genera named have subsequently proved to be erroneous (1828, 1834, 1842, 1843, 1846, 1850, 1851, 1853, 1859, 1862, 1881, 1882, 1898, 1899),

TABLE 1. Quality of materials used to name new dinosaur species and genera. Type specimens used to name the 188 species and 122 genera of new dinosaurs within the six five-year cohorts (1840–44, 1870–74, 1900–04, 1925–29, 1950–54, 1975–79), coded according to a numerical scheme: 1 (isolated bits and pieces); 2 (one complete or near-complete skull; 3 (several skulls); 4 (one complete or near-complete skeleton; 5 (several skeletons). The totals of each category of specimen is given, as well as totals of 2–5, and the ratio of 2–5 (more complete materials) to 1 (incomplete materials).

	Quality categories						Ratio
Cohort	1	2	3	4	5	2–5	(2–5):1
1840–44	13	0	0	0	0	0	0
1870–74	28	0	0	2	2	4	0.14
1900–04	17	2	2	2	4	10	0.59
1925–29	26	4	1	4	2	11	0.42
1950–54	11	3	1	3	3	10	0.91
1975–79	24	11	2	12	9	34	1.42

whereas only six such years after 1900, namely 1906, 1907, 1909, 1943, 1944, and 1945. These were all years in which only one to three new genera were named, except 1881, which was particularly disappointing, in that eight new genera were named, all of which are now regarded as erroneous. The broad decline in proportions of synonyms since the 1940s might reflect better taxonomic practices since the war, or it could reflect a ''pull of the recent'' effect, the relative under-correction of more recently named taxa (Alroy 2002).

Fossil quality is clearly crucial, and there is a general assumption that earlier workers were perhaps too cavalier in erecting new names for isolated teeth and other scraps. Current data (Table 1) bear this out. The earliest students of dinosaurs in the 1840s relied entirely on isolated teeth and bone scraps for their type specimens. Through the remainder of the nineteenth century, and until the 1950s, such isolated and fragmentary material still dominated the sample of type specimens of newly named dinosaurian species, most of which have been designated subsequently as nomina dubia (Weishampel et al. 1990, 2004). Only in the 1975–79 cohort do complete skulls and skeletons come to dominate the global sample. If this sampling study is borne out by a comprehensive study to follow (Benton 2008), it is clear, then, that there has been a marked improvement in the quality of material coming to hand and being used as a basis for new dinosaurian taxa; this should presumably mean that more recently established taxa are less likely to be found to be invalid than those named in the early decades of the subject.

How to Find a New Dinosaur

Is the discovery of new dinosaurian taxa limited by the number of paleontologists or the exploration of new areas? There is a close matching between cumulative total numbers of genera named and cumulative numbers of dinosaur workers (Fig. 4A). The recent dramatic upturn in the numbers of new dinosaurian genera being named, from 1980 onward, is matched, and probably driven, by a similar exponential rise in the number of paleontologists publishing papers about dinosaurs. The curve of valid dinosaurian genera, however, matches more closely the discovery curves of numbers of new countries and new sedimentary basins exploited (Fig. 4B). When the cumulative number of valid dinosaurian genera is plotted against cumulative totals of countries, basins, and workers, the best fit is against number of countries, and then number of basins (Fig. 4C). The number of authors has rocketed recently, and yet that has not been accompanied by a matching proportional increase in numbers of valid new dinosaurs discovered.

New countries have been added as sources of dinosaurs in recent years (e.g., Algeria, Niger, Zimbabwe, Mexico, South Korea, Thailand, Spain, Croatia, Poland; all since 1960), and one new continent (Antarctica), and there is clearly a limit to this pattern of addition as fewer and fewer countries (and no continents) remain that have not yielded at least one dinosaurian taxon. These additions might reflect a lack of effort by paleontologists in those countries in the past, and the first discoveries could trigger a deluge of new finds. However, this has not been the case for any of the countries named, and the apparent delay in reporting first dinosaurs from those countries might rather reflect the absence of suitable rocks and suitable fossils. Further, in many cases, dinosaur-bearing rock formations cross national borders, and so little new might be

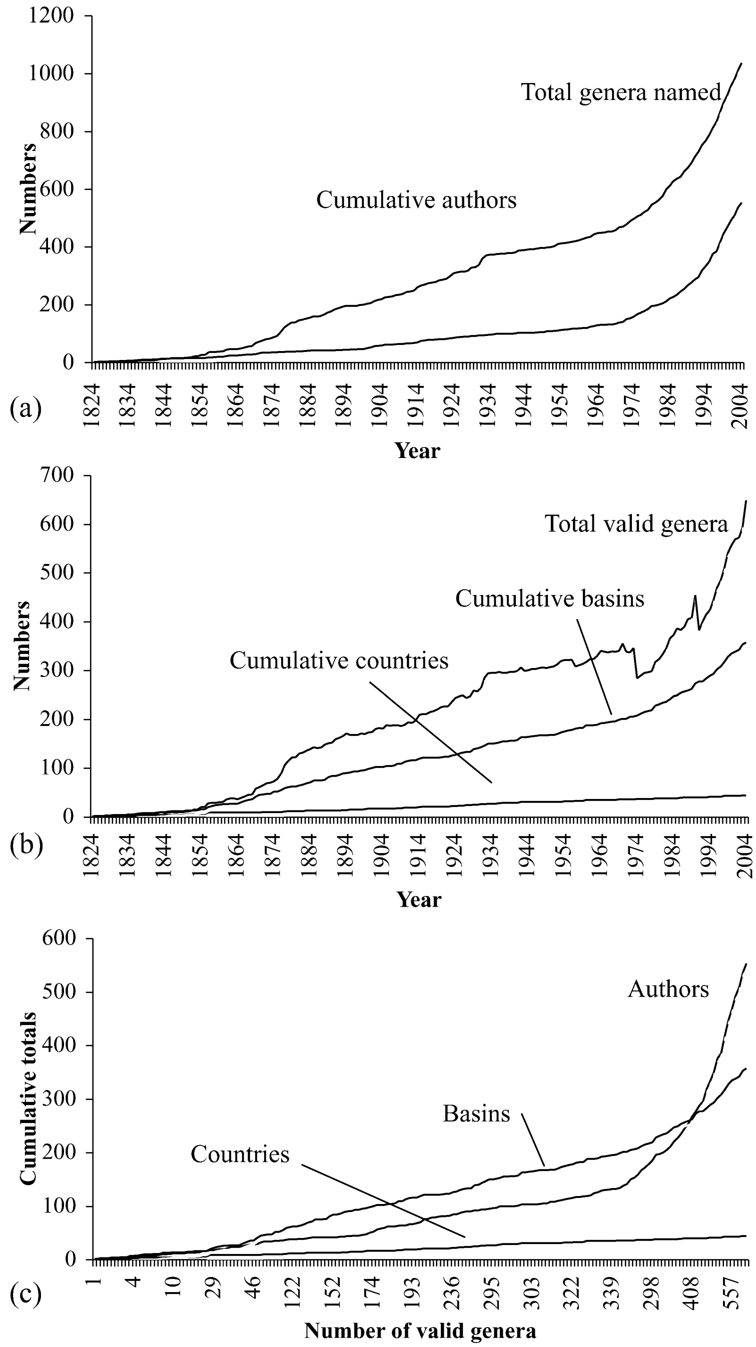
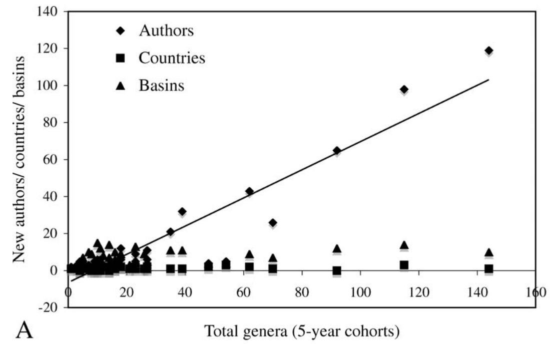


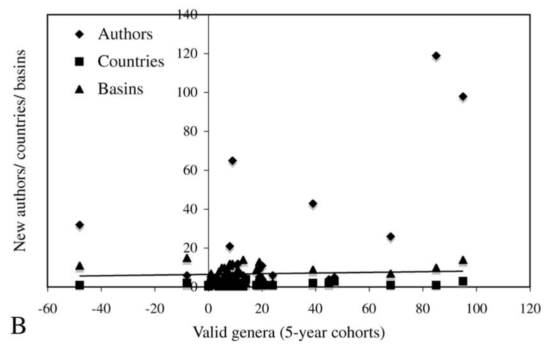
FIGURE 4. How to find a new dinosaur. A, Total number of dinosaur genera is proportional to the number of authors who are actively out there hunting. B, Total number of valid new dinosaur genera, however, depends on the number of new sedimentary basins or new countries entered. C, Cumulative total number of valid dinosaur genera (y-axis) is best explained by the cumulative total number of new countries explored ($y = 0.250x - 1.589$; $r^2 = 0.99$), and then by the cumulative total of new sedimentary basins entered ($y = 1.718x - 32.769$; $r^2 = 0.96$). The best-fitting curve for authors versus total genera is an exponential curve, $y = 6.519e^{0.022x}$ ($r^2 = 0.92$); the best-fitting straight line for authors vs. total genera is $y = 1.743x - 57.169$ ($r^2 = 0.68$).

TABLE 2. Naming new dinosaurian genera, and the influence of numbers of new workers, basins, and countries explored. The comparisons are made between figures for new genera (total and valid) versus numbers of new authors, new countries, and new basins introduced each year (annual), and in five-year cohorts. The Spearman rank (rho) statistic is indicated for comparisons of each series of values, and significance of correlation is indicated as: $p < 0.05$*, $p < 0.01$**, $p < 0.001$***.

	Authors	Countries	Basins
Annual figures			
Total new genera	0.687***	0.149*	0.686***
Valid new genera	0.496***	0.090	0.557***
Authors		0.023*	0.568***
Countries			0.388***
Five-year cohorts			
Total new genera	0.674***	0.301	0.405*
Valid new genera	0.370*	0.265	0.079
Authors		0.261	0.533**
Countries			0.096



A



B

FIGURE 5. The relationships between numbers of authors, countries, and basins and total number of genera (A) and number of valid genera (B). First differences (value for a study year minus the value for the previous study year) are taken for all cumulative figures, thereby giving annual measures. Regression lines show best fit for total annual number of genera named with annual number of new authors (A) and for annual number of valid genera with annual number of new basins (B). Data for goodness of fit given in Table 2.

expected from a small country that shares sedimentary basins with its neighbors.

These cumulative time series plots (Fig. 4) suggest some general correlations, but it is difficult to compare them. Therefore, the data were detrended to show year-by-year changes (that is, first differences) in the numbers of authors, countries, and sedimentary basins, and the relationship of each variable to numbers of genera, and numbers of valid genera named each year (Table 2, Fig. 5). The data were also grouped in five-year cohorts. For the year-by-year data, the total number of genera correlates equally with the number of new authors and number of new basins, whereas the number of valid genera correlates most strongly with the number of new basins, and then with number of new authors. In both cases, there is no correlation between number of new countries explored and number of new genera. For the five-year cohorts, the correlations are fewer and lower: total numbers of genera correlate most strongly with the number of new authors, and number of valid genera correlates somewhat less significantly with number of new authors. The strong correlation between number of valid genera and number of basins seen in the annual data is not replicated in the five-year-binned data. In both the annual and five-year-binned data, the number of authors correlates with the number of basins, and in the annual data also with the number of countries (Table 2).

The data suggest clearly (Figs. 4, 5) that a global strategist who wants to find more new dinosaurs has two choices: if you simply want to name new genera, then put more paleontologists on the job, but if you want to name *valid* new genera, then it is important to engage plenty of paleontologists, but also to go to a sedimentary basin that has never before yielded dinosaur specimens.

Genuine new dinosaurs are indeed found in well-trodden areas. For example, the Wealden rocks (Early Cretaceous) of southeast England have been a well-known source of dinosaurs since the 1820s, and yet remarkable new taxa are still being found (e.g., *Baryonyx* in 1983, *Neovenator* in 1996, *Eotyrannus* in 2001). More often, however, new basins/regions are the

TABLE 3. The authors who named most dinosaur species. Three over-active paleontologists, Friedrich von Huene in the twentieth century, and Othniel Marsh and Edward Cope in the nineteenth lead the table for most dinosaur species named, each with more than 60 names to their credit. The list then includes all other authors who named, or co-named, ten or more dinosaur species; some are still active and might climb the table in future years. The total number of species named includes only non-avian dinosaurs (some authors, such as Marsh, also named many Mesozoic birds), and the total includes new generic names for previously established species. The ''numbers still valid'' column is based on current assessments (primarily Weishampel et al. 2004), and the ''success rate'' is the ratio of names still regarded as valid to the total numbers named. The number of species named per year is based on the number of active ''naming'' years for each paleontologist, and persons who have been active predominantly in the last 50 years, and most of whom are still alive, are marked with an asterisk.

Author	No. dinosaur species named	Numbers still valid (2005)	Success rate	Years over which new names published	Species named/ year (*last 50 years)
1 Othniel Marsh	80	23	0.29	1870–1899	2.67
2 Friedrich von Huene	71	18	0.25	1902–1956	1.29
3 Edward Cope	64	9	0.14	1866–1892	2.37
4 Dong Zhiming	42	27	0.64	1973–2004	1.31*
5 Richard Owen	36	7	0.19	1841–1897	0.63
6 Harry Seeley	35	4	0.11	1869–1901	1.06
7 Young C.-C.	28	11	0.39	1931–1972	0.67
8 Charles Gilmore	25	13	0.52	1909–1946	0.66
9 José Bonaparte	25	24	0.96	1969–2000	0.78*
10 Xu Xing	24	24	1.00	1999–2006	3.00*
11 Richard Lydekker	21	8	0.38	1877–1895	0.91
12 Barnum Brown	21	10	0.48	1908–1943	0.58
13 Lawrence Lambe	20	11	0.55	1902–1929	0.71
14 Peter Galton	20	15	0.75	1971–2001	0.62*
15 Charles M. Sternberg	19	8	0.42	1926–1953	0.68
16 William Parks	17	5	0.29	1922–1935	1.21
17 Franz von Nopcsa	15	4	0.27	1900–1929	0.50
18 Dale Russell	15	15	1.00	1970–2004	0.43*
19 Joseph Leidy	14	3	0.21	1854–1872	0.74
20 Paul Sereno	14	13	0.93	1988–2004	0.82*
21 Zhao Xijin	13	12	0.92	1990–2004	0.56*
22 Henry F. Osborn	12	8	0.67	1903–1924	0.55
23 Albert de Lapparent	12	4	0.25	1955–1960	2.00
24 Rinchen Barsbold	12	11	0.92	1974–2001	0.43*
25 Alexander Nesov	12	1	0.08	1983–1995	0.92*
26 John Hulke	10	4	0.40	1871–1888	0.56
27 Werner Janensch	10	6	0.60	1914–1961	0.21
28 A. N. Ryabinin	10	2	0.20	1914–1945	0.31
29 Sidney Haughton	10	3	0.30	1915–1928	0.71
30 Evgeny Maleev	10	5	0.50	1952–1956	2.00*

source of repeated new finds, recently most notably the Liaoning basin in China, source of over 50 new genera of dinosaurs and birds since the first genus was named in 1992.

The Dinosaur Namers

The dinosaur taxon list has not been overly subject to the quirks of a limited number of systematists. Gaston and Mound (1993) noted that just four workers had authored almost half the 6112 species of Thysanoptera (thrips) named from 1901 to 1993, and one of these four authors was responsible for 1065 names. At times in the past there were particularly prolific namers of dinosaurs (e.g., Othniel C. Marsh, Friedrich von Huene, and Edward D. Cope, responsible respectively for 80, 71, and 64 species names). By 1900, Marsh and Cope together were responsible for 144 of the 359 (40%) dinosaur species names then in existence. Now, with a further century of study, the proportion of the total represented by their names has fallen to 10%.

Thirty prolific namers of dinosaurian species have been identified (Table 3), each responsible for more than ten species names. Marsh, von Huene, and Cope stand out as having named very many more new species of dinosaurs (64–80 each) than the remaining workers (10–42 each). These leading thirty active namers are responsible for 717 of the 1401 named species, so just over half (51.2%). Globally, 308 of their 717 new species (43%) are still regarded as valid.

Dinosaur namers have varied hugely in productivity, that is, the number of species named per year of activity (Table 3). The mean rate of naming species for all thirty prolific authors amounts to 1.00 per year, but the majority of authors of new dinosaur names appear to have named a new species roughly once every two years (rate = 0.2–0.9). Highly productive authors of new dinosaur names include the ''top three''—Marsh, Cope, and Huene—but the highest rate (three new species per year) was achieved by Xu Xing in the course of very few years. Further high rates (>1.00 per year) were achieved by Dong, Seeley, Parks, de Lapparent, and Maleev.

It might be worthwhile to determine whether prolific namers of dinosaurs have been uniformly successful in convincing the paleontological community that their new species truly are new. Using the current view of validity, it is simple to calculate a ''success rate'' for each dinosaur namer, the proportion of currently valid species to the total number named. Values range from 0.08 (Alexander Nesov) to 1.00 (Yu Xing and Dale Russell), with every gradation in between (Table 3). The success rate is not related to the total numbers of new species erected (although the top three—Marsh, von Huene and Cope—all score less than 0.5), but it is related broadly to the time when these paleontologists worked. When plotted against the midpoint of their active naming years, it is evident (Fig. 6) that prolific dinosaur namers of the nineteenth century have success rates in the range 0.1 to 0.4, those active from 1900 to 1950 achieve success rates of 0.2 to 0.7, and those operating after 1950 show success rates of 0.1–1.0. The mean of the success rates for the 30 listed prolific dinosaur namers is 0.43, considerably lower than the mean success rate averaged over all dinosaur species (0.52; the total minus the global taxonomic error rate of 48.2%). Perhaps the prolific authors were more careless/enthusiastic than the average, perhaps their material was poorer, or perhaps subsequent revisers have treated their species more harshly.

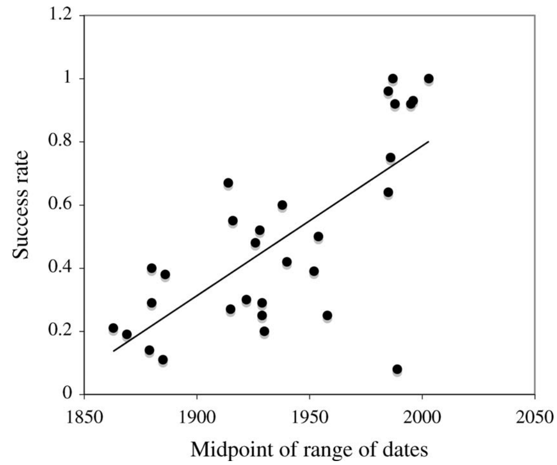


FIGURE 6. The success rates for the top 30 namers of new dinosaur species. The success rate is the proportion of currently valid dinosaur species to the total named during each worker's lifetime. Success rates are plotted against the midpoint of the active career span of each worker (the midpoint between the dates of publication of their first and last papers containing new dinosaur species names). There is a weak trend ($y = 0.005x - 8.71$; $r^2 = 0.5$) that may reflect some improvement in the quality of the new genera established by more recent workers, rather than being entirely a ''pull of the recent'' effect, where there has been insufficient time to revise and invalidate more recently named taxa; this is confirmed by the improvement in quality of specimens selected as types through research time (Table 1).

There is no evidence for a reduction in the enthusiasm of modern dinosaur paleontologists—three of the top ten, and eight of the top 30, prolific namers are still alive. As expected, their success rates (mean, 0.77) are better than those of the authors active before 1950 (mean, 0.35). The rising trend in success rate (Fig. 6) could be interpreted in several ways. A key aspect is surely that some earlier workers, notably Marsh, Cope, Huene, and Seeley, named many taxa on the basis of single or isolated fossils, whereas this practice has been rarer, but not completely excluded, in the past 50 years (Table 1). It would be gratifying also to suggest that a large part of the rise might also be accounted for by the greater care shown by modern paleontologists in comparing their putative new taxa with existing materials and publications. A part of the trend, though, must relate to the lack of revision of more recent work. The dinosaurs named by Marsh and

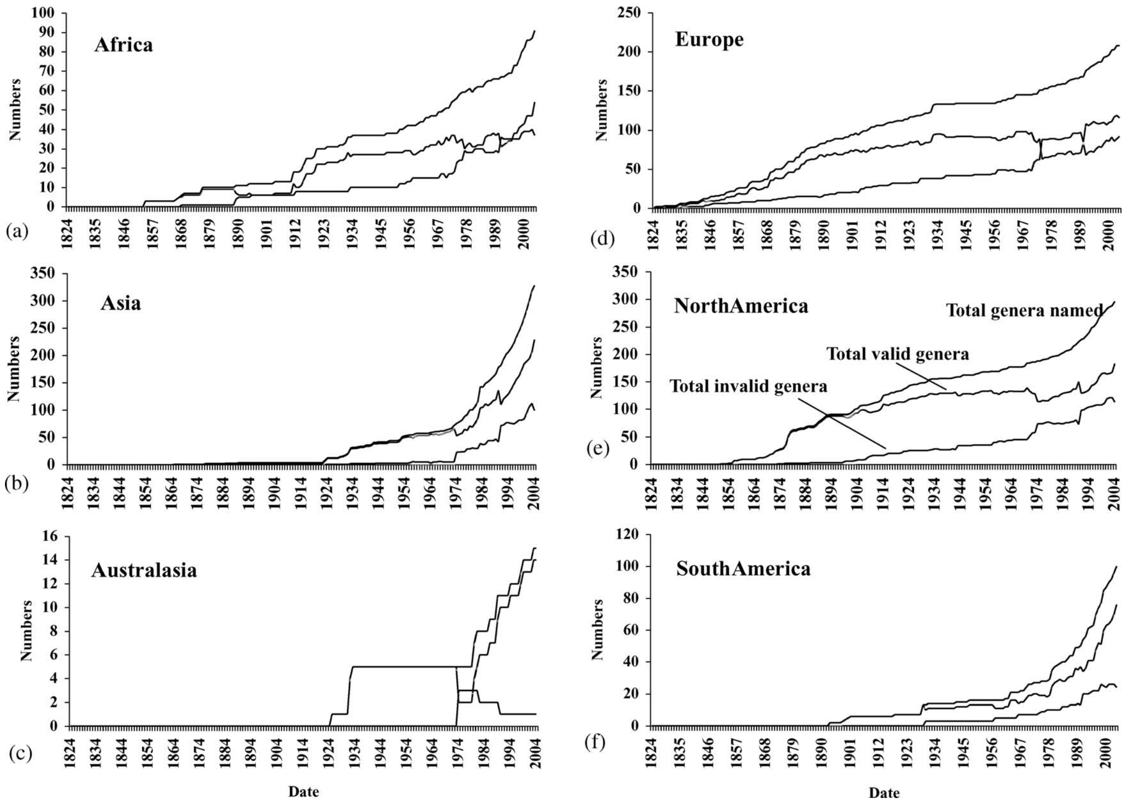


FIGURE 7. Regional trends in the discovery of dinosaur genera. A–F, Continent-by-continent plots of total number of genera named, total number of synonyms recognized, and net number of valid genera year-by-year through research time. Note that the start date ranges from 1824 (Europe) to 1924 (Australasia), and that Europe and North America have been more intensively studied (''mature'' discovery curves) than the other continents (''immature'' discovery curves).

Cope have been revised each generation since the late nineteenth century, whereas many recently named species await study by a first reviser.

Regional Trends

It is well known that dinosaurs have been studied to different extents on different continents. The first dinosaur from Europe (and the world) was named in 1824, but it took time before the first dinosaurs were named from other continents: Africa (1854), North America (1856), Asia (1865), South America (1893), Australasia (1924), Antarctica (1991). (Note that these dates postdate the first discoveries of dinosaur bones in each continent—first finds were often not named until later. Further, the previous ''first'' dinosaur from Australia, named in 1891, was erroneous [Vickers-Rich et al. 1999]. Since these first discoveries, the rate of discovery and naming has varied hugely from continent to continent, with over 300 genera named from North America and over 200 from Europe, whereas the other continents have produced rather lower numbers. The shapes of the discovery curves (Fig. 7) vary hugely, with those from Europe and North America having reached some kind of plateau around 1900, but then followed by an uplift in the past 50 years as increasing numbers of paleontologists entered the field. These plateaus have been noted earlier (Dodson and Dawson 1991; Benton 1998), before the rush of new discoveries in the past 15–20 years. The other continents follow a more exponential curve from their inception to the present time.

The shape of the discovery curve for dinosaurian genera (Fig. 1) reflects the balance of discovery and invalidation. In the early decades of collecting, generally rather incom-

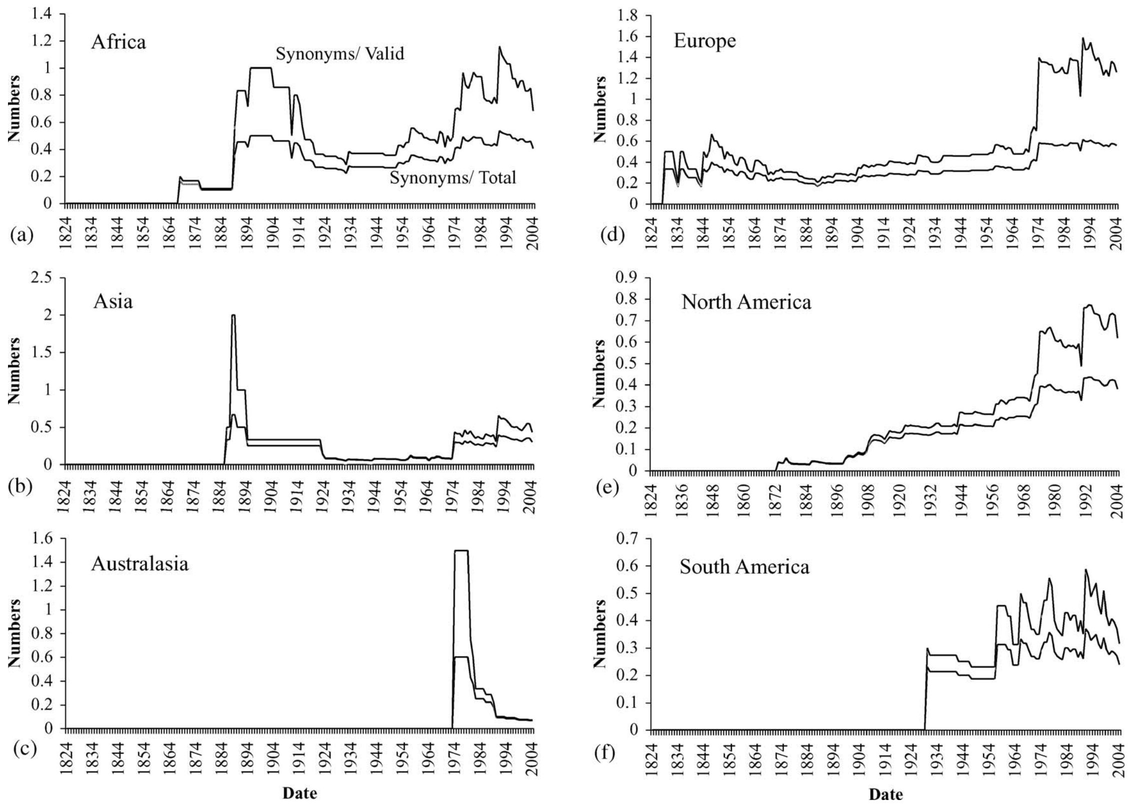


FIGURE 8. Regional trends in invalidation/synonymy of dinosaurian genera. A–F, Continent-by-continent plots of two taxonomic error rates: the usual invalid over total taxa measure, and the higher invalid over valid taxa measure. Note that current taxonomic error rates are about 40% for most continents, except Europe, where the value is 50%.

plete materials were reported. The first substantially complete dinosaur skeletons were not reported until 1861, *Compsognathus* from the Late Jurassic of Germany, and *Scelidosaurus* from the Early Jurassic of England. Up to that point, discoveries had come mainly from Europe, and consisted largely of isolated skulls, teeth, and limb bones. A ''golden age'' of collecting followed, from the 1880s to the 1920s, when paleontologists recovered many complete skeletons of dinosaurs from North America, Europe, Africa, and other continents. Once those obvious, large, and complete materials have been collected from particular geographic regions, dinosaurian researchers have to resort to searching out smaller, less complete, and rarer taxa. This three-stage cycle of early scraps, golden age, and the search for rare taxa has apparently been played out in Europe and North America, whereas we are experiencing the ''golden age'' phase in China and Argentina, and may yet do so in Antarctica, Australia, and some other regions.

Patterns of taxonomic error (Fig. 8) show some similarities, but also some striking differences between continents. In all cases, there appears to be an early burst of synonymy, but these peaks reflect low total numbers and mean little. The pattern for Australia (Fig. 8C) is hard to interpret, but total numbers of dinosaurs remain low to this day (Fig. 7C). For all other continents, initially low taxonomic error rates rise to a higher plateau from 1990 onward, and then drop to the present day, reflecting the recent rapid rise in number of new dinosaur genera being named in the past ten years, and perhaps the lag in invalidation. The taxonomic error rate over the past 20 years matches the global figure of 40% for all continents except Europe. The rate is just 40% for Africa and North America, and slightly lower for Asia and South America. But, for Europe, the rate is about 50%. This means that half the 200 or so dinosaur genera that have been named from Europe have subsequently been invalidated; it is likely that nearly everything that is to be found has been found, and new taxa tend to be spurious or synonyms. Perhaps the revisers of European dinosaur taxon lists have been harsher than workers elsewhere, but that seems less likely. Further, many European taxa were based on incomplete material, especially those named in the nineteenth century (Table 1), which could make the task of the systematist harder than that of the worker on Canadian dinosaurs, say, which are predominantly founded on essentially complete specimens.

Benton (1998) suggested that discovery curves might be plotted continent by continent for dinosaurs, with a view to determining whether discoveries had reached saturation point. His plots, taken up to 1990, showed a leveling off for Europe and North America: he suggested that these asymptotes could be taken to indicate that virtually all valid dinosaurs had been found in Europe and North America, the two taxonomically ''mature'' continents, where dinosaurs had been found early and where intense efforts had been devoted to finding and naming everything. These estimates could then be extrapolated to the taxonomically ''immature'' continents (Africa, Asia, Australasia, South America), perhaps scaled by gross area, or area of suitable rocks, in order to give a global total. Regrettably, it does not seem that the record is well enough sampled yet, even in those well-trodden northern continents. The raw data (Fig. 1A, total genera) show an exponential rise in discovery, and the ''corrected'' curve (Fig. 1A, valid genera) is not sufficiently damped to indicate an asymptote. This dashes any hope at present of using the shape of the discovery curve, either for the whole world or for some subset of it, to estimate the total number of dinosaurs in the rocks. Note that Bebber et al. (2007) provide mathematical reasons why a sample should be 90% complete before its total size is extrapolated through the discovery curve method. But note also that alternative methods have been used to estimate total untapped dinosaurian diversity by Dodson (1990), Russell (1995), and Wang and Dodson (2006).

Conclusions

In answer to the questions posed earlier: (1) the overall synonymy rate for dinosaurs is similar to that for extant groups, and this does not seem to be much affected by inadequacies of the fossil material; (2) the discovery rate of new dinosaurian species depends primarily on the numbers of systematists, but the discovery rate of valid new dinosaurian species is dependent both on the number of paleontologists, and on access to new material, especially in sedimentary basins that have not previously been explored; (3) 30 prolific namers have been responsible for nearly half of all named dinosaurian species, and yet their success rate of valid to total named species (0.43) is lower than the mean for all dinosaur species (0.52); (4) patterns of naming and revision of species differ from continent to continent, with the highest rejection rate of species in Europe; (5) synonymy rates may reflect the intensity or ''maturity'' of study, with European dinosaurs having been studied for longest.

Some might object that a detailed review of the naming history of Dinosauria is not helpful for understanding the diversity of modern groups. However, as Alroy (2002) argued in his study of fossil mammal taxa from North America, the differences are not so great. Clearly, fossil specimens preserve fewer characters than extant taxa, but type materials of fossil species were sampled from just as many localities, the diagnoses and anatomical descriptions are just as detailed, and revision has been just as thorough as for extant taxa. The reliability of species lists for extant groups varies hugely, although the potential for more detailed study is there; in many cases, the work has not been done because of a shortage of systematists, and the taxonomy of some extant groups is hugely reliant on the work of a small number of people. In the end, empirical assessments have shown similar synonymy rates in the 30–60% range for both fossil and extant groups of plants and animals.

The magnitude of those taxonomic error rates is striking. When, 15 years ago, May

(1990), Wilson (1992), and others used a synonymy rate of 20% as their rule of thumb, species lists could be so modified. Now, if the proportion of erroneous taxa is nearer 50% than 20%, there is cause for serious concern. Until a thorough, synoptic review of the fundamental taxonomy of a clade has been undertaken, those species lists should be treated with caution. A striking finding, however, has been that, despite such high error rates in many databases of fossil taxa, thorough taxonomic revision does not produce substantially different estimates of ancient diversity, or other broad macroevolutionary and macroecological conclusions (Maxwell and Benton 1990; Sepkoski 1993; Adrain and Westrop 2000; Wagner et al. 2007).

Acknowledgments

Many thanks to P. Donoghue, M. Ruta, G. Lloyd, and J. Tarver for valuable discussions, and D. Weishampel, P. Dodson, W. Kiessling, and two further anonymous referees for extremely helpful review comments. Funded by Natural Environment Research Council Grant NEC518973/1.

Literature Cited

Adrain, J. M., and S. R. Westrop. 2000. An empirical assessment of taxic paleobiology. Science 289:110–112.

Alroy, J. 2002. How many named species are valid? Proceedings of the National Academy of Sciences USA 99:3706–3711.

Altaba, C. R. 1996. Counting species names. Nature 380:488–489.

Bebber, D. P., F. H. C. Marriott, K. J. Gaston, S. A. Harris, and R. W. Scotland. 2007. Predicting unknown species numbers using discovery curves. Proceedings of the Royal Society of London B 274:1651–1658.

Benton, M. J. 1998. The quality of the fossil record of vertebrates. Pp. 269–303 *in* S. K. Donovan and C. R. C. Paul, eds. The adequacy of the fossil record. Wiley, New York.

———. 2008. Fossil quality and naming dinosaurs. Biology Letters. doi:10.1098/rsbl.2008.0402.

Benton, M. J., M. Wills, and R. Hitchin. 2000. Quality of the fossil record through time. Nature 403:534–538.

Cain, S. A. 1938. The species-area curve. American Midland Naturalist 19:573–581.

Colwell, R. K., and J. A. Coddington. 1995. Estimating terrestrial biodiversity through estimation. Pp. 108–118 *in* D. L. Hawkesworth, ed. Biodiversity—measurement and estimation. Chapman and Hall, London.

Dodson, P. 1990. Counting dinosaurs: how many kinds were there? Proceedings of the National Academy of Sciences USA 87:7608–7612.

Dodson, P., and S. S. Dawson. 1991. Making the fossil record of dinosaurs. Modern Geology 16:3–15.

Gaidet, N., H. Fritz, S. Messad, S. Mutake, and S. Le Bel. 2005. Measuring species diversity while counting large mammals: comparison of methods using species accumulation curves. African Journal of Ecology 43:56–63.

Gaston, K. J., and L. A. Mound. 1993. Taxonomy, hypothesis-testing and the biodiversity crisis. Proceedings of the Royal Society of London B 251:139–142.

Huene, F. von. 1956. Paläontologie und Phylogenie der niederen Tetrapoden. Gustav Fischer, Jena.

Kuhn, O. 1961. Die Familien der rezenten und fossilen Amphibien und Reptilien. Meisenbach, Bamberg.

Lapparent, A. F. de., and R. Lavocat. 1955. Dinosauriens. Pp. 785–962 *in* J. Piveteau, ed. Traité de Paléontologie, Vol. 5. Masson, Paris.

Magurran, A. E., and R. M. May, eds. 1999. Evolution of biological diversity. Oxford University Press, Oxford.

Mao, C. X., R. K. Colwell, and J. Chang. 2005. Estimating the species accumulation curve using mixtures. Biometrics 61: 433–441.

Maxwell, W. D., and M. J. Benton. 1990. Historical tests of the absolute completeness of the fossil record of tetrapods. Paleobiology 16:322–335.

May, R. M. 1990. How many species? Philosophical Transactions of the Royal Society of London B 330:292–304.

———. 2004. Tomorrow's taxonomy: collecting new species in the field will remain the rate-limiting step. Philosophical Transactions of the Royal Society of London B 359:733–734.

May, R. M., and S. Nee. 1995. Taxonomy—the species alias problem. Nature 378:447–448.

Olszewski, T. D. 2004. A unified mathematical framework for the measurement of richness and evenness within and among multiple communities. Oikos 104:377–387.

Ostrom, J. H., and P. Wellnhofer. 1986. The Munich specimen of *Triceratops* with a revision of the genus. Zitteliana 14:111–158.

Peters, S. E., and M. Foote. 2002. Determinants of extinction in the fossil record. Nature 416:420–424.

Preston, F. W. 1948. The commonness, and rarity, of species. Ecology 29:254–283.

Purvis, A., and A. Hector. 2000. Getting the measure of biodiversity. Nature 405:212–219.

Romer, A. S. 1966, Vertebrate paleontology, 3d ed. University of Chicago Press, Chicago.

Rozhdestvensky, A. K., and L. P. Tatarinov. 1964. Amphibia, Reptilia, Aves. *In* J. A. Orlov, ed. Osnovy Paleontologi, Vol. 12. Izdatelstvo Nauka, Moscow.

Russell, D. A. 1995. China and the lost worlds of the dinosaurian era. Historical Biology 10:3–12.

Sepkoski, J. J., Jr. 1993. Ten years in the library: new data confirm paleontological patterns. Paleobiology 19:43–51.

Solow, A. R., L. A. Mound, and K. J. Gaston. 1995. Estimating the rate of synonymy. Systematic Biology 44:93–96.

Steel, R. 1969. Ornithischia. Handbuch der Paläoherpetologie 15:1–83. Springer, Stuttgart.

———. 1970. Saurischia. Handbuch der Paläoherpetologie 14:1–87. Springer, Stuttgart.

Tarver, J. E., S. J. Braddy, and M. J. Benton. 2007. The effects of sampling bias on Palaeozoic faunas and the implications for macroevolutionary studies. Palaeontology 50:177–184.

Vickers-Rich, P., T. H. Rich, G. C. McNamara, and A. C. Milner. 1999. *Agrosaurus*: Australia's oldest dinosaur? Records of the Western Australian Museum Supplement 57:191–200.

Wagner, P. J., M. Aberhan, A. Hendy, and W. Kiessling. 2007. The effects of taxonomic standardization on sampling-standardized estimates of historical diversity. Proceedings of the Royal Society of London B 274:439–444.

Wang, S. C., and P. Dodson. 2006. Estimating the diversity of dinosaurs. Proceedings of the National Academy of Sciences USA 103:13601–13605.

Web of Knowledge©. 1990–1992. http://www.isiwebofknowledge.com

Weishampel, D. B., P. Dodson, and H. Osmólska, eds. 1990. Dinosauria. University of California Press, Berkeley.

———, 2004. Dinosauria, 2d ed. University of California Press, Berkeley.
White, T. E. 1973. Catalogue of the genera of dinosaurs. Annals of the Carnegie Museum 44:117–155.
Wickström, L. M., and P. C. J. Donoghue. 2005. Cladograms, phylogenies and the veracity of the conodont fossil record. Special Papers in Palaeontology 73:185–218.
Wilson, E. O. 1992. The diversity of life. Penguin, London.
Wortley, A. H., and R. W. Scotland. 2004. Synonymy, sampling and seed plant numbers. Taxon 53:478–480.
Zittel, K. A. 1890. Handbuch der Paläontologie. I. Abtheilung Paläozoologie. III Band. Vertebrata (Pisces, Amphibia, Reptilia, Aves). Oldenbourg, Munich.