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Palaeontology

Fossil quality and naming dinosaurs

Michael J. Benton*

Department of Earth Sciences, University of Bristol, Bristol BS8 1RJ, UK *mike.benton@bristol.ac.uk

The intense interest in dinosaurs through the past 30 years might have led to an increase in poor practice in naming new species. A review of the data shows that the reverse is the case. For 130 years, from the 1820s to the 1950s, most new species of dinosaurs were based on scrappy and incomplete material. After 1960, the majority of new species have been based on complete skulls or skeletons, and sometimes on materials from several individuals. This switch in the quality of type specimens corresponds to the recent explosive renaissance of interest in dinosaurs, during which the number of new species named per year has risen, from three or four in the 1950s, to thirty or more today. The pattern of specimen quality varies by continent, with the highest proportion of new species based on good material in North America, then Asia, then South America, then Africa and finally Europe. This ranking reflects a complex pattern of perhaps overstudy in Europe, immensely rich reserves of new dinosaur materials in North America and Asia, and a relative paucity in South America and Africa.

Keywords: synonymy; systematics; dinosaurs; nomenclature; type specimens; biodiversity

1. INTRODUCTION

In estimating biodiversity, it is important to be sure that all species counted are valid (Wilson 1992; Purvis & Hector 2000). Validity of species names depends on the quality of work by systematists, and this is especially true of fossil taxa. Dinosaurs have been subject to intense study over the past 200 years, and never more so than at present. There is a risk, however, that systematists might be tempted to name new species on the basis of incomplete and undiagnostic materials, particularly if the group is of intense public interest, and there is a career premium in naming new species.

Dinosaurs have been subject to varying levels of study (figure 1a). The rate of naming was low from 1820 to 1870, and then picked up during the so-called 'bone wars' in North America, from 1870 to 1890, a time of intense activity during which up to 15 species were named each year by arch rivals Edwin Cope and Othniel Marsh. After their deaths, species discovery waned, and there were particularly low levels of work through the two world wars. The peak in the 1920s corresponds to particularly active work on many continents by the German palaeontologist

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Friedrich von Huene. The time since 1990 has seen a second, even more extraordinary, phase of discovery and naming of new species, some 30 per year.

The aims of this study are to explore the recent burst of dinosaur work and to resolve whether the new phase is illusory or not. It could be that palaeontologists are producing poor-quality work, perhaps fuelled in part by excessive interest from museums and the media worldwide. There is a risk that undue pressure from funding agencies, or even from scientific journals, might lead palaeontologists to name new species when they do not feel a new name is warranted: it is well known, for example, that the press prefers a story about a 'new species of dinosaur', rather than another example of a previously named form. On the other hand, it could be that the new species being reported every few weeks are generally valid, and that there really is a great deal yet to discover about these giant fossil creatures.

2. SYNONYMY AND INVALIDITY

Discussions about valid and invalid species have mainly focused so far on the issue of synonymy (e.g. May 1990; Wilson 1992; May & Nee 1995). Synonyms are species, or higher taxa, that have been given a name in error by an investigator who is unaware that the species had already been named. There are other reasons for rejecting a species name as incorrect or invalid: it may be a nomen vanum (improperly established name for something that is already named), a nomen nudum (no type material identified), a nomen oblitum (name never used after its establishment), a nomen dubium (based on undiagnostic and incomplete material), preoccupied (given a name that has already been given to some other organism) or misassigned (correctly named, but belonging to another group).

There is some debate over the global proportions of invalid taxa, whether synonyms or any of the other error categories just noted. Wilson (1992) assumed a global synonymy rate of 22 per cent among living taxa, a figure modified to approximately 20 per cent by May & Nee (1995); these authors assumed a more-or-less 'standard' rate for all taxa, large and small, marine and non-marine, plant and animal. Detailed studies of particular groups of living taxa have suggested that these global estimates might be too low. For example, there is a wide range of synonymy rates, from 7 to 80 per cent (mean 31%), among insect groups (Gaston & Mound 1993), and from 33 to 88 per cent (mean 66%) among seed plants (Wortley & Scotland 2004). Further, these are 'static' synonymy rates, based on our current view of what is valid and what is not. It is likely that many of the new species named in the past 20 or 30 years may not yet have been revised, and so they have not been tested for possible synonymy. In view of this omission, the global estimates of 'eventual' synonymy rates, when all current taxa have been revised, might well be higher than current estimates; and indeed, owing to a substantial rise in naming activity for many groups in recent years, the effect of this omitted error might be substantial.

In order to attempt to estimate true synonymy rates, Solow et al. (1995) presented a modelling approach to take account of recently named taxa. In a case study, they found that the error rate for thysanopteran insects is 22 per cent, based on a survey of all 6112 named species. 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 per cent, roughly twice the static estimate. Alroy (2002) stressed that acts of invalidation are themselves subject to scrutiny, and species once invalidated may subsequently be revalidated. So, he applied a 'flux ratio' approach to his dataset of North American fossil mammals, and found a corrected error value of 50 per cent, compared with the static estimate of 31 per cent invalid taxa.

Among dinosaurs, Benton (2008) found that 726 (51.8%) of the 1401 species named up to the end of 2004 are currently regarded as invalid. This figure is comparable with Alroy's (2002) figure for North American fossil mammals, and it is also in line with measures for particular groups of living plants and animals. In more detail (Benton 2008), 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).

3. RESULTS

Dinosaur fossils are relatively large and hard to miss in the rocks, so it might be assumed that they are more or less collected out and we should be on the asymptotic phase of the species discovery curve. This is apparently not the case (figure 1a)—although there is a substantial concern that the majority of species named in the past 30 years might actually be invalid.

This is not supported by the data (figure 1b). In fact, the quality of type materials of new dinosaurian species has improved steadily since the first dinosaur was named in 1824. The measure of quality of type material (ratio of good to poor specimens) remained below 1.0 until 1960, and after this crossover point more new species of dinosaurs were based on complete skulls or complete skeletons than on less complete materials. In this context, 'good' type material consists of a complete or partial skull, or a complete or partial skeleton, where 'partial' means that at least 50 per cent of the skull or skeleton is preserved. 'Poor' type material consists of anything from a single tooth to a collection of 10 or 15 isolated elements from different regions of the skull and skeleton. Note that the high figure for 1940, in figure 1b, reflects a rather small sample size (n=41)for that decade.

These global figures mask significantly different trends by continent (table 1; electronic supplementary material, figure 1; note, Australia, Madagascar and Antarctica are omitted because the total number of dinosaurs from these regions is too small for analysis). The highest proportion of new species based on good material has been in North America, then Asia, then South America, then Africa, and finally Europe. Indeed, the quality crossover point for dinosaurs

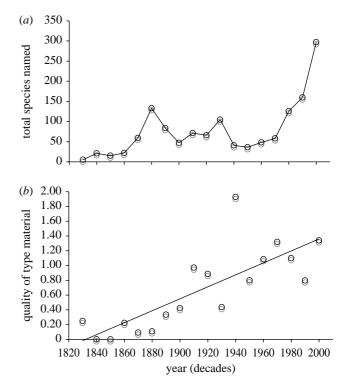


Figure 1. Naming new dinosaurs. (a) The total numbers of new dinosaurian species named, by decades, from 1824 to 2004; totals per decade range from 5 to 297. These are all new species named, whether they have subsequently been invalidated (inadequate type materials, synonymy, not a dinosaur). (b) Quality of type materials for new dinosaur species, plotted by decades; the measure of quality is the ratio of incomplete materials (isolated teeth or bones; collections of individual elements) to complete materials (complete skull(s) or skeleton(s)). The best-fitting line (y=0.0811x-0.098) shows highly significant correlation (Spearman's rho=0.788; t=5.12; p<0.0001). In these plots, 'dinosaur' is used in the cladistic sense, and includes Mesozoic birds, totalling some 100 of the 1401 total species.

ranges from 1920 in North America to 1970 in South America, and is not yet attained in Europe and Africa. This suggests that there are multiple factors involved in the choice of type materials for new species. The figures do not reflect nationality or regional practices because Europeans and North Americans have long sought materials from all continents. Perhaps more complete materials have been used in North America and Asia simply owing to the relative richness of dinosaur-bearing deposits. The quality of type materials employed is not simply a function of maturity of study—dinosaurs were first named from Europe, and that continent had a head start of some 30 years before dinosaurs were named from Africa, and yet the quality ratio, although exceeding 1.00 in 1960, has remained well below 1.00 since then. The key conclusion might be that European dinosaur deposits have long been more or less worked out, and palaeontologists are increasingly driven to using incomplete materials as a basis for new species, whereas North America and Asia have a great deal of potential, but Africa and South America have yet to produce truly abundant dinosaur remains, despite there being a small number of exceptional sites in each continent.

Table 1. Variations in the quality of fossil material used as a basis for new species of dinosaurs, recorded by continents. (The total number of species includes all species named, whether valid or invalid. The 'type quality' is the ratio of 'good' to 'poor' specimens (see the text), indicated as a mean for all years since the first putative dinosaur was named, and for the years 1885–2004, providing a standardized time span for all samples. The crossover decade, is the 10-year time span during which, on average, more new dinosaur species were named on the basis of complete than incomplete material; X, not yet achieved.)

	global	Europe	Africa	N. America	Asia	S. America
total number of species	1401	325	113	430	415	101
first putative dinosaur named	1824	1824	1854	1856	1865	1893
first valid dinosaur named	1824	1824	1854	1858	1877	1893
type quality (all years)	0.67	0.26	0.41	1.25	1.02	0.68
type quality (1885–2004) crossover decade	0.95 1960	0.35 X	0.54 X	1.65 1920	1.19 1940	0.68 1970

4. DISCUSSION

So, far from having exhausted all the potential sites for discovery of new dinosaur species, it looks as if there is much more to come. The historical rate of invalidity, more than 50 per cent, may not apply to the species named more recently because the quality of type materials has improved. Indeed, evidence of past invalidation tends to support this. Of the 726 currently invalid dinosaurian species, 582 (80.2%) were based on isolated teeth and bones, whereas only 247 of the 675 currently valid dinosaurian species (36.6%) were based on such limited materials. As the use of incomplete specimens declines, past performance suggests that dinosaurian systematists ought to be establishing a higher proportion of valid species now than they did in the past.

There is likely to be a limit to the number of new dinosaurs to be named at some point in the near future, however. By using various approaches, Dodson (1990) estimated that there had been perhaps 1000 genera of dinosaurs (which scales to approx. 1200 species), a figure revised upward to 1850 genera (and perhaps 2220 species) by Wang & Dodson (2007). These estimates suggest that we have identified approximately one-quarter of known dinosaur species (the 1990 estimate) or approximately one-third (the 2007 estimate). Further evidence that a limit will be reached at some point is that the number of valid new dinosaur species is correlated with the number of new sedimentary basins from which dinosaurs have been recovered (Benton 2008). The burst of new discoveries from various geological formations in China, Mongolia and Argentina in particular have fuelled much of the recent rise; there will surely be fewer and fewer such unexplored new basins as time goes on.

These data suggest that continuing rigorous scrutiny of species lists is required to provide a meaningful measure of the biodiversity of any group, whether living or extinct. If as many as 50 per cent of named species may turn out to be invalid, current species lists for unrevised groups may be entirely misleading. The invalidity may be evenly spread through geographical regions and ecological categories, but equally it might be found that invalidity is clumped around small taxa, or species from one region of the world for example.

It could be claimed that fossils are less well understood than extant taxa. In particular, fossil species are

morphospecies, and genetic and breeding tests cannot be carried out: this is not perhaps such a problem as might be thought at first, however, because most systematics of living species is also based on the morphospecies model. Further, it is not clear that taxonomic practice has been uniformly worse (or better) among palaeontologists than among systematists of living taxa. The equivalent synonymy rates for extant and fossil groups indeed suggest that there is not much difference in practice. Among fossil groups, dinosaurs, and the North American mammals presented by Alroy (2002), have been subject to heavy scrutiny. Indeed, there have now been several cycles of revision of the species established in Victorian times, and this intense scrutiny continues. If other, less well studied, fossil or living groups are subjected to the same level of revision, invalidity rates of 50 per cent or more might be found to be more the norm than the figures of 20 to 22 per cent suggested by Wilson (1992) and May & Nee (1995).

The apparent improvement in the quality of type materials, for dinosaurs at least (figure 1b), suggests that such scrutiny may help the community of active systematists to define better practice in identifying new species. If such improvements are occurring, then this must be factored into the statistical techniques that have been used to estimate ultimate synonymy rates based on historical levels of synonymy (Solow et al. 1995; Alroy 2002).

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