

Body size evolution in palaeognath birds is consistent with Neogene cooling-linked gigantism

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ABSTRACT

Palaeognathae is an extant clade of birds with body masses ranging over several orders of magnitude of kilograms, including the largest-yet described terrestrial avian species. Most studies have suggested flight loss and increasing body size began early in its evolutionary history, prior to the divergence of the major extant lineages. However, recent phylogenetic work suggests body size increases occurred more recently and independently within many extant lineages. Here, we use linear regression equations to estimate the masses of extinct taxa from both the crown and stem of Palaeognathae to test these hypotheses. We allocate fragmentary specimens to discrete body mass categories to accommodate additional species for which more precise body mass estimation is not possible. The first fossil evidence for an increase in maximum palaeognath body size, from approximately that of a rhea (20 kg) or smaller to ostrich size (100 kg), is Miocene in age (approximately 20 Ma). The heaviest taxa, those exceeding 120 kg, all occur within the last 9 million years. Molecular divergence dating estimates for the crown ages of palaeognath subclades pre-date the oldest preserved material, often significantly; however, plotting the lightest member of each clade at the estimated crown ages does not change the observed pattern. These results may be affected by the predictive model used to estimate the mass of extinct taxa, but the observed trends in body mass do not change when four models from different studies are used. Both island-dwelling and continental clades show broad temporal congruence in the timing of their estimated gain of large body sizes, meaning geographical restriction on islands does not alone explain the observed trend. We suggest large and giant Palaeognathae body sizes may be more closely linked to global cooling which creates selective pressures on body size for thermoregulation, as well as causing landscape changes which alters dietary and locomotory requirements. Global cooling has received extensive attention as a driver of mammalian body size extremes but has been relatively little discussed with respect to birds.

1. Introduction

The variety in size and geographic distribution in palaeognath birds has presented an enduring evolutionary puzzle (e.g. Cracraft, 1973, 1974; Yonezawa et al., 2017). The Palaeognathae are an early divergent avian clade comprised of volant tinamous and the flightless “ratites” — kiwis, emu, ostriches, cassowaries, and rheas. Ratite body size ranges over several orders of magnitude from the little spotted kiwi (*Apteryx owenii*, 1.20 kg) to ostrich (*Struthio camelus*, 111 kg; Dunning, 2007). Flightless extinct forms include the giant Moas as well as the elephant bird *Aepyornis maximus*, the largest terrestrial avian species known. Phylogenetic relationships within Palaeognathae have supported different proposed histories of body size evolution. Early morphological studies suggested ratites to be monophyletic (Parkes and Clark, 1966; Cracraft, 1973, 1974), implying a single origin of gigantism and

vicariance or dispersal via terrestrial connection of large-bodied flightless taxa deep in the Mesozoic.

Molecular phylogenetic studies of extant taxa indicate ratites are instead paraphyletic with respect to tinamous (Harshman et al., 2008; Hackett et al., 2008). Those studies that have included extinct species of Palaeognathae also support paraphyly, recovering sister relationships between tinamous and moas as well as between kiwis and elephant birds (Baker et al., 2005, 2014; Mitchell et al., 2014; Grealy et al., 2017; Yonezawa et al., 2017). These results indicate that large body sizes evolved multiple times in ratites (Baker et al., 2005; Hackett et al., 2008; Harshman et al., 2008; Baker et al., 2014; Mitchell et al., 2014; Grealy et al., 2017; Yonezawa et al., 2017), but the causes and timing of these events are less clear. Most hypotheses generally imply these shifts occurred early in the history of the group. Large size has been proposed, for example, to be a response to the ecological opportunities following

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the end-Cretaceous mass extinction (Phillips et al., 2010; Mitchell et al., 2014), following dispersal onto new continents (Yonezawa et al., 2017), or to allow consumption of a wider range of dietary items in the Cretaceous (Cracraft, 1974).

Broad interest in body size extremes in birds and the relationship of body mass with key life history traits has led to a continuing concern with specific estimation of body masses in extinct birds that sample a greater range than observed in extant taxa (e.g. Amadon, 1947; Alexander, 1983; Field et al., 2013). Estimation of the size of extinct taxa generally relies on predictions based on the scaling of skeletal element measurements with body mass. Several studies have identified skeletal correlations with body mass in birds with high predictive power, but palaeognath taxa have either not been included (Field et al., 2013), included in very few numbers (Maloiy et al., 1979; Prange et al., 1979), or with a limited number of measured elements (Campbell and Marcus, 1992). Few studies have concentrated specifically on Palaeognathae and largest terrestrial avian taxa (Alexander, 1983; Cubo and Casinos, 1997; Dickison, 2007), and there has been significant variation in estimates of palaeognath masses (Wiman, 1935; Amadon, 1947; Campbell and Marcus, 1992; Dickison, 2007). Mass estimates of extinct taxa are also possible through the integration of x-ray computed tomography data in whole skeleton and muscle mass reconstruction (e.g., Brassey et al., 2013); however, as many species are described from extremely limited material, researchers will likely continue to rely on predictions made from individual skeletal elements.

A frequently studied relationship is between global climate and body size evolution. In particular, larger body sizes allow species to more effectively retain heat in colder conditions (Glazier, 2010). These relationships have been more extensively evaluated in mammals, where changes in global climate have been shown to drive evolution of large sizes (Smith et al., 2010; Saarinen et al., 2014). Studies of mammals have also shown changes in climate may also produce additional selective pressures. For example, as global climate changed through the Cenozoic there was a pronounced correlated shift in the relative abundances of different habitats which, by themselves, can also drive changes in body size (Lovegrove and Mowoe, 2013). These trends have been less frequently studied in avian taxa.

Here we evaluate the hypothesis that large Palaeognathae body sizes evolved early in the history of the group by estimating the mass of extinct palaeognath taxa and assess any temporal trends. We assess skeletal measurement predictors of body mass for the clade against results from previous regressions and factor in molecular divergence estimates for the origin of extant palaeognath crown clades. Finally, we estimate the probability of sampling extinct avian species in discrete time intervals for all Cenozoic birds to inform the relative likelihood of as-yet-unsampled species diversity affecting conclusions drawn from the observed temporal body mass distribution.

2. Materials and methods

We predicted the mass of all described palaeognath taxa for which skeletal material was available, but excluding species only described from eggshell (Table S1, S2). We estimated the masses of 40 extinct taxa using allometric scaling equations derived from extant palaeognaths (Table 1). We used specimens of extant palaeognaths which had a

recorded specimen weight, with this preferred over mean species weight. Using the mean species weight in allometric equations may affect results as absolute mass variability will be greater for heavier species (Fig. S1). This effect would be due to the lower probability of using a limb measurement from a specimen of mean species weight (Field et al., 2013).

The range in body masses used here to calculate allometric equations of body size covered the majority of weight variation seen in Palaeognathae. Masses ranged from a species of tinamou, White-bellied Nothura (*Nothura boraquira*, 0.32 kg), to Ostrich (*Struthio camelus*, 80.92 kg). Published data for *N. boraquira* ranges between 0.24 and 0.34 kg (Dunning, 2007), and *S. camelus* between 86 and 145 kg (Dunning, 2007). The ostrich is the heaviest extant Palaeognathae species, the smallest is the dwarf tinamou *Taoniscus nanus* which weighs only approximately 0.04 kg (Dunning, 2007); however, this species is exceptionally small for a tinamou which average 0.50 kg as a group.

We focused on length measurements, predominantly of hindlimb elements (femur, $n = 15$, tibiotarsus, $n = 13$, tarsometatarsus, $n = 8$, Table 1, Table S2) as well as humerus length ($n = 10$, Table 1, Table S2) for volant taxa (e.g. Lithornithidae). Circumference measurements are more likely to be unobtainable if a fossil element had been crushed. Additionally, the cross-sectional shape of hindlimb elements is variable among species, with circumference and length equations performing comparably in estimating the mass of Neognath taxa (Field et al., 2013). If a species had multiple available measurements, either multiple limb element measurements from a single species and/or measurements of the same element from different studies, we estimated its mass iteratively using each of these available values and recorded the mean and range. All measurements were log-transformed prior to performing regressions. The raw data for the predictive equations is given in Table S2. We estimated body masses and performed all subsequent analyses using the statistical program R (R Core Team, 2017).

To evaluate our equations for mass prediction, we used measurement and mass data for extant taxa from Dickison (2007) and Dunning (2007). How we used the data depended on the methodology of the respective study. Dickison (2007) aggregated mass data from palaeognath museum collections as mean species values, but did not report measurements for individual specimens, meaning they could not be used directly in calculating our regressions. However, they provide a reliable benchmark for assessing our regressions. Dunning (2007) amassed a wealth of data on extant species masses from disparate sources, meaning the sample sizes used to calculate the mean mass for an extant species is greater. Using these data, we evaluated our equations in three ways.

We tested the ability of our linear models, based on femur, tibiotarsus and tarsometatarsus measurements of individuals, to predict the mean species masses of extant taxa reported by Dickison (2007). We did not use humerus length as these data are not reported by Dickison (2007). For the three hind limb measurements, we performed a linear regression between these values, and used the r^2 values as an indicator of predictive power (Fig. 1). We compare our results against the r^2 values when equations from several previous studies (Cubo and Casinos, 1997; Field et al., 2013) were used with the same measurement data. These previous studies used avian data not limited to palaeognaths or did not include palaeognaths, respectively (Table S3).

Table 1
Equations for predicting body mass from this study. n is the number of measurements used for the prediction, r^2 is the proportion of the variation explained. In the equations y is body mass in kilograms and x is the measurement in millimeters. Specimen weight and species weight refer to the source of the weight data used to calculate the regression. All of the equations were estimated to be significant at the 0.001 level.

Measurement	n	r^2	Specimen weight	Species weight
Femur length	15	0.99	$\log(y) = -13.457 + 3.169 \cdot \log(x)$	$-14.013 + 3.299 \cdot \log(x)$
Tibiotarsus length	13	0.99	$\log(y) = -12.507 + 2.712 \cdot \log(x)$	$-12.867 + 2.787 \cdot \log(x)$
Tarsometatarsus length	8	0.99	$\log(y) = -10.111 + 2.415 \cdot \log(x)$	$-9.809 + 2.333 \cdot \log(x)$
Humerus length	10	0.89	$\log(y) = -10.582 + 2.548 \cdot \log(x)$	$-11.190 + 2.694 \cdot \log(x)$

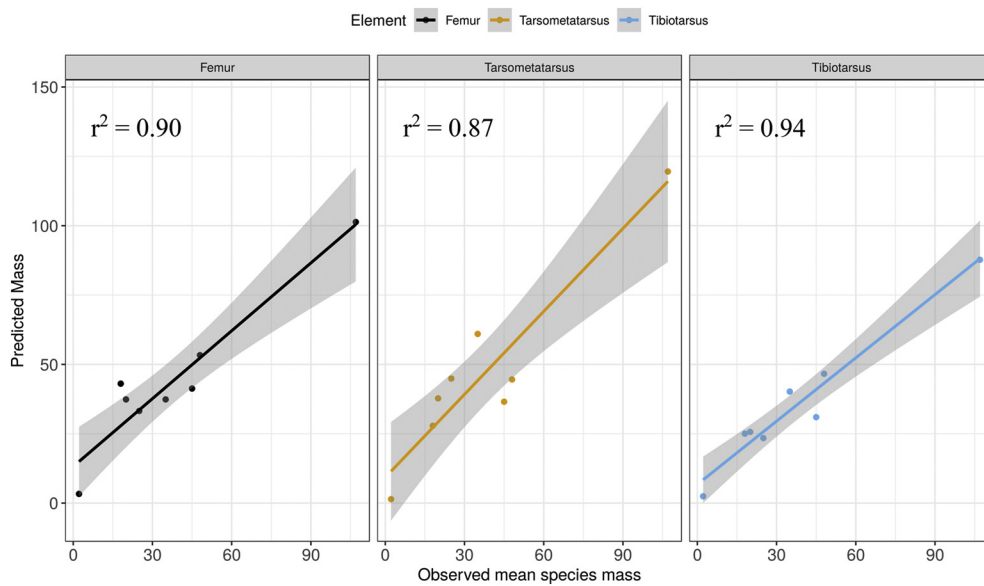


Fig. 1. Estimated predictive power of the linear models derived in this study. Predictive power was calculated by comparing the masses predicted from our equations using the measurements in [Dickison \(2007\)](#) against mean species masses from [Dickison \(2007\)](#). Here we report the goodness of fit between the observed and predicted values.

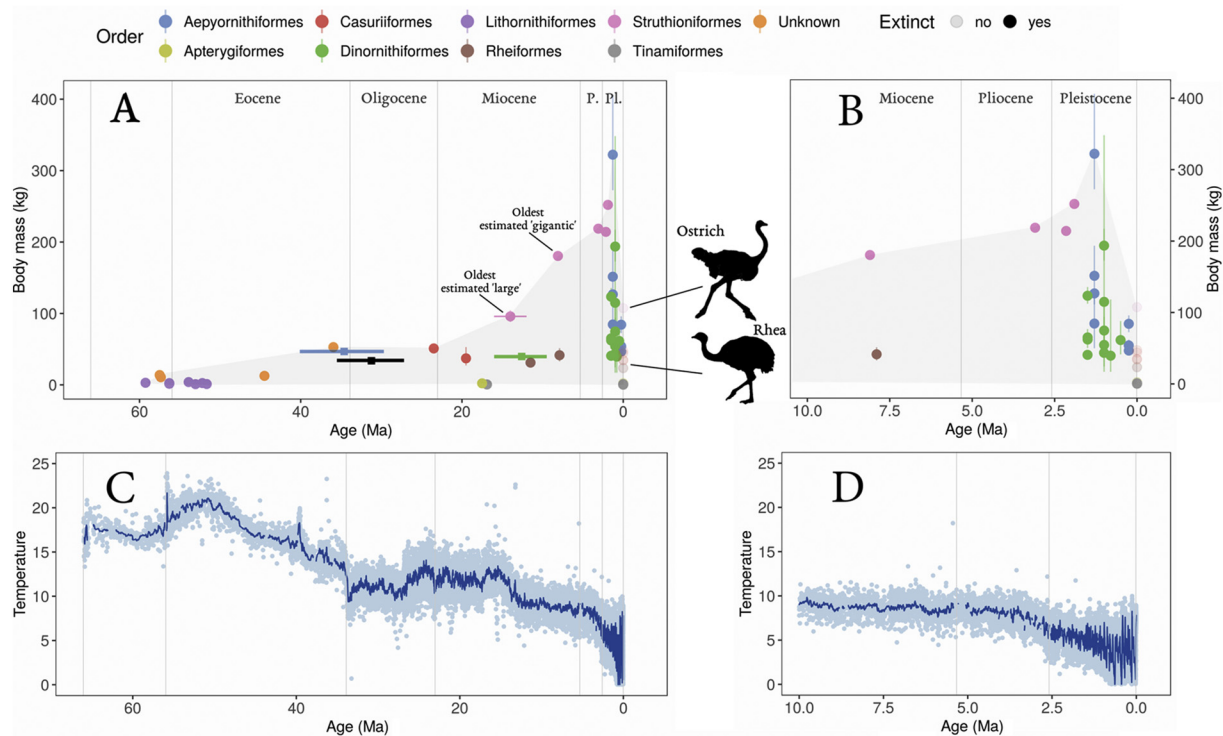


Fig. 2. The age and estimated masses of 40 extinct and 51 extant Palaeognathae taxa, compared to temporal changes in global climate ([Friedrich et al., 2012](#)). A) Temporal distribution of the masses of all taxa in the study. Dots shown mean mass estimates and bars, where present, the range in mass estimates. Squares and horizontal lines show the mean and 95% HPD molecular crown age estimates from [Yonezawa et al. \(2017\)](#) for three clades, with Casuariiformes shown in black. [Mitchell et al. \(2014\)](#) estimate the moa crown at 5.5–10.1 Ma, the elephant bird crown at 11.3–24 Ma, and the Casuariiformes crown at 25–30.1 Ma. The y intercepts for the lines is the minimum estimated or observed mass for the respective clade. Highlighted are two extant species: rhea (23 kg) and ostrich, the heaviest extant palaeognath species (111 kg). B) Distribution of body masses of taxa only within the last ten million years. C) Changes in global temperature over the last 66 million years ([Friedrich et al., 2012](#)). D) Changes in global climate over the last ten million years ([Friedrich et al., 2012](#)).

Next, we asked if the regressions we calculated from individual measurements were significantly different from those calculated using the species mean values of [Dunning \(2007\)](#). Finally, to see how the estimated masses for extinct taxa compare among our equations and those of previous studies, and whether they change the observed trend ([Fig. 2](#)), we compared estimated masses using equations from [Prange et al. \(1979\)](#), [Maloiy et al. \(1979\)](#), [Cubo and Casinos \(1997\)](#), and [Dickison \(2007\)](#) and the same measurement data ([Fig. 3](#)).

In combination with specific mass estimates, we categorized extant and extinct taxa into discrete body mass categories. Placing taxa into body mass ranges helps take into account uncertainty in estimated mass variation and variation due to sexual dimorphism ([Bunce et al., 2003](#); [Huynen et al., 2003](#); [Olson and Turvey, 2013](#)). It further allows specimens which lack preserved material germane to inclusion in allometric analyses (e.g. cranial fragments, pedal phalanges, synsacrum) to be assessed to these general categories. We defined four mass categories

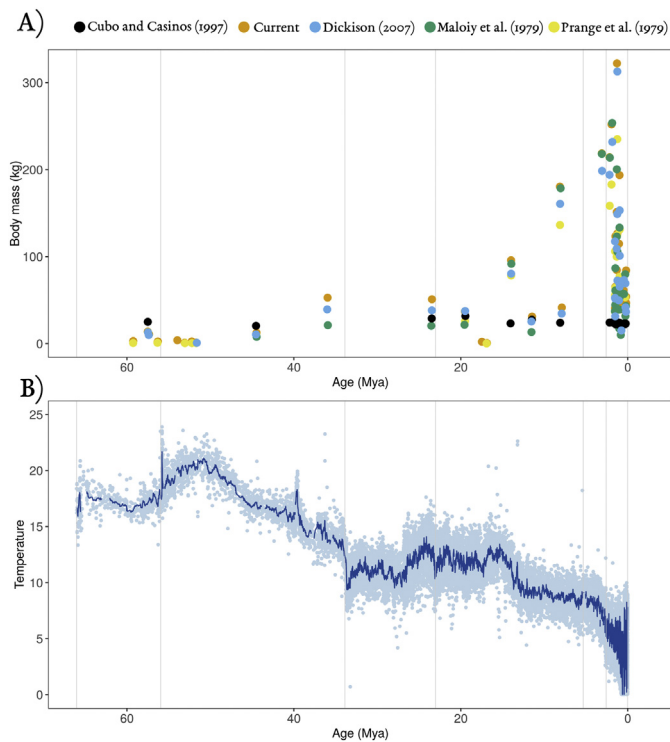


Fig. 3. Comparison of trends in body size over time using different linear models. A) Temporal distribution of species masses using models derived in previous studies compared to the models from the current study. B) Changes in global temperature over the last 66 million years (Friedrich et al., 2012).

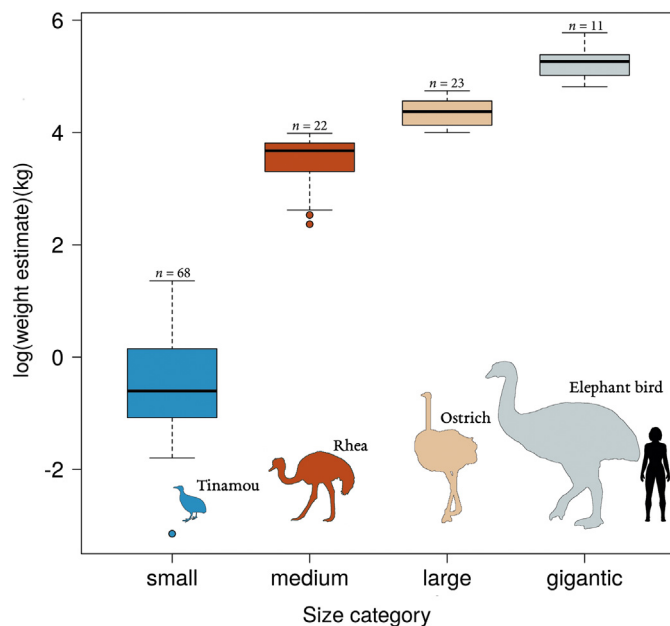


Fig. 4. Distribution of estimated and measured body sizes by the discrete categories of avian mass used in this study. Legend shows example taxa from each size category drawn approximately to scale. *n* is the number of species in each category including those for which a specific mass was not available.

that were of approximately uniform size given the distribution of the log-transformed data (Fig. 4). The categories, in log(kg), were small (< 2.20, 9 kg), medium (2.21–4.01, 9.1–55 kg), large (4.02–4.75, 56–116 kg), and gigantic (> 4.76, 117 kg with a maximum of 5.78, 324 kg, Fig. 4, Table S1). In total we categorized 23 extinct species without specific mass estimates (Table S1).

The number of taxa in the ‘small’ weight category (68) far exceeded the numbers seen in ‘gigantic’ (11), ‘large’ (23), and medium (22) categories (Fig. 4). A predominance of ‘small’ taxa is due to the higher relative diversity of extant tinamous (47 species) and the distribution of masses of extinct taxa (Fig. 2). Three taxa in the ‘gigantic’ category are known only from limited material and categorized without directly estimating mass here: *Struthio pannonicus*, *S. linxiaensis*, and *S. novorossicus*. *S. pannonicus* was categorized on the size of its pedal phalanges (Sauer, 1979), *S. linxiaensis* on the relative size of the pelvis (Hou et al., 2005), and *S. novorossicus* on the dimensions of the distal end of its tarsometatarsus (Boev and Spassov, 2009). *S. novorossicus* is the oldest species from the ‘gigantic’ category (9.0–5.3 Ma; Boev and Spassov, 2009). The ‘large’ mass category had the largest number of species assigned to it without a specific mass estimate (12 taxa, Table S1). This was due to a large number of extinct ostrich species which lacked preserved skeletal material from which a mass could be estimated from preserved limb lengths.

We evaluated the robustness of our recovered temporal trends to potential sampling deficits first by assessing the effect of using the estimated timing of crown subclade origin based on recent timetrees from molecular sequence data (Mitchell et al., 2014; Yonezawa et al., 2017). These dates are older than the earliest fossils from these clades. Specifically, we plotted, to the 95% confidence age interval estimated by Yonezawa et al. (2017), size estimates for the moa and elephant bird crown clades (Fig. 2). We used as the smallest observed size in these crowns (Table S1) for the minimum ancestral value; The hypothesis that these clades independently gained large size (Baker et al., 2005, 2014; Mitchell et al., 2014; Grealy et al., 2017; Yonezawa et al., 2017) predicts the largest observed values are derived. These divergence dating estimates were compared to evaluate potential effects of underestimating the timing of crown subclade origin on our inferred temporal trends in body mass.

Hypotheses about temporal changes in body size may be compromised if species are missing from the fossil record, and the fossil record of Palaeognathae is sparse. In this study, we use two approaches to estimating sampling probability. First, we use the True Richness estimated using a Poisson Sampling model (TRiPS) technique of Starrfelt and Liow (2016). TRiPS incorporates the number of observations of different taxa in the fossil record over a specified period of time to determine both sampling biases and approximate true species richness (Starrfelt and Liow, 2016). We performed this analysis using the online portal <https://starrfelt.shinyapps.io/TRiPS/>, with the analysis performed on January 18th, 2019, specifying a maximum number of occurrences downloaded of 5 million. We supported this analysis using PyRate (Silvestro et al., 2014a, 2014b), specifying a time-variable Poisson process plus gamma model, which allows both temporal and across-lineages variation in preservation rates. We downloaded data from the Paleobiology Database for these analyses on January 21st, 2019, and calculated that 1023 out of the 2990 unique species names were extant species, required for the PyRate analysis. We ran the PyRate analysis for 10 million generations. The values output from PyRate are not probabilities, i.e. fall between 0 and 1. Rather, they require the comparison of the estimated rates among all sampled time intervals. Specifically, a significant difference in preservation rates can be assumed between time intervals if the 95% confidence intervals do not overlap (Silvestro et al., 2015).

3. Results

There was high predictive power across all of the measurements tested here for body mass, a result consistent with prior studies (Campbell and Marcus, 1992; Cubo and Casinos, 1997; Field et al., 2013; Campione et al., 2014). Lengths of femora, tibiotarsi, and tarsometatarsi all had coefficient of determination (r^2) values of 0.99, whereas humerus length was 0.89 (Table 1). Fit for palaeognath species mean data from Dickison (2007) was significantly better for the new

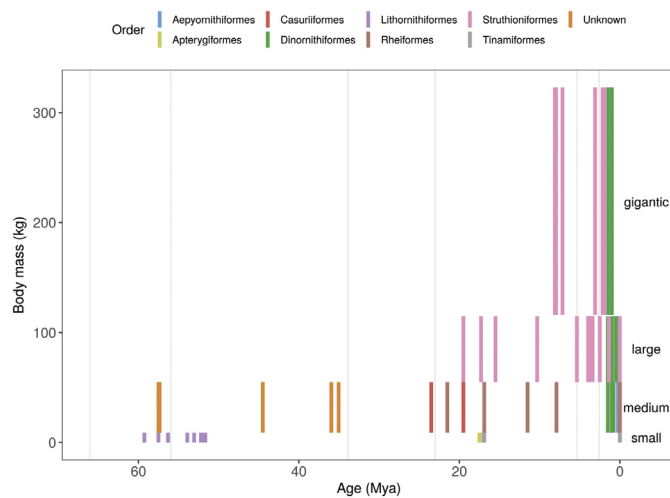


Fig. 5. Temporal distribution of mass categories. Line heights represent the range in mass covered by each category (data for individual species is provided in Table S1).

regressions than for recent equations based on larger avian datasets but excluding palaeognaths (Field et al., 2013; r^2 : 0.46–0.58) and for the most recent palaeognath focused study (Cubo and Casinos, 1997; r^2 : 0.44–0.55) (Fig. 1, Table S3). Regressions using palaeognath species mean data from Dunning (2007) were not significantly different from those based on individual measurements (Table 1). Thus, use of species means in future analyses may be justified.

There was a pronounced temporal trend of increasing body size through time (Fig. 2). The oldest ‘large’ species, *Struthio coppensi* (Mourer-Chauviré et al., 1996), is from the early Miocene (Fig. 5). The largest taxa are concentrated within the last 9 Ma. *S. novorossicus* is the oldest species from the ‘gigantic’ category (9.0–5.3 Ma; Boev and Spassov, 2009). The largest body mass estimate was for the Giant Elephant-bird, *Aepyornis maximus*, with a mean mass exceeding 300 kg, but estimates ranged between 272 kg and 406 kg depending on the hind limb measurement used. Conversely, the smallest mass estimate was for *Crypturellus reai*, an extinct species of tinamou from Argentina (Chandler, 2012), with a predicted mass of approximately 0.5 kg. This trend is robust to estimation of body mass values using previously proposed scaling equations (Fig. 3). Indeed, our estimated pre-Miocene body masses are slightly higher, not lower, than those using these previous equations.

The oldest preserved fossils of moas (Dinornithiformes) and elephant birds (Aepyornithiformes), two clades containing some of the

largest palaeognath taxa, are notably younger than their estimated crown molecular divergence estimates (Fig. 2A). Here, we plotted divergence estimates from Yonezawa et al. (2017) as they are older than Mitchell et al. (2014), and were therefore more likely to invalidate our hypothesis of late Cenozoic change in body size. Specifically, Yonezawa et al. (2017) estimated the moa crown age at 9.7–15.8 Ma while the oldest fossil material is unlikely to be older than 2.5 Ma; Worthy et al., 1991). Elephant bird crown age was estimated at 29.9–39.9 Ma and that of Casuariiformes at 27.4–35.3 Ma (Yonezawa et al., 2017). Mitchell et al. (2014) estimate the moa crown at 5.5–10.1 Ma, the elephant bird crown at 11.3–24 Ma, and the Casuariiformes crown at 25–30.1 Ma. Despite this difference in estimated clade origin, if the minimum recovered mass for any species within the respective group is plotted at the age of the crown divergence estimates these data fit with the mass trend described (Fig. 2A). Large, ostrich-sized or heavier remain uniquely Neogene in age. Rhea (‘medium’) and smaller taxa are known earlier (Fig. 2).

Estimating the probability of sampling extinct taxa in the fossil record is challenging. Sampling probabilities estimated using TRiPS shows peaks of relatively high sampling probabilities (i.e. > 0.6) in between time periods of low sampling probability (lower than 0.3). Peaks of high sampling probability of 0.69 and 0.68 are estimated for age intervals of 13.82–15.97 Ma and 15.97–20.44 Ma respectively, considerably older than the oldest known ‘gigantic’ taxa. By contrast, PyRate analyses suggest an extremely low probability of having sampled any taxa older than the Pliocene (5.33 Ma, Fig. 6). Both the records used and the model estimates deserve further refinement for Aves.

4. Discussion

Earlier hypotheses based assumptions of large body size on inferred vicariance of flightless cursorial taxa in the Mesozoic (Cracraft, 1973, 1974). Although flightless taxa appear early, volant palaeognath taxa have a known fossil record throughout the same interval (Fig. 2). More recent research has used the presence of palaeognath taxa from the Paleocene (for example, the flightless *Diogenornis fragilis*) to suggest that trend toward large body sizes generally began early in the clade (Yonezawa et al., 2017). Our results offer little support for this hypothesis. *Diogenornis fragilis* is estimated to be approximately 11 kg, smaller than a rhea (Table S1). Although it is heavier than the largest volant taxa estimated here – *Paracathartes howardae* at 3.9 kg – it is dramatically smaller than the large and gigantic groups, which range from 55 kg to 323 kg, for *Aepyornis maximus*. Our results suggest that species did not reach 100 kg, the size of a modern ostrich, until the Miocene, < 20 million years ago (Fig. 2), and known fossil palaeognaths exceeding 200 kg do not appear until the Quaternary (Fig. 2). Our results are robust to use of equations from different studies (Fig. 3).

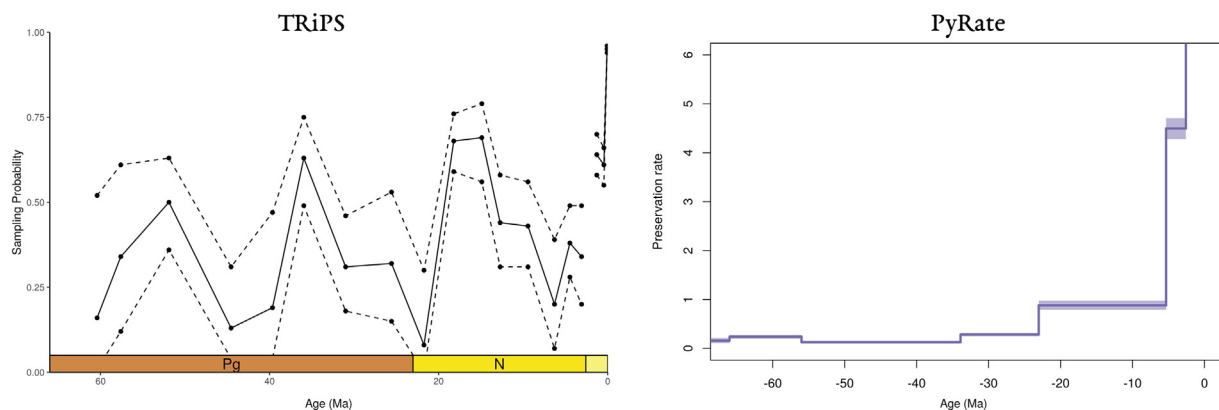


Fig. 6. Comparison of the two procedures for estimating sampling probabilities of extinct taxa. True Richness estimated using a Poisson Sampling model (TRiPS) plot shows maximum likelihood estimate (solid line) with upper and lower confidence intervals (dashed lines). Repeating the PyRate analysis downloading only palaeognath species from the Paleobiology Database produced a similar pattern.

Our hypothesis of Neogene rather than Mesozoic body mass increase recovered in Palaeognathae would be compromised if ages of the oldest observed 'large' species are a severe underestimate. Limited palaeognath sampling in key regions such as Africa, Madagascar and New Zealand is well known (Fig. S2) and may influence our results. PyRate results suggest an extremely low sampling rate for avian taxa older than the Pliocene (Fig. 6). Conversely, estimated sampling probabilities using TRIPS suggests a peaky distribution, with some age brackets, including pre Miocene intervals have a relatively high sampling probability (> 0.6). However, both of these methods only estimate the likelihood of sampling any species, and not whether the species we observe are a biased representation of body mass through time. Nevertheless, it could be expected that, within the same preservational environment, palaeognath taxa should have a higher sampling probability than the average for Aves given that large-bodied taxa are generally more readily preserved (Plotnick et al., 2016; Gardner et al., 2016). At the same time, there is a temporal gap in preserved palaeognath material and molecular divergence estimates. For example, the oldest crown subclade estimates from Yonezawa et al. (2017) place the mean crown age for elephant birds close to 35 Ma, that for Casuariiformes at ~31 Ma with Moas around ~12 Ma. If these earlier dates for minimum body masses values for these subclades are correct, the first smaller increases would have occurred close to the Eocene/Oligocene boundary. Other divergence dates suggest all of these clades are younger still (elephant bird crown 11.3–24 Ma, Casuariiformes crown at 25–30.1 Ma and moa crown, 5.5–10.1 Ma; Mitchell et al., 2014).

Large and giant body masses seen in Palaeognathae also evolved in at least two other flightless terrestrial clades: Gastornithiformes (proposed to be related to waterbirds and game birds) and Cariamiformes (Seriemas, reviewed by Mayr, 2009). However, only Gastornithiformes evolved sizes comparable to that seen in Palaeognathae in the Paleogene. Cariamiformes show their earliest evidence of large body sizes in the Miocene. That there are known Paleogene records for Gastornithiformes indicates that there is not simply a preservation bias against large bodied taxa. Although we believe recent mass estimates for some of these taxa reported by Worthy et al. (2017) to be over-estimates (see Fig. S3), and some subclades appear to increase significantly in body size in the Miocene (e.g., Phorusrachidae), other early Paleogene species were undoubtedly large (Table 2, see also Fig. 4 of Worthy et al., 2017).

Variation in body mass and its relationship with climate change is has been commonly investigated in mammals than birds (e.g., Smith et al., 2010; Lovegrove and Mowoe, 2013; Baker et al., 2015; Huang et al., 2017; though see Olson et al., 2009; Smith, 2016). Incorporating divergence date estimates for palaeognath subclades puts loss of flight and body size increases around the Eocene/Oligocene boundary, a period of pronounced global cooling (Friedrich et al., 2012). Only fossil first occurrences for ostriches predate the onset of Miocene cooling around 14 Ma (Holbourn et al., 2014; Shevenell, 2016; Song et al., 2018). *Struthio coppensi*, dates to approximately 20 Ma, before the Mid-Miocene Thermal Optimum and subsequent cooling (Friedrich et al., 2012). It is the oldest palaeognath species in the 'large' category. Material for this species is fragmentary, however. A more precise weight estimate is possible for the large *Struthio brachydactylus* (Fig. 2; Table S1). However the precise age of this species is unclear; different

estimates for the age of the fossiliferous units age range from 12 to 16 Ma (Janoo and Sen, 1998; Mayada et al., 2014; Čerňanský et al., 2017). The onset of Miocene cooling is more confidently estimated between 14 and 14.7 Ma (Holbourn et al., 2014; Shevenell, 2016; Song et al., 2018). The degree of Miocene cooling was dramatic, with evidence for extensive Antarctic ice sheets by 13.8 Ma (Holbourn et al., 2014; Pierce et al., 2017). All other records of the heaviest species are confined to the coolest period of the Cenozoic, particularly the last 9 million years (Fig. 2). We propose that body size increases in palaeognath subclades are more likely driven by landscape induced changes related to Eocene/Oligocene boundary and later Neogene cooling.

Cenozoic landscape changes include by a transition from woodland to grassland dominated ecosystems by the late Miocene (Retallack, 2001; Osborne, 2008; Strömberg, 2011). This change has been proposed to induce a shift in palaeognath diet to include lower quality forage such as roots, leaves, and seeds (Baker et al., 2005; Clarke et al., 2006; Attard et al., 2016) as seen in extant ratites. Lower quality forage necessitates longer retention time of food, therefore this dietary shift may have driven larger body sizes to enable longer gut lengths and greater digestive efficiency (Demment and Van Soest, 1985; Illius and Gordon, 1992; Janis et al., 2002). Increasing body size also allows organisms to migrate more easily between resource patches (Saarinen et al., 2014). In ratites, this locomotory shift is demonstrated in extinct ostriches which, as they increased in size through the Neogene and Quaternary, showed a general decrease in the angle between the longitudinal axis of the tarsometatarsus and their second toe (trochlea IV, Koufos et al., 2016). A narrower angle reduces the separation between the two pedal digits causing them to act almost as a single digit, with pedal digit reduction suggesting a preference for open habitats as it is often linked with increased locomotor efficiency (Schaller et al., 2011; McHorse et al., 2017). Finally, cooler climates drive selection of larger body sizes to allow more efficient thermoregulation by decreasing an organisms' surface to volume ratio (Glazier, 2010). These selective forces are not unique to avian taxa and have been extensively characterized in mammalian taxa (Smith et al., 2010).

Competitive release on islands from mammalian taxa has been suggested to be important in driving body size extremes in both the Malagasy elephant birds and New Zealand moas (Meiri et al., 2010, references therein). However, island dwelling alone cannot explain increasing body sizes across ratites as the continental radiation of extinct ostriches reached equally large sizes. The range in sizes of extinct members of *Struthio* fall easily within the range seen in the Malagasy elephant birds (Table 3), and the mean weight estimates of three taxa (*S. oldowayi*, 252 kg, *S. transcaucasicus*, 219 kg, and *S. dmanisensis*, 215 kg) exceed the estimate of the heaviest Moa (*Dinornis robustus*, 194 kg, Table S1). Instead, the temporal congruence with which these separate groups gained their large sizes is more suggestive of potential climatic driven effects. Isolation timing varies for the island groups (New Zealand, Madagascar, South America, Australia), while all become isolated much earlier by the Late Cretaceous/earliest Cenozoic (e.g., Müller et al., 2016).

Further work comparing support for the timing of body size increases in Aves are needed. Why Palaeognathae and Cariamiformes do not have a fossil record consistent with earlier Paleogene body mass increases seen within gastornithiform birds is unclear. However, morphology, ecology and distribution differ markedly among these groups. Cariamiform taxa, which also show Neogene increases in body size, are predatory. By contrast, although the large bodied gastornithiforms are to be primarily herbivorous (e.g., Angst et al., 2014), they have a high beaked rostral morphology unlike that known in any palaeognath. Incorporating extinct taxa may change the observed pattern and inferred process of trait evolution (Slater et al., 2012; Hunt and Slater, 2016; Schnitzler et al., 2017), and inference of ancestral body mass may require consideration of shifts among clade specific scaling relationships. Synoptic consideration of temporal trends in body mass across diverse

Table 2

Exemplar masses of large flightless birds outside of Palaeognathae from the Cenozoic. Masses were estimated using linear models derived in this study.

Clade	Species	Age (Ma)	Mass (kg)
Gastornithiformes	<i>Gastornis gigantea</i>	50.3–55.8	137.0
	<i>Gastornis parisiensis</i>	48.0–59.2	52.3
	<i>Dromornis stirtoni</i>	5.3–11.6	263.0
Cariamiformes	<i>Brontornis burmeisteri</i>	17.5–16.3	247.4

Table 3
Comparison of a selection femur lengths between the largest members of *Struthio* and members of *Aepyornis*.

Clade	Species	Femur length (mm)	Reference
Struthioniformes	<i>Struthio karatheodori</i>	360	Burchak-Abramovich and Vekua (1990)
	<i>Struthio dmanisensis</i>	380	Burchak-Abramovich and Vekua (1990)
	<i>Struthio oldowayi</i>	400	Burchak-Abramovich and Vekua (1990)
Aepyornithiformes	<i>Aepyornis maximus</i>	465	Gatesy (1991)
	<i>Aepyornis maximus</i>	440	Amadon (1947)
	<i>Aepyornis medius</i>	368	Gatesy (1991)
	<i>Aepyornis gracilis</i>	322	Gatesy (1991)

clades of terrestrial vertebrates could identify potential causal factors in their varied responses to shifts in global climate. Because body mass is linked to other key aspects of life history (Illius and Gordon, 1992; Glazier, 2010; Lovegrove and Mowoe, 2013; Hirt et al., 2017), selection on one or more of these linked attributes should be considered alongside potential direct selection on body mass itself in these taxa as well as in Palaeognathae.

5. Conclusions

Understanding the pattern and timing of body size evolution has numerous paleoecological implications due to its association with multiple aspects of life history. Here, we test whether large body sizes seen in Palaeognathae arose early as predicted by previous hypotheses of terrestrial vicariance explaining their distribution. Predicting the masses of extinct taxa using predictive equations derived from extant species, in combination with discrete categories of mass, we find little support for large body sizes arising before the Neogene. Initial body size increases may occur as early as the Eocene/Oligocene boundary. However, the heaviest taxa, those exceeding 120 kg, are only found in the last 9 million years. We found these trends, and the appearance of large body sizes in the late Cenozoic ice house Earth to be unaffected by the specific equation used for predicting the masses of extinct taxa, and by the discrepancies in age between the oldest preserved material and molecular divergence estimates for each palaeognath subclade.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.palaeo.2019.05.046>.

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