

Cope's Rule in the Pterosauria, and differing perceptions of Cope's Rule at different taxonomic levels

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Abstract

The remarkable extinct flying reptiles, the pterosaurs, show increasing body size over 100 million years of the Late Jurassic and Cretaceous, and this seems to be a rare example of a driven trend to large size (Cope's Rule). The size increases continue throughout the long time span, and small forms disappear as larger pterosaurs evolve. Mean wingspan increases through time. Examining for Cope's Rule at a variety of taxonomic levels reveals varying trends within the Pterosauria as a whole, as pterodactyloid pterosaurs increase in size at all levels of examination, but rhamphorhynchoid pterosaurs show both size increase and size decrease in different analyses. These results suggest that analyses testing for Cope's Rule at a single taxonomic level may give misleading results.

Introduction

Many clades show increasing body size through time, a phenomenon often loosely called Cope's Rule (Benton, 2002). This has been a part of evolutionary biology theory for over a century (Cope, 1896), yet it has never gained common acceptance. It has been demonstrated to operate in some groups (Arnold *et al.*, 1995; Poulin, 1995; Alroy, 2000) but not in others (Jablonski, 1997; Gould & McFadden, 2004; Moen, 2006), and yet Cope's Rule has been dismissed by some as imaginary, either an artefact of passive evolution (small ancestors can only produce similar-sized or larger descendants; Stanley, 1973), an increase in variance (where small forms remain as part of the evolving clade, and larger forms are added as the clade becomes more diverse), rather than a uniform driven trend (Gould, 1988), or even psychological ('bigger is better'; Gould, 1997). However, Cope's Rule has recently attracted much attention (Knouft & Page, 2003; Kingsolver & Pfennig, 2004; Laurin, 2004; Webster *et al.*, 2004; Hone & Benton, 2005; Hone *et al.*, 2005; Hunt & Roy, 2006; Moen, 2006) and merits further investigation to determine whether it is a

feature of many lineages, or just a rare and unusual occurrence, and to clarify that simple size increase through time is not in itself enough to warrant special explanation.

Large size is expected to convey certain advantages in both interspecific and intraspecific competition (Schmidt-Nielsen, 1984; Benton, 2002; Hone & Benton, 2005) and thus Cope's Rule might be expected to be observed widely, yet this is apparently not the case. Counter selection for smaller size should appear when size limits are achieved or ecological pressures are applied, e.g. limits on resources, dramatic environmental change, competition from superior, larger species etc. (Kingsolver & Pfennig, 2004; Hone & Benton, 2005) but within a context of general size increase. Apparent variation in selection pressures may be partly a result of testing for Cope's Rule at differing levels of phylogeny. As Alroy (2000) showed, large-scale trends like Cope's Rule may only be apparent at certain phylogenetic levels. Short-term or low-level trends may be masked over extended periods of time or at high phylogenetic levels (as seen in some dinosaurian clades in Hone *et al.*, 2005). Similarly, analyses over short time periods or at low taxonomic levels may miss large-scale trends that take millions of years to become apparent. Therefore there remains an apparent conundrum: even if Cope's Rule is detected, is it a true evolutionary effect, or merely a medium-term pattern not seen over shorter or longer time spans?

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Pterosaurs were the first vertebrates to achieve powered flight and so represent an important part of vertebrate evolutionary history. Although pterosaur remains are relatively scarce compared with their large-bodied contemporaries, the dinosaurs and marine reptiles, they represent an important component of Mesozoic faunas as the only flying vertebrates for 60 million years (Myr) (Unwin, 2006).

Pterosaurs consist of many families in two major suborders – the paraphyletic 'Rhamphorhynchoidea' (relatively small, with a long tail, from the Late Triassic to the Early Cretaceous) and the Pterodactyloidea (relatively large, reduced tail, from the mid-Jurassic to the end Cretaceous) (Wellnhofer, 1991). As flying organisms, their body sizes must have been constrained by the aerodynamic demands of flight (Alexander, 1998). Even so, pterosaurs include the largest flying organism so far known – *Quetzalcoatlus* with a wingspan of 12 m (Wellnhofer, 1991, pp. 142–143), and their minimum size was large compared with both birds and bats: *Jeholopterus* spanned 0.35 m (Wang *et al.*, 2002). Smaller nonadult records include a young *Pterodactylus* with a wingspan of just 0.18 m (Wellnhofer, 1991, p. 88) and new evidence suggests that even tiny, newly hatched pterosaurs could fly (Wang & Zhou, 2004; Unwin, 2006).

Pterosaurs have attracted a great deal of interest recently, with considerable effort devoted to their origins (Bennett, 1996; Peters, 2000), phylogenetics, (Kellner, 2003; Unwin, 2003) and biology (Bennett, 2001; Bonde & Christiansen, 2003; Frey *et al.*, 2003; Wilkinson *et al.*, 2006). Pterosaurs are represented by many complete specimens and they were diverse, with approximately 60 genera in 20 families (Unwin, 2003, 2006). The aim of this paper was to assess whether or not pterosaurs show evidence of Cope's Rule. Coupled with this analysis is an investigation into the effects of testing for Cope's Rule at different phylogenetic levels based on the pterosaurs.

Materials and methods

In order to test for the presence of Cope's Rule, both within a single lineage and across multiple lineages, a measure of body size, and ancestor/descendant relationships must be established. Testing must also be performed at an appropriate taxonomic level, as testing at high levels (e.g. families) may miss generic-level trends (Alroy, 2000, and corroborated by Kingsolver & Pfennig, 2004).

Determining body mass accurately for extinct organisms is very difficult, so most authors have used an easily measured morphological feature as a proxy for body mass. For example, Alroy (1998) used molar tooth size for mammals, Jablonski (1997) used shell height and length for molluscs, and Moen (2006) used carapace length in turtles. Here, total wingspan is used as a proxy for body mass in pterosaurs.

In pterosaurs, the wing shape was far more constrained than in birds or bats (Hazlehurst & Rayner, 1992) and

even the most disparate wing shapes of pterosaurs are still very similar. Furthermore, wingspan must correlate with body mass, as the amount of lift generated by the wings must be sufficient to maintain flight. However, two factors could complicate this rather simple assumption. First, in larger pterosaurs, a reduction in the thickness of long bones allowed for an increase in overall weight without an increase in wingspan (Bonde & Christiansen, 2003). Secondly, the pterodactyloids also reduced their net wing area per unit length, as the main flight wing, the cheiropatagium, was probably attached to the knee, and not the ankle as in rhamphorhynchoids (Bennett, 2000). However, these differences may be ignored in within-family comparisons, and comparisons between families will involve relatively large differences and so the results should not be affected.

In most cases, complete wing specimens were used, but on occasion missing terminal phalanges were scaled from close relatives. Single wings can be doubled in total length to provide an estimate for total wingspan. Although the width of the torso is missing from this estimate, the elbow would naturally be flexed, so reducing the total wingspan. Thus the underestimate for the missing body is balanced by the overestimate of measuring the total length of all forelimb bones. This simple doubling of the total length of the wing bones therefore provides an accurate representation of the actual wingspan of the animal in life (Bennett, 2001). Pterosaurs do show variation in the scaling of the bones that make up the wing (Hazlehurst, 1991) but these are constrained within both families and genera, and so estimates are adequate for comparison of closely related taxa.

Pterosaur nomenclature used here is based on the revisions by Unwin (2003). Measurements were collected from the literature and from other researchers, and, where possible, these measures were taken from multiple sources to corroborate and cross check the methods. The data are presented in Appendix S1 (see Supplementary Material), with sources. Slack *et al.* (2006) have carried out a superficially similar analysis of pterosaur wingspan, but not directed at assessing the validity of Cope's Rule. Their data set is larger than ours, but it includes a high number of invalid taxa and incomplete specimens, and the basis for some of the wingspan estimates is not clear.

Putative 'ancestor-descendant' pairs may be determined from stratigraphy (e.g. Alroy, 1998), or from a phylogeny (e.g. Hone *et al.*, 2005). For pterosaurs, most published phylogenies are characterized by large ghost-lineages (times when the taxon was assumed to exist from evidence of its phylogenetic affinities, but for which no fossils are known) and therefore family groups were established using phylogenetic analysis, and within-family 'ancestor/descendant' pairs were then based on stratigraphic differences. Of the available, recent, complete pterosaur phylogenies, that of Unwin (2003) was chosen as being the most suitable for this analysis. In comparison with a similar analysis by Kellner (2003), Unwin's (2003)

phylogeny consists of family groups rather than a mix of genera and families and thus provides a framework for familial relationships. Unwin's (2003) analysis also shows significantly shorter ghost ranges, and may therefore be a better estimate of relationships.

Comparisons were therefore made between the wingspans of genera of different stratigraphic age (specifically the youngest and oldest) within 10 pterosaurian families, those that contained more than two genera. Where two or more genera shared the same stratigraphic age, an average of their wingspans was used. This is perhaps a crude method, but it gives a good indication of trends within the clade. Because the pterosaur phylogenetic tree distinguishes families, but not genera, extra pairs of genera could not be compared, as in previous studies (Hone *et al.*, 2005).

Wingspan measurements were logarithmically transformed to normalize for data distribution (Freckleton *et al.*, 2002) and plotted against average stratigraphic age. Midpoint stratigraphic ages were taken from the relevant stages of the first appearance of a given taxon (e.g. the Norian is taken as 221–210 mya, and so is given a midpoint age of 226.5 mya). Many pterosaur taxa are limited to single stages (often single formations) and thus are only known from a single point in time. In order to examine patterns of size change at different taxonomic levels, the Pterosauria were then split into the suborders 'Rhamphorhynchoidea' and Pterodactyloidea, and then the largest clades within each (the superfamilies Rhamphorhynchoidea and Azhdarchoidea respectively) were also plotted.

Results

The results of the intra-familial comparisons are presented in Table 1. No wingspan data were available for the lonchodectids and so they are omitted. The low number of just nine intrafamilial comparisons makes further evaluation difficult, but in general the results are strongly positive.

Table 1 Comparisons of pterosaurian wingspans.

Family	Earlier taxa	Later taxa	Time (Myr)	Log size difference
Dimorphodontidae	<i>Peteinosaurus zambellii</i>	<i>Dimorphodon weintraubi</i>	56	0.567
Anurognathidae	<i>Bactrognathus Volans</i>	<i>Jeholopterus ningchengensis</i>	32.5	-0.319
Campylognathidae	<i>Austriadactylus cristatus</i>	<i>Campylognathoides zitteli</i>	34	0.164
Rhamphorhynchidae	<i>Dorygnathus banthensis/D. purdoni</i>	<i>Rhamphorhynchus muensteri/R. 'longiceps'/Scaphognathus crassirostris</i>	40	0.470
Ornithocheiridae	<i>Haopterus gracilis</i>	<i>Anhanguera santanae/Arthurdactylus conandoylei</i>	9	0.510
Pteranodontidae	<i>Nyctosaurus gracilis/N. lamagoi</i>	<i>Pteranodon longicps/P. sternbergii/P. ingens</i>	4.25	0.435
Lonchodectidae	–	–	–	No size data
Ctenochasmataidae	<i>Huanhepterus quingyangensis</i>	<i>Caeradactylus atrox</i>	33	0.342
Dsungaripteridae	<i>Germanodactylus cristatus</i>	<i>Noriopteris complicidens</i>	33	0.200
Azhdarchoidea	<i>Tupuxuara leonardii</i>	<i>Quetzalcoatlus northropi/Q. s</i>	5.35	0.126

Families are given sensu Unwin (2003). Time is the difference in millions of years between the midpoint of estimated ages of both named taxa; in other words, the duration of the time of size change in a lineage. Size difference is the difference in wingspan between the first and last named taxon in a lineage; it is quoted in metres and as a percentage.

A graph of data for all available pterosaurs was completed to show the distribution of size across the Mesozoic and a least-squares regression line calculated. The results show an overall trend to increase in wingspan from the Late Triassic to the end of the Cretaceous (Fig. 1) with a strong positive trend towards large size.

The 'Rhamphorhynchoidea' (Fig. 2a) shows a general size decrease, although the data distribution is highly scattered. In comparison, the Pterodactyloidea (Fig. 2b) shows much greater clustering of the data, with a highly significant positive correlation of size increase. Both the Rhamphorhynchoidea and Azhdarchoidea (Fig. 3a,b respectively) also show strong increases in size over time, although each based on relatively few data points.

Discussion

The nine complete intrafamilial comparisons (Table 1) strongly support Cope's Rule in action. All of the comparisons except one show a notable size increase in

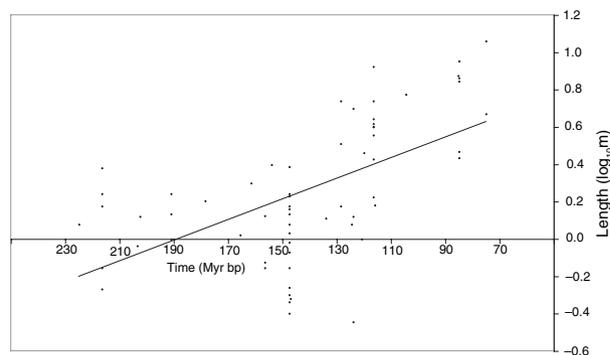


Fig. 1 Graph of log wingspan vs. time for all pterosaur genera with a best-fit regression line (formula of line $y = -0.0055x + 1.0438$), with the correlation coefficient ($R^2 = 0.33$) and P value ($P = 0.0001$). Wingspans measured from juveniles, and taxa for which the data are incomplete, were excluded.

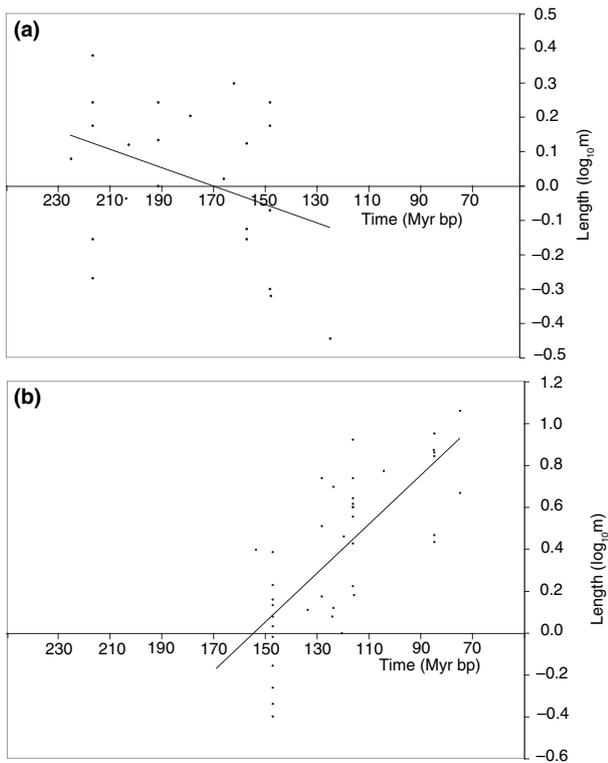


Fig. 2 Graph of log wingspan vs. time for all of the 'Rhamphorhynchoidea' ($y = 0.0027x - 0.4511$, $R^2 = 0.13$, $P = 0.05$) (a) and all Pterodactyloidea ($y = -0.0117x + 1.8022$, $R^2 = 0.54$, $P = 0.0001$) (b) with regression lines. Wingspans measured from juveniles, and taxa for which the data are incomplete, were excluded.

the descendants, with only a minor decrease in the anurognathids. The gross change in size across the whole Pterosauria (Fig. 1) shows a similar trend to large size. Most importantly, there is a clear trend of increasing maximum and mean size towards the end of the Cretaceous, coupled with the progressive loss of smaller forms.

Small pterosaurs were lost at the Jurassic-Cretaceous (JK) boundary, and there may have been a modest extinction event or turnover event at that time (Fig. 1). Indeed, almost all of the rhamphorhynchoids went extinct at the JK boundary, and only two families survived, the anurognathids and scaphognathids. Small to medium-sized pterosaurs continued to be lost through the Cretaceous, and these losses make the minimum and maximum lines bounding the overall distribution of pterosaur sizes roughly parallel.

Small size is a high priority for flying or gliding organisms as it minimizes the animals' mass and so minimizes the required wing area and power requirements (Pennycuik, 1988). Furthermore, achieving large size is difficult for known flying vertebrates (Pennycuik, 1986), although it does reduce the relative metabolic cost of transport (Alexander, 2006). Small size is a characteristic of almost all known gliders, such as

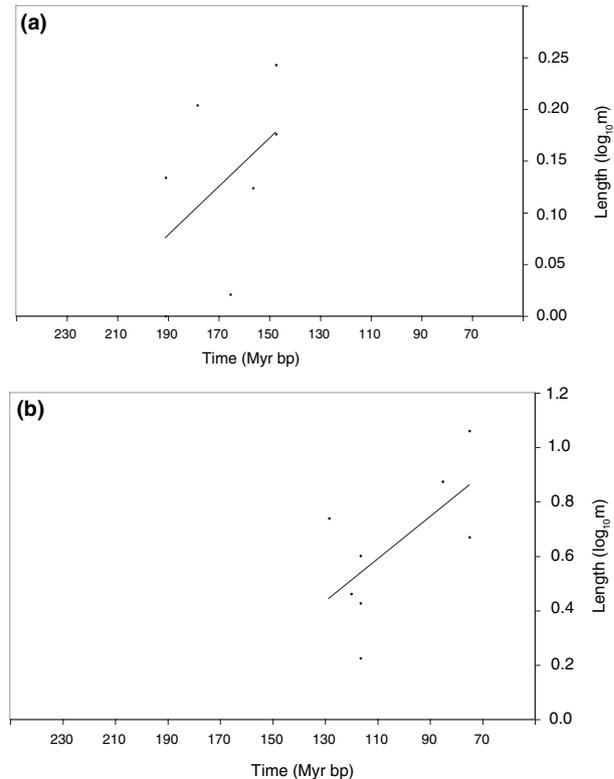


Fig. 3 Graph of log wingspan vs. time for the Rhamphorhynchoidea ($y = -0.0023x + 0.5235$, $R^2 = 0.24$, $P = 0.13$) (a), and all Azdarchoidae ($y = -0.0078x + 1.445$, $R^2 = 0.41$, $P = 0.04$) (b) with regression lines. Wingspans measured from juveniles, and taxa for which the data are incomplete, were excluded.

Sharovipteryx and *Coelurosauravus*, and early powered fliers, such as *Archaeopteryx* and *Icaronycteris* (Wellnhofer, 1991; Padian, 2003; Unwin, 2006).

Despite the heavy constraints placed on body form and anatomy by powered flight, the pterosaurs were able to achieve huge size in two families, the Azdarchidae and Pteranodontidae (Alexander 1998). Large size is hard to achieve for flying organisms for two reasons: the constraints placed on the anatomy by powered flight, and perhaps the absence of ecological niches. The dinosaurs, on the other hand, achieved large size earlier than the pterosaurs (both groups originated at the same time), and a number of families achieved giant size (Hone *et al.*, 2005). As with the dinosaurs (Hone *et al.*, 2005), in most families (six of nine) the largest known taxon is the most recent in that clade, and indeed the largest pterosaur taxa are known from the very end of the Cretaceous (*Pteranodon* and *Quetzalcoatlus*). It is possible that extreme size in pterosaurs was facilitated by the warmer climate of the Cretaceous and with it an increase in thermals used for soaring (suggested by an unnamed reviewer).

There may be hierarchical effects in the appearance of Cope's Rule that depend on the taxonomic level

under study (Alroy, 2000). Comparisons of the whole clade (Fig. 1) with its two main subdivisions (Fig. 2), and two further lower-level subdivisions (Fig. 3). All plots show significant size increases except that for 'Rhamphorhynchoidea' (Fig. 2a), which shows a negative correlation. The slope is shallow, and sample size. This plot may be biased by the numerous anurognathid taxa from the Cretaceous of China. The fossil record of this family is especially poor (just six specimens in four genera) and is concentrated in the Jehol deposits (Unwin, 2006). Without them, this plot would show no overall change in size. Note that the plot of Rhamphorhynchoidea (Fig. 3a), a major subclade of 'Rhamphorhynchoidea', shows a significant positive correlation.

These results are unlikely to be a result of taphonomic bias. Despite the fact that some 90% of specimens and 50% of taxa are known from just four deposits we can have some confidence in these results. Notably, the deposits that dominate the data (Solnhofen, Santana, Jehol) include not only pterosaurs but also numerous other small fossils, such as fishes, amphibians, birds and insects that do not always preserve well in other deposits. Thus the lack of small pterosaurs in the Cretaceous Santana cannot be put down to their lack of preservation or simply not having been found.

So, do pterosaurs obey Cope's Rule? Or do they simply reflect Stanley's (1973) observation that early members of a clade are small, and so they can only diversify and so evolve to larger sizes? Two observations suggest that Cope's Rule is in action as an active trend:

- 1 Body size increases continuously across almost all taxa (the only exception being the 'Rhamphorhynchoidea' and Anurognathidae), and within families, through the Late Jurassic and Cretaceous, a time span of 100 Myr or so, a far more sustained trend than might be expected with passive evolution away from small size.
- 2 Small taxa of pterosaurs disappear. The explanation of Cope's Rule as increase in variance (Gould, 1988) is rejected for the pterosaurs, as small forms disappear through the Cretaceous as ever-larger taxa evolve. This exclusion of the small is an unusual observation, not seen in mammals (Alroy 1998), dinosaurs (Hone *et al.*, 2005), or other clades, but perhaps important as a test for Cope's Rule.

The survival of large forms and progression of size increase is also coupled with a fundamental change in body form. The pterodactyls achieved far greater size than the rhamphorhynchoids, in association with a number of morphological changes (Unwin, 2006). The pterodactyls lost the long tail and reduced the associated large hind-wing seen in rhamphorhynchoids, they developed the notarium (a fused section of dorsal vertebrae to support the wing musculature), they proportionally increased their wingspans, and they reduced relative skeletal mass (Wellnhofer, 1991).

Potential benefits of large size have been detailed in a number of studies and reviews (Schmidt-Nielsen, 1984; Benton, 2002; Hone & Benton, 2005), and Kingsolver & Pfennig (2004) have provided good evidence for mechanisms that might drive Cope's Rule by demonstrating the intraspecific benefits of large size across single generations (e.g. increased survivability, increased number of offspring and increased offspring survival). Pterosaurs show strong sexual dimorphism (Bennett, 1996) both in size and the morphology of their often elaborate head crests (Frey *et al.*, 2003). It therefore remains a strong possibility that this trend to large size was driven (at least in part) by sexual selection for large size or sexual signalling.

Why were the small pterosaurs lost? It has been suggested (e.g. Unwin, 1987; Penny & Phillips, 2004) that the steady loss of smaller pterosaurs maps neatly on to the appearance of birds through the Cretaceous. Slack *et al.* (2006) indicate this, although they urge caution about making a simple link from matching events to an assumption of competitive exclusion. Diet suggests that caution is warranted: most Cretaceous birds were insect-eaters, with some flightless fish-eaters and shorebirds in the Late Cretaceous, whereas insectivorous pterosaurs are known only from the Late Jurassic and Early Cretaceous, and most later ones were probably coastal fish-eaters. Further, there was always a substantial size gap between the largest birds and the smallest birds at any time. The suggestion that birds somehow drove the pterosaurs towards large size, and perhaps to final extinction, is currently not supported.

Conclusions

It should be remembered that Cope's Rule is a rule and thus 'a generally prevailing condition' (Benton, 2002) – it does not need to be found in *all* clades and lineages to be valid. With current evidence, Cope's Rule does appear to be widespread: there are more palaeontological case studies that support the rule (Arnold *et al.*, 1995; Poulin, 1995; Maurer, 1998; Alroy, 2000; Kingsolver & Pfennig, 2004; Hone *et al.*, 2005; this study) than reject it (Jablonski, 1997; Gould & MacFadden, 2004). [Although see Moen (2006) for details of both palaeontological and neontological studies of Cope's Rule]. It should be admitted that the majority of these studies have concentrated on amniotes, and these might be exceptional in comparison with other organisms, but a century on from its first appearance, Cope's Rule appears to be in rude health.

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Supplementary material

The following supplementary material is available for this article:

Appendix S1: Data used for the analyses.

This material is available as part of the online article from <http://www.blackwell-synergy.com/doi/full/10.1111/j.1420-9101.2006.01284.x>

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