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Little is known about the olfactory capabilities of extinct basal (non-neornithine) birds or the evolutionary changes in olfaction that occurred from non-avian theropods through modern birds. Although modern birds are known to have diverse olfactory capabilities, olfaction is generally considered to have declined during avian evolution as visual and vestibular sensory enhancements occurred in association with flight. To test the hypothesis that olfaction diminished through avian evolution, we assessed relative olfactory bulb size, here used as a neuroanatomical proxy for olfactory capabilities, in 157 species of non-avian theropods, fossil birds and living birds. We show that relative olfactory bulb size increased during non-avian maniraptoriform evolution, remained stable across the non-avian theropod/bird transition, and increased during basal bird and early neornithine evolution. From early neornithines through a major part of neornithine evolution, the relative size of the olfactory bulbs remained stable before decreasing in derived neoavian clades. Our results show that, rather than decreasing, the importance of olfaction actually increased during early bird evolution, representing a previously unrecognized sensory enhancement. The relatively larger olfactory bulbs of earliest neornithines, compared with those of basal birds, may have endowed neornithines with improved olfaction for more effective foraging or navigation skills, which in turn may have been a factor allowing them to survive the end-Cretaceous mass extinction.

Keywords: theropoda; Aves; olfactory bulb; *Archaeopteryx*; basal birds; olfactory ratio

1. INTRODUCTION

Several anatomical, physiological and behavioural traits of living birds are known to have first evolved among non-avian theropods [1–14]. However, little is known about the extent to which birds inherited their sensory modalities from their non-avian theropod ancestors. Aspects of visual, auditory and vestibular senses have been investigated in some extinct birds in order to understand the sensory changes associated with the origin of flight during the non-avian theropod/bird transition [5,15–17]. In comparison, changes in olfaction (i.e. sense of smell) have received limited attention, which may be due, in part, to the preconceived notion that olfaction was a declining sensory modality during bird evolution [18–21] and to the historical misconception that birds have a poor sense of smell [22]. Birds are now known to have a wide range of olfactory capabilities, which are used for a variety of purposes, such as foraging, orientation and social interactions [22–24].

Among birds and extinct theropods, investigations of the olfactory system have emphasized the role of the olfactory bulbs, anterior projections of the forebrain, in olfaction. The relative size of the olfactory bulbs has been suggested to be related to the olfactory capabilities of living birds [25–29] and extinct theropods [5,16,30–33]. A recent study of olfactory bulb size in non-avian theropods and *Archaeopteryx* led to the inference that the oldest known bird had olfactory capabilities typical of a similar-sized non-avian theropod [33]. Although this suggests that olfaction remained unchanged during the non-avian theropod/bird transition [33], a large-scale study of relative olfactory bulb size in extinct and extant theropods is necessary to shed light on the hypothesis that olfaction declined progressively through avian evolution. Here, we present the most inclusive study to date of early avian olfactory evolution by analysing relative olfactory bulb size in 157 species of non-avian theropods, fossil birds and living birds, while taking into consideration the effects of body mass and phylogeny, in order to assess changes in olfaction through theropod evolution.

2. OLFACTORY BULB SIZE AND OLFACTORY CAPABILITIES

Olfactory bulb size has long been suggested to be correlated with olfactory capabilities in vertebrates [34] based on the well-established principle of proper mass [35], which states that the relative size of a brain region reflects the relative importance of the neural function of that region to the biology of the animal. Various studies have demonstrated that olfactory bulb size is correlated with olfactory ability in birds and mammals [36–38]. The relationship between olfactory bulb size and olfactory ability may be related to: (i) the number and size of mitral cells in the bulb [29,39]; (ii) the number of glomeruli in the bulb [40]; and (iii) the number of olfactory receptor genes [41,42].

In birds, relative olfactory bulb size has long been considered a neuroanatomical proxy for olfactory capabilities [25–27,37,41,42] and is quantified in a metric termed the olfactory ratio, defined as the ratio between the greatest linear dimension of the bulb and the greatest linear dimension of the cerebral hemispheres, regardless of their orientation [25,27]. Recent studies have supported the validity of this proxy because olfactory ratios are: (i) positively correlated with the number of olfactory receptor genes (i.e. the larger the olfactory ratio, the greater the number of olfactory receptor genes) [41,42], and (ii) negatively correlated with the odour detection threshold (lowest detectable odorant concentration) across bird orders [37], both suggesting that larger ratios indicate better olfactory capabilities. Given these correlations, olfactory ratios are an appropriate measure of the relative importance of olfaction through large-scale evolution of non-avian and avian theropods. Furthermore, defining the olfactory ratio in terms of the longest linear dimensions of the olfactory bulbs and cerebral hemispheres regardless of orientation, rather than the measurement of a standardized orientation (e.g. rostrocaudal diameter), allows for the documented changes in shape or orientation of these brain components that occurred during theropod evolution [16,20,31,35,43,44] to be taken into consideration. Thus, the olfactory ratio is a useful comparative statistic to reflect the relative importance of olfaction in comparison with other sensory modalities, even when, for example, the cerebral hemispheres were undergoing substantial evolution throughout the non-avian theropod/bird transition.

3. MATERIAL AND METHODS

(a) *Olfactory ratio calculations*

Olfactory ratios, calculated from the greatest linear measurements of the olfactory bulb and cerebral hemisphere, have been the standard measure of the relative size of these features in extant birds [25,27]. Although complex parameters (e.g. mass or volume of brain components) may seem to be the more appropriate measurements for size, single linear measurements are often used to estimate complex parameters that are otherwise not readily obtainable [45–50]. Furthermore, for fossil specimens, linear measurements of endocranial features are often the most appropriate, if not the only, measurement possible because of incomplete preservation or ossification of bones (e.g. the sphenethmoid [51]).

The olfactory ratios of 20 species of non-avian theropod dinosaurs representing eight families/superfamilies, seven species of fossil birds representing six orders, and 130 species of living birds representing 26 orders were considered in this study (see the electronic supplementary material). Olfactory ratios were calculated as the ratio between the longest diameter of the olfactory bulb and the longest diameter of the cerebral hemisphere, regardless of orientation, multiplied by 100 [27,33] (figure 1).

Olfactory ratios for extant and extinct birds were derived from the literature and from computed tomographic (CT) data of skull material. The olfactory ratios for most living birds studied were obtained from the literature and are based on linear measurements of soft tissue [28,52]. However, the olfactory ratios for two species (*Struthio camelus* and *Eudromia elegans*) were obtained from virtual endocasts
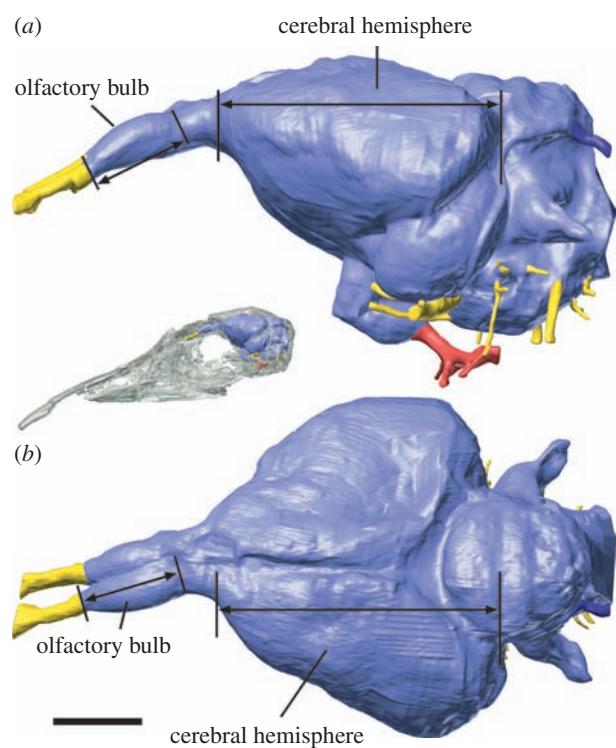

Figure 1. Virtual brain endocast of *Lithornis plebius*, (a) in left lateral and (b) dorsal view, showing the location of the olfactory bulbs and cerebral hemispheres. The greatest linear dimension of the olfactory bulb and cerebral hemisphere, regardless of orientation, was used to calculate olfactory ratios (only rostrocaudal dimensions illustrated). Red features represent blood vessels, yellow features represent cranial nerves. Scale bar, 5 mm. Inset (not to scale) shows the position of the brain endocast within the skull of *Lithornis promiscuus*.

(i.e. a representation of the endocranial cavity produced using CT data; see below). The fact that endocast-derived and soft tissue-derived olfactory ratios are comparable (see the electronic supplementary material) and that endocranial volume and brain mass are highly correlated in birds [53] supports the inclusion of virtual endocast data in our study. Olfactory ratios for extinct birds were derived from virtual endocasts, except for *Confuciusornis sanctus*, which was calculated from measurements made on a CT-scanned skull using the software AMIRA v. 5.3, and *Archaeopteryx lithographica*, which was obtained from the literature [33]. Because the posterior portion of the cerebral hemispheres in the *Hesperornis* endocast is crushed, both minimum and maximum cerebral hemisphere lengths were estimated, resulting in a maximum and a minimum olfactory ratio. The mean of these two values was used for ancestral state reconstructions. The Cretaceous bird *Cerebavis cenomanica* [5] was not included in our study owing to uncertainties related to the dimensions of key endocranial features and to its taxonomic affinity.

Olfactory ratios of most non-avian theropod species were obtained from the literature [33]. Some published non-avian theropod specimens (e.g. *Gorgosaurus*, *Albertosaurus*, subadult *Tyrannosaurus rex*) were excluded owing to uncertainties in their olfactory ratios [33]. We augmented the dataset from Zelenitsky *et al.* [33] with olfactory ratios of additional non-avian theropod species (*Deinonychus antirrhopus* and *Tsaagan mangas*) and additional specimens of the previously studied species (*Allosaurus fragilis*, *Tyrannosaurus rex* and *Tarbosaurus*

bataar); all new olfactory ratios are based on virtual endocasts. Mean olfactory ratios for each non-avian theropod species were calculated prior to bivariate analysis and ancestral state reconstruction.

All virtual endocasts used in this study were produced using CT data in the WitmerLab at the Ohio University College of Osteopathic Medicine following a previously published method [54]. To ensure consistency in structure identification and to eliminate inter-observer error in the measurement of the olfactory bulb and cerebral hemisphere dimensions, all measurements taken on virtual endocasts and on fossil specimens were made by a single individual (F.T.).

(b) Body mass estimates

Body masses for extant bird species are calculated as the mean of mean female and mean male body masses published in Dunning [55] (see the electronic supplementary material).

Body masses for fossil birds were estimated from regressions for living birds with comparable lifestyles or body plans (electronic supplementary material). Body masses for volant fossil birds (except *Archaeopteryx*) were estimated from a least-squares regression of log-transformed humerus length versus body mass (log(body mass, in kilogram) = $0.4822 \times$ log(humerus length, in millimetre) + 2.0722, $r^2 = 0.97$) derived from published data for 17 living volant birds [56]. Body mass for the non-volant diver *Hesperornis* was estimated from a published regression of femur length versus body mass for extant diving birds [57].

Body mass estimates for *Archaeopteryx* and non-avian theropod species, except *Deinonychus* and *Tsaagan*, were obtained from the literature [33] (see the electronic supplementary material). The body mass estimate for *Deinonychus* is based on a three-dimensional virtual model [58], whereas that of the dromaeosaurid *Tsaagan* is considered equivalent to the dromaeosaurid *Velociraptor* owing to the similarity in skull size.

(c) Regression analysis

A log-transformed bivariate plot of olfactory ratio versus body mass was produced for non-avian theropods and birds in order to assess the influence of body size on olfactory ratio. Least-squares regressions, rather than reduced major axis regressions, were used to quantify the relationship between olfactory ratio and body mass because these regressions are considered more accurate when plotting a ratio as a function of a direct measurement [59]. The influence of phylogenetic relationships among taxa was accounted for by producing phylogenetically corrected regressions through the method of phylogenetically independent contrasts [60] using the PDAP module v. 1.14 [61] of the software MESQUITE v. 2.72 [62] (see the electronic supplementary material). It was not possible to determine individual branch lengths for the calculation of phylogenetically independent contrasts owing to the large number of taxa considered, the fact that not all of these species have been subjected to a molecular phylogenetic analysis, and the uncertainty of the divergence time between some taxa. Consequently, the alternative, but equally valid method of assigning a branch length of one was used, which in effect assumes that all evolutionary changes took place during speciation events [63].

(d) Phylogenetic hypotheses

Two recent hypotheses for the high-order phylogenetic relationships of extant neornithines were considered in our analyses, one based on molecular data [64] and one based on morphological data [65]. Each of these high-order phylogenetic hypotheses was combined with several phylogenetic hypotheses below the ordinal level [65–82] to establish the phylogenetic relationships of all 130 extant species considered in this study (see the electronic supplementary material).

Inclusion of extinct birds in our analysis based on the molecular phylogeny [64] was problematic because this phylogeny did not include fossil taxa. Consequently, the phylogenetic position of the extinct birds had to be inferred from previous morphological phylogenetic analyses. The phylogenetic position of *Presbyornis* and basal birds was readily determined using published morphological analyses [83,84]. The phylogenetic placement of the extinct genus *Lithornis*, however, was problematic owing to differences in tree topology between morphological and molecular phylogenies for palaeognaths and because of the variable position of *Lithornis* in morphological phylogenies (i.e. as a basal palaeognath or as the sister taxon to Neornithes). In order to include *Lithornis* in the analysis based on the molecular phylogeny, we used the inter-relationships of palaeognaths and *Lithornis* from the morphological phylogenetic hypothesis of Dyke & Van Tuinen [85].

The phylogenetic relationships among non-avian theropods follow the cladogram compiled from the literature by Zelenitsky *et al.* [33], supplemented by the dromaeosaurid phylogeny of Csiki *et al.* [86].

(e) Ancestral state reconstruction

Changes in relative olfactory bulb size through higher order nodes of theropod (including bird) phylogeny were examined via maximum-parsimony ancestral state reconstructions using MESQUITE v. 2.72 [62]. Ancestral states of olfactory ratios were reconstructed for the phylogeny of Aves (electronic supplementary material). Ancestral states of olfactory ratio residuals (relative to the non-avian theropod regression), rather than of olfactory ratios, were reconstructed for the phylogeny of the non-avian theropod/bird transition in order to take into consideration the influence of body mass on olfactory ratios because a strong correlation exists between these two variables in non-avian theropods [33] (also see §3). This approach permits the comparison of relative olfactory bulb size between early birds and non-avian theropods.

Major changes in olfactory ratios through avian evolution were identified when the reconstructed ancestral state at a given higher order node fell outside of the 95% confidence interval of the mean of the ancestral states for the four preceding higher order nodes.

(f) Statistical analyses

Statistical analyses were conducted with the software PASW Statistics v. 17.0.2 and GRAPHPAD PRISM v. 5.0.

4. RESULTS/DISCUSSION

(a) Comparison of olfactory ratios and olfactory abilities among non-avian theropods and birds

A bivariate analysis reveals that a strong positive correlation exists between olfactory ratio and body mass among non-avian theropods ($r^2 = 0.8$, $p < 1.27e - 7$), whereas the data for Aves are uncorrelated ($r^2 = 0.009$, $p = 0.26$) and widely scattered (figure 2). When basal birds are investigated alone, the slope of the regression between olfactory ratio and body mass is not significantly different from zero ($p = 0.4$). These results indicate that olfactory ratios can be compared among avian taxa regardless of body mass differences, whereas the effect
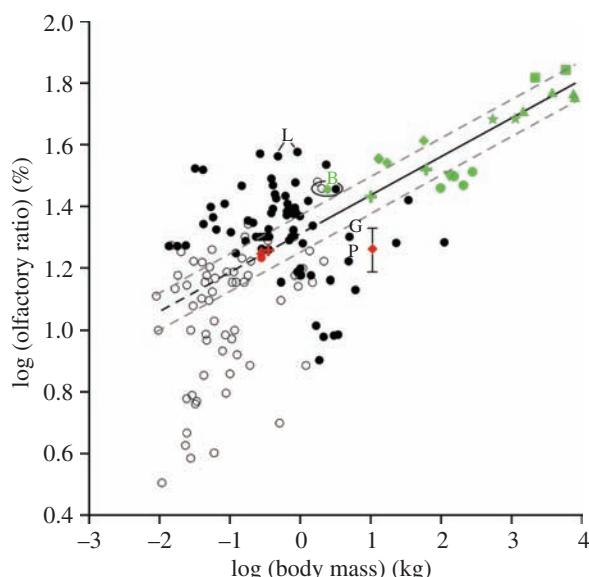
Figure 2. Plot of log-transformed olfactory ratio versus log-transformed body mass in avian and non-avian theropods. No significant correlation is observed between olfactory ratio and body mass among birds when phylogeny is considered ($r^2 = 0.009$, $p = 0.26$). In contrast, a significant positive correlation is observed between olfactory ratio and body mass among non-avian theropods ($r^2 = 0.8$, $p < 1.27e - 7$), indicating that olfactory ratios increase with body mass among non-avian theropods. The non-avian theropod regression (solid black line) and its extrapolation (black dashed line) bisect the distribution of olfactory ratios for birds. The majority of neornithine species basal to the common ancestor of Charadriiformes and Passeriformes have higher olfactory ratios than more derived taxa. Most basal birds fall near the non-avian theropod regression. The fossil diving bird *Hesperornis* plots near the extant divers *Gavia immer* (loon, G) and *Pygoscelis adeliae* (Adelie penguin, P). The error associated with *Hesperornis* reflects the uncertainty of its cerebral hemisphere length (see §3). The dromaeosaurid *Bambiraptor* (B) plots near *Cathartes aura* (turkey vulture, open circle) and *Phoebastria nigripes* (black-footed albatross, solid circle). The extinct palaeognath *Lithornis* (L) has high olfactory ratios. Green diamonds, dromaeosaurids; green squares, tyrannosaurids; green triangles, allosauroids; green stars, ceratosaurs; green circles, ornithomimosaurs; inverted green triangle, *Citipati*; green crosses, *Dilong* and *Troodon*; red circle, *Archaeopteryx*; red triangle, *Confuciusornis*; red cross, *Ichthyornis*; red diamond, *Hesperornis*; black circles, neornithines basal to charadriiform–passeriform common ancestor (based on molecular phylogeny); white circles, neornithines more derived than charadriiform–passeriform common ancestor (based on molecular phylogeny).

of body mass must be taken into consideration when comparing olfactory ratios between non-avian theropods and birds.

The data for Aves are evenly distributed about the non-avian theropod regression with 53.3 per cent of avian species plotting above the regression and 46.7 per cent below it (figure 2). Olfactory ratios of most basal birds (i.e. *Archaeopteryx*, *Confuciusornis*, *Ichthyornis*) fall near the regression line, suggesting that they had olfactory capabilities expected for non-avian theropods of their respective sizes (figure 2). One exception is *Hesperornis*, which had a lower olfactory ratio than that predicted for a non-avian theropod of its size (figure 2), suggestive of weaker olfactory capabilities than a similar-sized non-

avian theropod. Neornithine birds display a greater range of olfactory ratios about the regression line than non-avian theropods or basal birds (figure 2; see residuals in the electronic supplementary material), indicative of a greater diversity of olfactory abilities than their ancestors. At large body sizes (greater than 4.85 kg), neornithines tend to have lower olfactory ratios than predicted for non-avian theropods, whereas at smaller body sizes neornithines are more evenly distributed about the regression (figure 2).

Comparison of neornithine olfactory ratios with those of similar-sized non-avian theropods can elucidate aspects of olfaction and behaviour in these extinct taxa (see the electronic supplementary material). Relative to extant birds of similar size, the small dromaeosaurid *Bambiraptor* has an olfactory ratio similar to that of *Cathartes aura* (turkey vulture) and *Phoebastria nigripes* (black-footed albatross) (figure 2), carnivorous birds with high olfactory ratios (greater than 28%) known to rely heavily on olfactory cues while foraging (i.e. olfactory foraging) [28,87–89]. Given the correlation that exists between high olfactory ratios and olfactory foraging among birds (for statistical test, see the electronic supplementary material), it is possible that *Bambiraptor* also relied considerably on olfaction to locate food, supporting the previous behavioural interpretations made for non-avian theropods with high olfactory ratios [33].

Similarly, inferences can be made about the olfactory capabilities and behaviours of extinct birds through comparison of their olfactory ratios with those of living neornithines. Basal birds had olfactory ratios that are just above average for neornithines (figure 3), but significantly lower than those of olfactory foraging neornithines ($p < 0.004$; see the electronic supplementary material). Consequently, vision must have played a more important role than olfaction while foraging in these taxa. Nevertheless, olfaction was probably important in basal bird ecology as these birds possessed olfactory capabilities similar to domestic pigeons (olfactory ratio = 18.2%), birds that have been reported to use olfactory cues for aerial navigation and homing [90–94]. The basal bird *Hesperornis* is a specialized non-volant diver [57] that plots near extant divers *Pygoscelis adeliae* (Adelie penguin) and *Gavia immer* (loon), birds that are primarily visual foragers [95,96] (figure 2). The similarity between *Hesperornis* and these extant divers probably reflects evolutionary convergence related to comparable lifestyles. Among extinct neornithines, the volant palaeognath *Lithornis* has a high olfactory ratio (mean = 37.1%), which is not significantly different ($p = 0.051$) from those of known olfactory foraging taxa (mean = 30.6%), such as Procellariiformes (tube-nosed seabirds) [88,97–101], birds that also use olfaction to navigate over open seas [98,102–104], and *Apteryx* (kiwi) [105–107] (figure 2). This result suggests that olfaction was a key sense for food location in *Lithornis* and could also have played a role in navigation.

(b) *Evolution of olfaction among non-avian theropods and birds*

Ancestral state reconstruction of olfactory ratios and olfactory ratio residuals was used to document changes in olfactory capabilities through non-avian theropod and
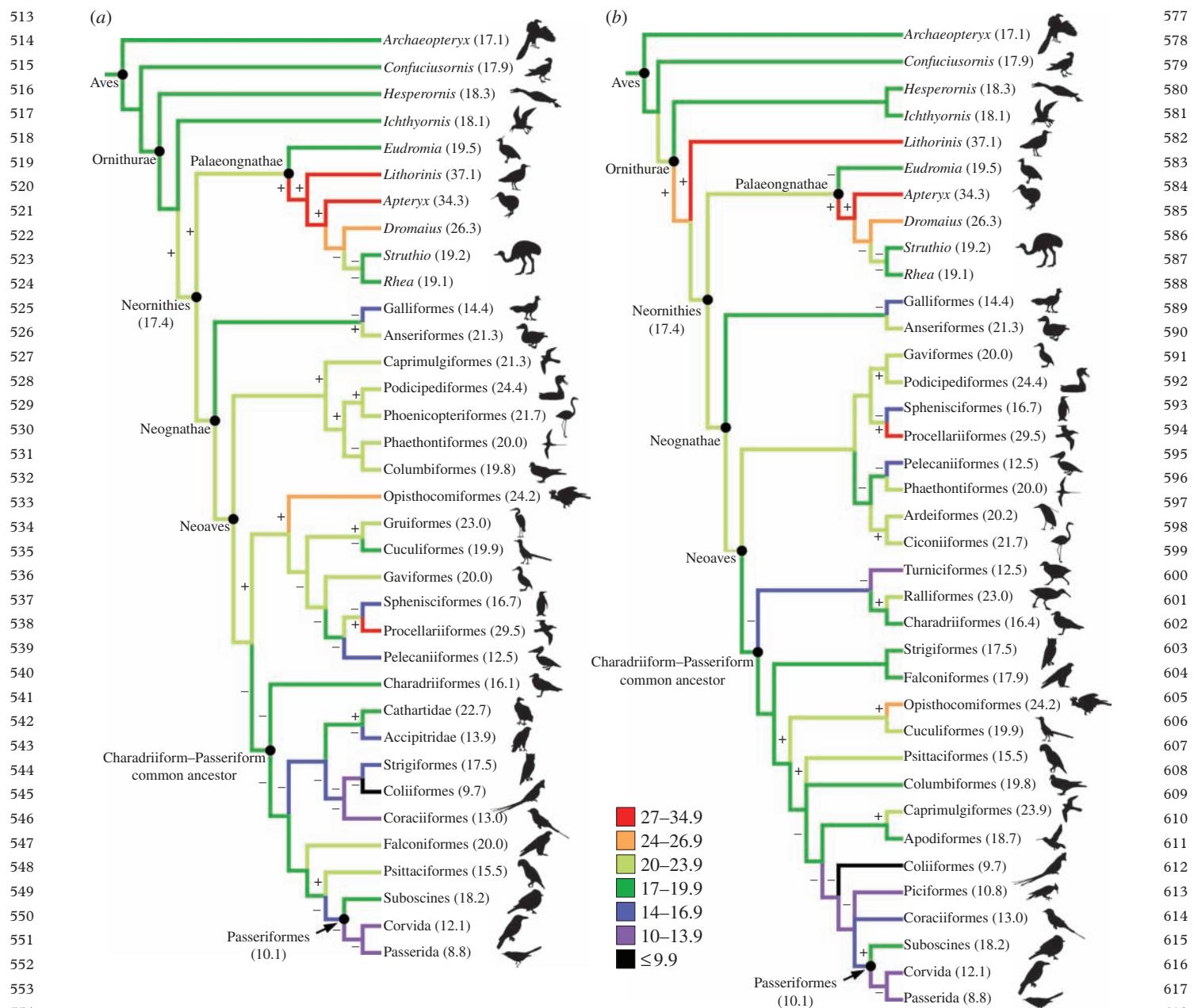
Figure 3. Higher order phylogeny of Aves showing maximum-parsimony ancestral state reconstruction of olfactory ratios. (a) Molecular phylogeny based primarily on Hackett *et al.* [64]. (b) Morphological phylogeny based on Livezey & Zusi [65]. Major increases or decreases in olfactory ratio ancestral states are denoted with (+) and (−), respectively. Through avian evolution, major increases in olfactory ratios have occurred independently in many different lineages, primarily in clades basal to the common ancestor of Charadriiformes and Passeriformes. Significant decreases in olfactory ratios are prevalent in clades more derived than this common ancestor. Numbers between parentheses represent mean olfactory ratios for clades. See the electronic supplementary material for details.

bird evolution. Olfactory ratio residuals initially decrease in the Maniraptoriformes common ancestor and subsequently increase in the Eumaniraptora common ancestor (figure 4). Interestingly, the residuals of the Eumaniraptora, Aves and Pygostylia common ancestors remain the same (figure 4), supporting the previous suggestion that olfactory capabilities were unchanged across the non-avian theropod/bird transition [33]. Olfactory ratios and residuals show an increase through basal birds, with a major increase occurring at the common ancestor of neornithines (figures 3 and 4). These results indicate that the relative size of the olfactory bulbs increased through the evolution of non-avian maniraptoriforms and basal birds. Olfaction was therefore not a

declining modality, as previously suggested [19,20,31], but rather became relatively more important during early bird evolution. This suggests that olfaction likely played a significant ecological role during the evolution of basal birds, as it is doubtful that olfactory bulb size would have continued to increase without conferring a selective advantage.

Analysis of both molecular and morphological phylogenies results in similar trends in olfactory ratios among Neornithes, despite differences in tree topology. Olfactory ratios remained relatively high (usually greater than 20%) well into neornithine evolution, until the most recent common ancestor of Passeriformes and Charadriiformes (figure 3). A continual decrease in olfactory ratios
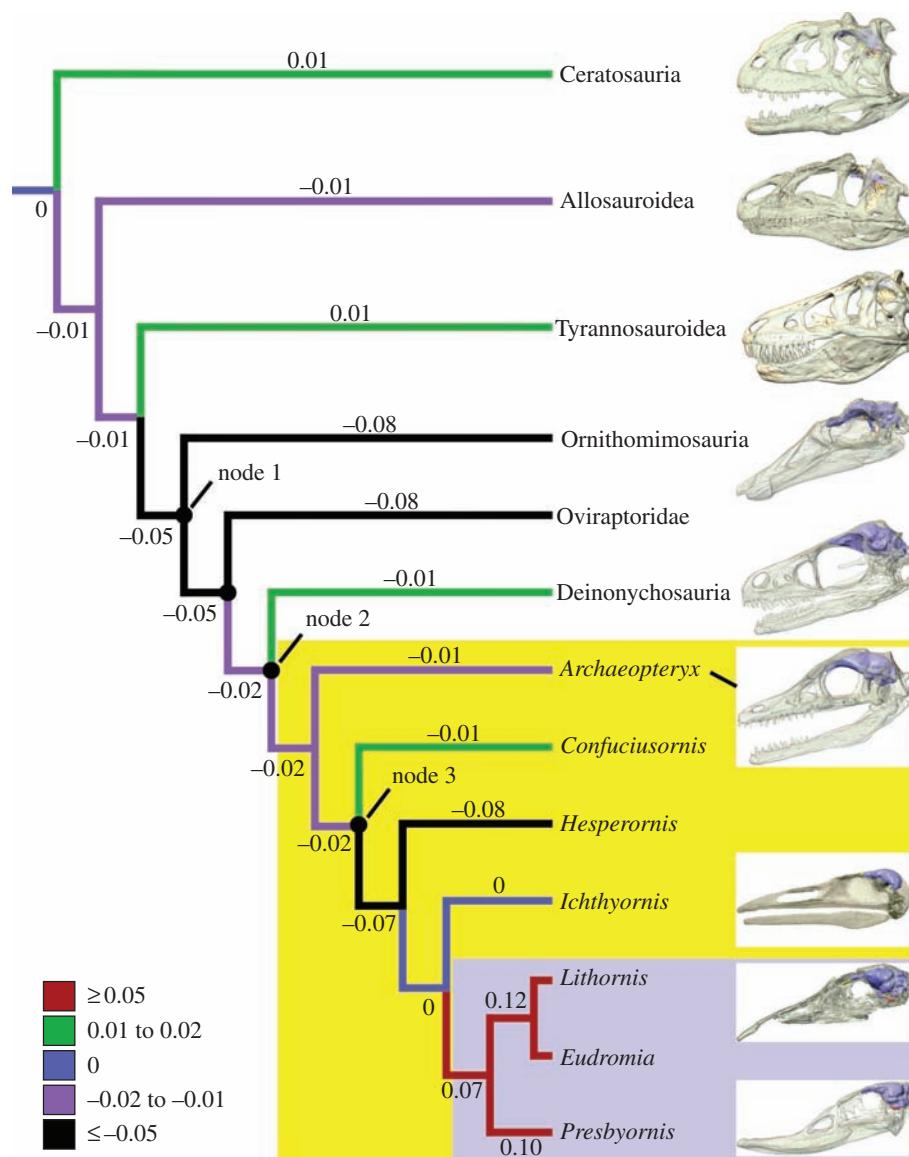
Figure 4. Phylogeny of non-avian theropods and early birds showing maximum-parsimony ancestral state reconstruction of olfactory ratio residuals relative to the non-avian theropod regression. Residuals increase from the Maniraptoriformes common ancestor (node 1) to the Eumaniraptora common ancestor (node 2). Residuals then remain constant across the non-avian theropod/bird transition, between the Eumaniraptora common ancestor (node 2) and the Pygostylia common ancestor (node 3). Within Aves, residuals increase from negative values in basal birds to strongly positive values in neornithines, indicating that olfactory ratios increase and surpass values predicted by the regression for non-avian theropods. These results reveal that olfactory capabilities improved during the evolution from non-avian theropods to modern birds. Yellow box, Aves; blue box Neornithes. Skulls with endocasts are, from top to bottom, *Majungasaurus crenatissimus*, *Allosaurus fragilis*, *Tyranno-saurus rex*, *Struthiomimus altus*, *Bambiraptor feinbergi*, *Archaeopteryx lithographica*, *Ichthyornis dispar*, *Lithornis* sp. and *Presbyornis* sp. Skulls are not to scale.

occurs from this common ancestor to the common ancestor of Passerida (approx. 10.5%) (figure 3). Olfactory ratios are generally well below 20 per cent among clades more derived than the charadriiform–passeriform common ancestor. These results indicate that relative olfactory bulb size remained large during a major part of neornithine evolution before a reduction occurred in derived Neoaves clades.

Among palaeognaths, relatively larger olfactory bulbs evolved in basal forms, such as *Lithornis* and *Apteryx*, and olfactory bulbs then decreased in size continually towards the more derived Struthioniformes (figure 3a); the same trend is observed if *Lithornis* is treated as the sister taxon to Neornithes (figure 3b). This trend may reflect behavioural changes among palaeognaths, from

olfactory foraging in more basal forms (e.g. *Apteryx* [107]), to non-olfactory or visual foraging in more derived taxa (e.g. *Struthio*, *Dromaius* [108,109]). If the molecular tree topology for palaeognaths is analysed and *Lithornis* is excluded from the study, the opposite trend is observed, where olfactory bulb size increased continually through palaeognath evolution, from basal *Struthio* to derived *Apteryx* (not illustrated).

Among neognaths, increases in the relative size of the olfactory bulb occur mainly among clades basal to the common ancestor of Charadriiformes and Passeriformes, whereas reductions in size are prevalent among more derived clades (figures 2 and 3a). This pattern suggests that olfaction is a relatively more important modality in taxa basal to the charadriiform–passeriform common

ancestor, which is consistent with reports on the use of olfaction in such taxa [22,24,88,90,91,93,97–102,104, 105,107,110–113]. Increases in olfactory ratio are more frequent in clades more derived than the charadriiform–passeriform common ancestor in the morphological analysis than in the molecular analysis owing to differences in tree topologies (i.e. some clades that are more basal in the molecular phylogeny are more derived in the morphological phylogeny; figure 3).

The greatest reduction in relative olfactory bulb size among neognaths occurs at the common ancestor of Passeriformes (in the molecular phylogeny, figure 3a) or among Passeriformes (in the morphological phylogeny, figure 3b). If the highly divergent psittaciform *Strigops habroptila* is removed from the ancestral state reconstruction, major decreases in olfactory bulb size are then observed in the common ancestor of Psittaciformes and Passeriformes as well as in the Psittaciformes common ancestor in both molecular- and morphological-based analyses (not illustrated). Passeriformes and Psittaciformes are clades noted for advanced cognitive abilities [114], such as true tool use and high frequency of foraging innovations [115–117]. The coincidence between increased cognitive abilities and reduced olfactory capabilities may indicate that enhanced cognition reduced selective pressures for the use of olfaction at a late stage in neornithine evolution.

5. CONCLUSION

Early avian sensory evolution has been characterized previously by enhancements to visual, auditory and vestibular senses [15], while olfaction was considered to have been a deteriorating modality [19,20,31]. In contrast, our results show that olfaction continued to become relatively more important during the transition from non-avian theropods to early neornithines, thus indicating that olfaction was another significant sensory modality during early avian evolution. The diversification of olfactory abilities among neornithines and the enhancement of olfaction in several basal neornithine and neoavian clades suggest that olfaction retained its significance well into neornithine evolution. The heightened olfactory abilities of ancestral and early neornithines may have provided these birds with a competitive advantage, in the form of increased efficiency at foraging and navigation, over other Cretaceous bird lineages and increased their survivability through the end-Cretaceous extinction.

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Electronic Supplementary Material - Zelenitsky et al.

1. Accuracy of endocast-derived olfactory ratios

Because the braincase closely conforms to brain shape in birds [1, 2], olfactory ratios based on soft-tissue measurements should theoretically be comparable to olfactory ratios based on measurement of endocasts. To test this assumption, we compared endocast-derived olfactory ratios for *Apteryx australis* (USNM 18278) and *Dromaius novaehollandiae* (OUVC 10515) with published soft-tissue-derived values for these taxa [3]. For each taxon, the absolute difference between endocast-derived and soft-tissue-derived olfactory ratios was less than 1.0%, thus verifying that olfactory ratios derived from virtual endocasts are comparable to those derived from soft tissues.

Olfactory ratios for extinct theropods were calculated from endocranial measurements. Like birds, the brains of non-avian maniraptoriform theropods mostly filled the endocranial cavity [4-9] so endocranial proportions should accurately reflect brain proportions. For non-maniraptoriform theropods, we follow the assumption of Larsson et al.[10] that the size proportion between the soft-tissue structures of the brain are equal to the size proportion of the endocranial cavity housing them, even though their brains did not completely fill the endocranial cavity, as in extant crocodylians [11, 12]. Moreover, the disparity between the dimensions of the neural tissues of the telencephalon (which includes the olfactory bulb and cerebral hemispheres) in extant reptiles and the enclosing bony braincase is the smallest for any region of the brain [12]. Therefore, olfactory ratios of non-avian theropods, as we have calculated from measured endocasts, should accurately reflect the proportions of the cerebral hemispheres and olfactory bulbs [13].

2. High olfactory ratios and olfactory-associated behaviours

Among birds, olfaction is involved in a variety of behaviours, such as foraging, navigation, orientation, homing, individual recognition, social displays, predator avoidance, and nest material selection [14-17]. There is a tendency for olfactory-associated behaviours to be reported more often in birds with above average olfactory ratios [3, 18]. Here we wanted to test for significant correlations between olfactory ratios and the frequencies of specific olfactory behaviours (e.g., olfactory foraging, navigation, mate recognition, etc.) among the bird species considered in this study. This was not possible in most cases due to a general paucity of behavioural studies related to olfaction in birds [17]. The only behaviour we could test was olfactory foraging because it represents the only behaviour documented in a reasonable number of species (n = 13). We compared the olfactory ratios of birds known to practice olfactory foraging (i.e., *Apteryx australia, Cathartes aura septentrionalis, Daption capense, Fulmarus glacialis, Oceanites oceanicus, Oceanodroma leucorhoa leucorhoa, Pachyptila desolata, Pagodroma nivea, Puffinus pacificus, Puffinus gravis, Phoebastria nigripes, Puffinus opisthomelas, Strigops habroptila*) against those of all other birds, which primarily use other senses for foraging, through an independent sample t-test in PASW Statistics v. 17.0.2. For this analysis, although we could not find data on *Puffinus opisthomelas*, we considered it as part of the olfactory foraging group because at least six closely related species (*P. gravis, P. griseus, P. creatops, P. bulleri, P. puffinus, P. tenuirostris*) are reported to practice olfactory foraging [19]. Our results reveal that olfactory foraging species have significantly higher (p < 0.0001) olfactory ratios (mean = 30.6%) than other species (mean = 13.8%).

3. Institutional abbreviations

 AMNH, American Museum of Natural History, New York City, NY; BMNH, Natural History Museum, London, UK; CMN, Canadian Museum of Nature, Ottawa; FMNH PR, Field Museum of Natural History, Chicago, IL; GIN, Paleontological Center of Mongolia, Ulaan Bataar, Mongolia; IGM, Institute of Geology, Mongolian Academy of Sciences, Ulaan Bataar, Mongolia; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China; KUVP, University of Kansas Natural History Museum, Lawrence, KS; MOR, Museum of the Rockies, Bozeman, MT; MUCPv-CH, Museo de la Universidad Nacional del Comahue, El Chocón collection, Neuquén; MWC, Museum of Western Colorado, Fruita, CO; OMNH, Oklahoma Museum of Natural History, Norman, OK; OUVC, Ohio University Vertebrate Collection, Ohio University, Athens, OH; PIN, Paleontological Institute, Moscow; SGM, Ministère de l'Énergie et des Mines, Rabat, Morocco; TMP, Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta; UMNH, Utah Museum of Natural History, Salt Lake City, UT; USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.; UUVP, University of Utah Museum of Natural History, Salt Lake City, UT; YPM, Yale-Peabody Museum, New Haven, CT.

4. Phylogenetic independent contrasts

Least-squares regression of the standardized, positivized independent contrasts of olfactory ratio and body mass based on molecular and morphological phylogenies for Aves are presented below.

Figure S1. Least-squares regression of the standardized, positivized independent contrasts of olfactory ratio and body mass based on the molecular phylogeny for Aves (figure S3).

$y = -0.008x$
$R^2 = 0.0008$
p-value 2-tailed = 0.77
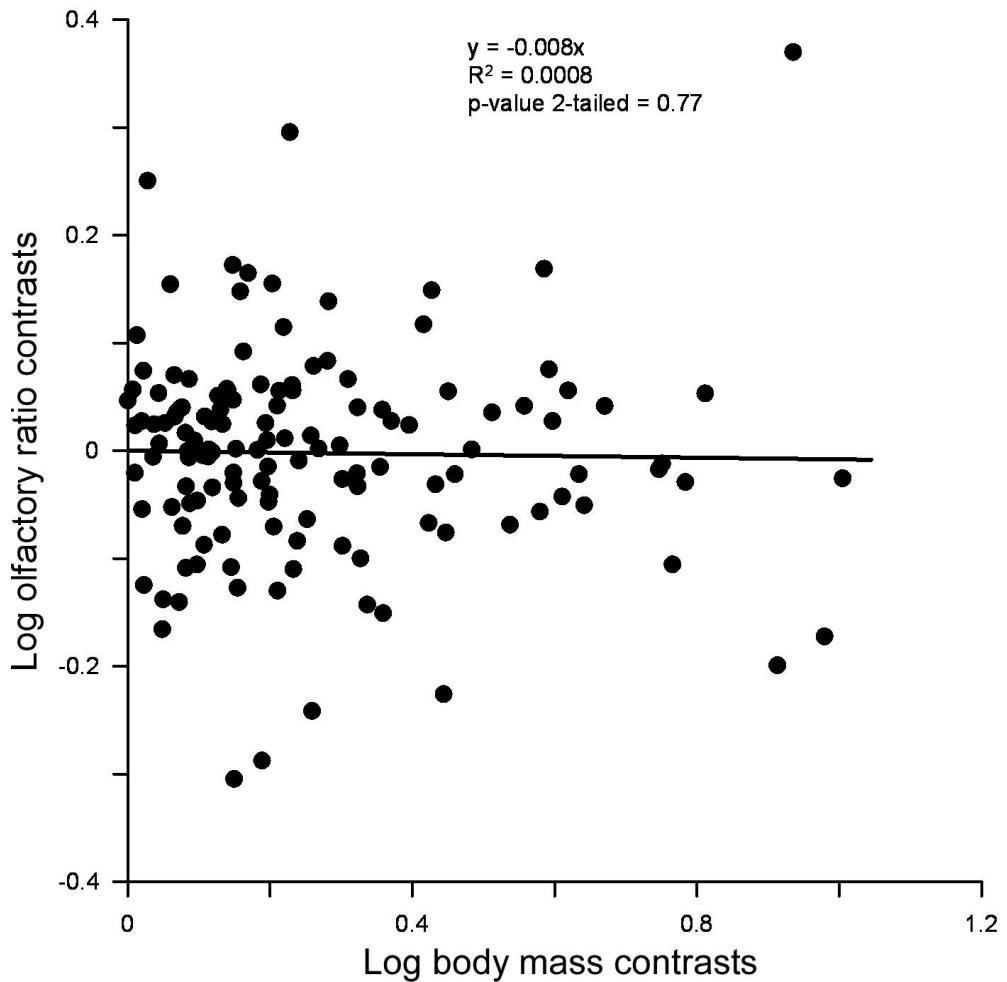
Figure S2. Least-squares regression of the standardized, positivized independent contrasts of olfactory ratio and body mass based on the morphological phylogeny for Aves (figure S4).

y = -0.0064x
R^2 = 0.0005
p-value 2-tailed = 0.81
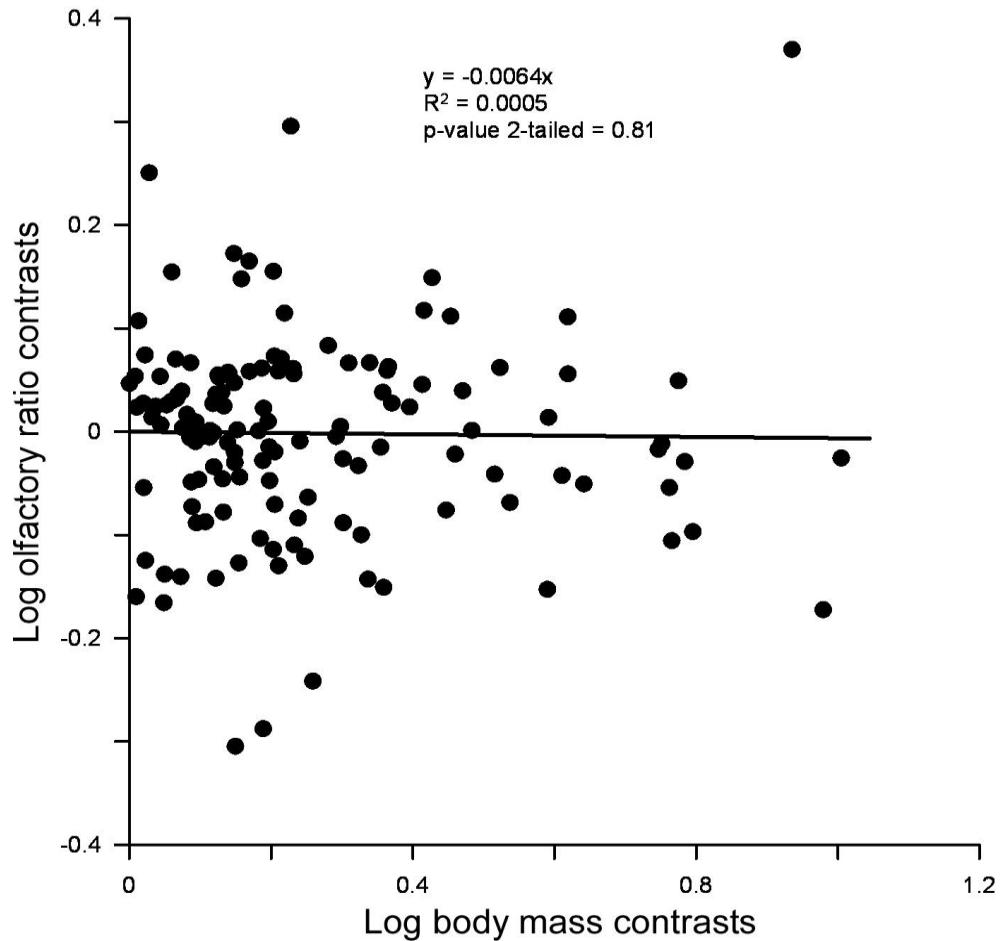
Figure S3. Molecular phylogeny of Aves used for maximum parsimony ancestral state reconstruction of olfactory ratios. Olfactory ratios for each node, except those for terminal taxa, are provided in table S3. Olfactory ratios for terminal taxa are listed in table S1.
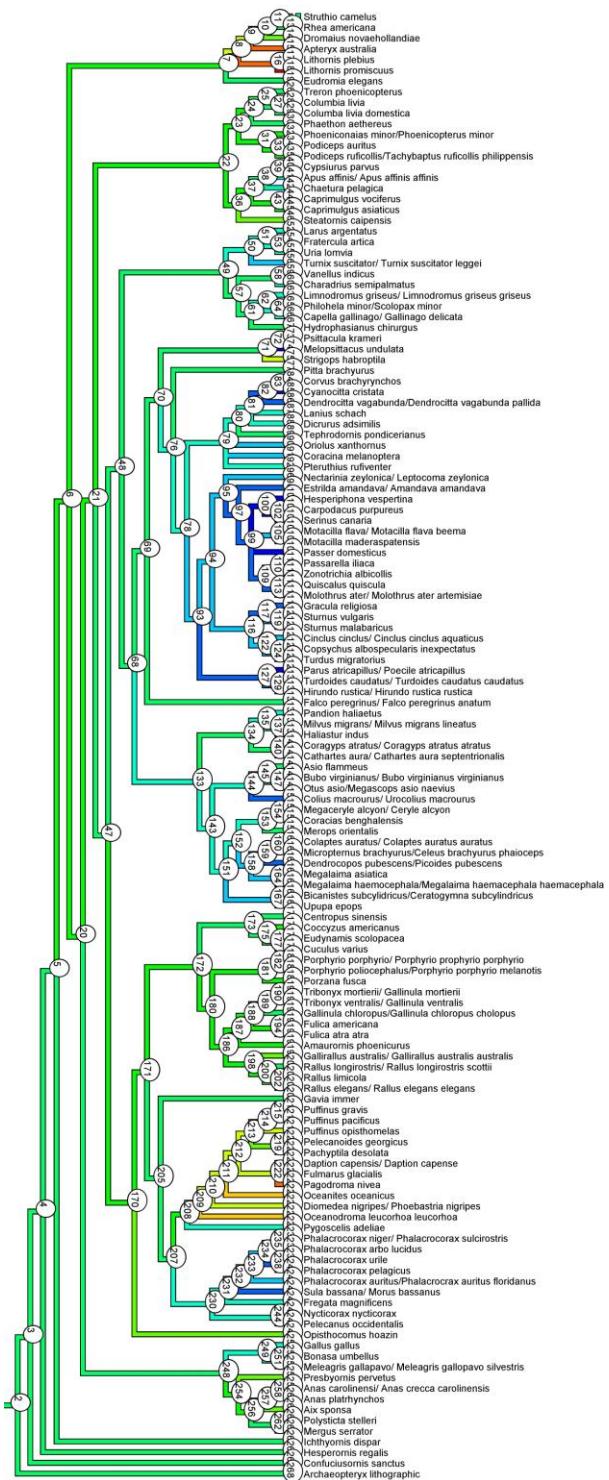
Figure S4. Morphological phylogeny of Aves used for maximum parsimony ancestral state reconstruction of olfactory ratios. Olfactory ratios for each node, except those for terminal taxa, are provided in table S4. Olfactory ratios for terminal taxa are listed in table S1.
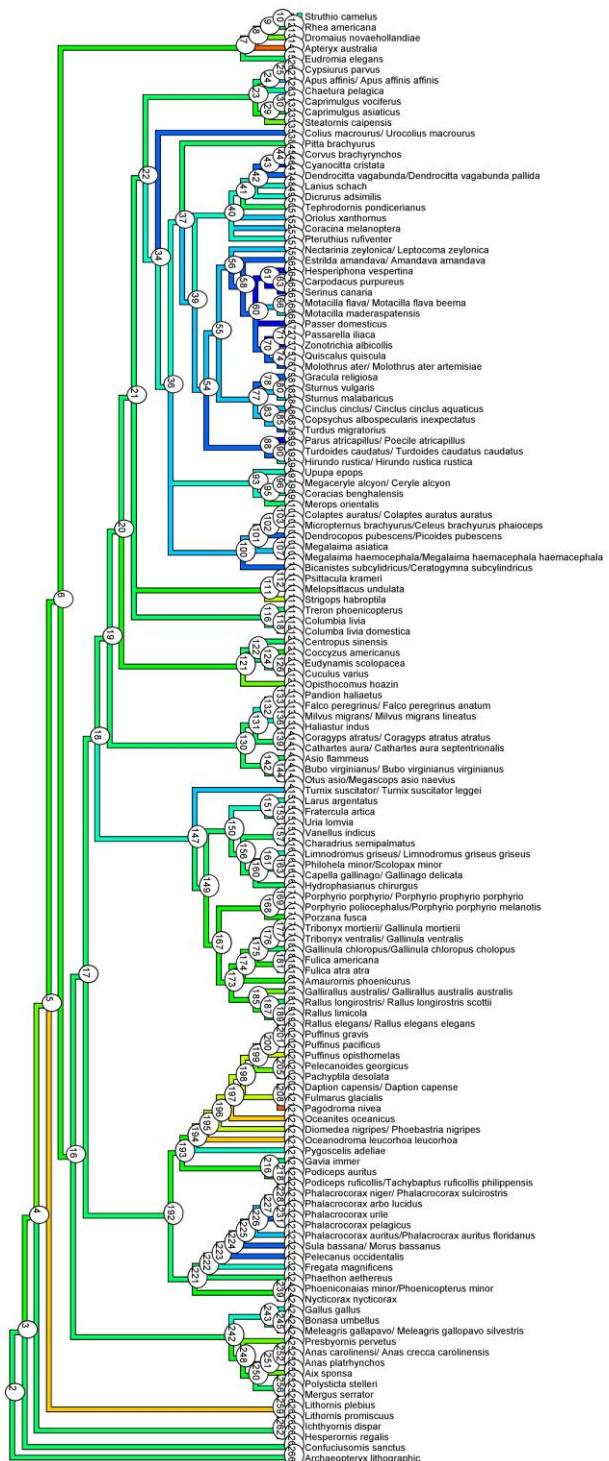
Table S1. Olfactory ratios and body masses of avian taxa considered in this study. Olfactory ratios for extant birds are sourced from Bang [3] and body masses are derived from Dunning [20], unless otherwise noted. Ordinal-level categories of living birds are based on the phylogeny of Hackett et al. [21], and follow the revised nomenclature of Chesser et al. [22]. Sources of olfactory ratios and body masses for extinct birds are provided in the text (see Materials and Methods). Limb-element lengths for extinct birds were measured by the authors, unless otherwise noted. Residuals for all birds were calculated relative to a phylogenetically-corrected least-squares regression of olfactory ratio against body mass for non-avian theropods (figure 2). Dagger "†" denotes fossil taxon. *From virtual endocast. **From Hagelin [23].

Taxon	Olfactory ratio (%)	Body mass (kg)	Olfactory ratio residual
Basal birds Archaeopterygiformes† *Archaeopteryx lithographica*† (BMNH 37001)	17.1	0.280	-0.01
Confuciusornithiformes† *Confuciusornis sanctus*†(TMP 1998.14.2) (TMP 1998.14.1 mean humerus length = 63.65 mm)	17.9	0.277	0.01
Hesperornithiformes† *Hesperornis regalis*† (KUVP 71012) (femur length = 105 mm; from Marsh [24])	15.3-21.3 mean=18.3	10.608	-0.26 to -0.11 mean=-0.18
Ichthyornithiformes† *Ichthyornis dispar*† (YPM 1728) (mean of all known complete humeri = 62.4 mm; from Clarke [25])	18.1	0.350	0.00
Palaeognathae Apterygiformes *Apteryx australis*	34.3	2.330	0.18
Lithornithiformes† *Lithornis plebius*† (USNM 336534) (humerus = 83 mm; from Houde [26])	36.5	0.480	0.29
Lithornis promiscuus† (USNM 391983) (USNM 336535 humerus = 112.7 mm; from Houde [26]	37.7	0.908	0.27

Tinamiformes			
Eudromia elegans (OUVC 10602)	19.5*	0.695	0.00
Casuariformes			
Dromaius novaehollandiae	26.3	34.200	-0.08
Struthioniformes			
Rhea americana	19.1	23.000	-0.20
Struthio camelus (OUVC 10491)	19.2*	111.000	-0.28
Neognathae			
Galliformes			
Gallus gallus	15.4	0.904	-0.12
Bonasa umbellus	14.3	0.532	-0.12
Meleagris gallopavo/Meleagris gallopavo silvestris	13.5	6.050	-0.28
Anseriformes			
Presbyornis sp. (USNM 299846) (humerus = 95.64 mm; from Ericson [27])	24.2	0.646	0.10
Aix sponsa	25.6	0.658	0.12
Polysticta stelleri	23.7	0.808	0.07
Anas carolinensis/Anas crecca carolinensis	20.0	0.341	0.05
Anas platyrhynchos	19.0	1.082	-0.04
Mergus serrator	15.0	1.022	-0.14
Caprimulgiformes			
Caprimulgus vociferus	25.0	0.053	0.25
Steatornis caipensis	24.7	0.408	0.13
Caprimulgus asiaticus	22.0	0.042	0.20
Chaetura pelagica	18.8	0.024	0.17
Apus affinis/Apus affinis affinis	18.7	0.018	0.18
Cypsiurus parvus	18.7	0.014	0.19
Podicipediformes			
Podiceps auritus	26.7	0.453	0.16
Podiceps ruficollis/Tachybaptus ruficollis philippensis	22.2	0.213	0.12
Phoenicopteriformes			
Phoeniconaias minor/Phoenicopterus minor	21.7	1.500	0.00
Phaethontiformes			
Phaethon aethereus	20.0	0.750	0.01
Columbiformes			
Columba livia	21.2	0.355	0.07
Treron phoenicopterus	20.0	0.235	0.07
Columba livia domestica	18.2	0.355	0.00
Opisthocomiformes			
Opisthocomus hoazin	24.2	0.696	0.09
Gruiformes			
Tribonyx mortierii/Gallinula mortierii	26.1	1.293	0.09
Rallus limicola	25.6	0.084	0.23
Fulica atraata	24.9	0.836	0.09

Tribonyx ventralis/Gallinula ventralis	23.9	0.387	0.12
Gallirallus australis/Gallirallus australis australis	24.2	0.852	0.08
Fulica americana	23.5	0.642	0.08
Porzana fusca	23.1	0.058	0.21
Porphyrio poliocephalus/Porphyrio porphyrio melanotis	23.4	0.988	0.06
Amaurornis phoenicurus	22.6	0.180	0.14
Porphyrio porphyrio/Porphyrio prophyrio porphyrio	21.1	0.797	0.02
Gallinula chloropus/Gallinula chloropus chloropus	20.0	0.305	0.05
Rallus longirostris/Rallus longirostris scottii	20.0	0.269	0.06
Rallus elegans/Rallus elegans elegans	20.0	0.361	0.05
Cuculiformes			
Coccyzus americanus	21.1	0.064	0.16
Cuculus varius	20.7	0.103	0.13
Eudynamis scolopacea	19.4	0.167	0.07
Centropus sinensis	18.3	0.283	0.02
Gaviiformes			
Gavia immer	20.0	4.980	-0.10
Sphenisciformes			
Pygoscelis adeliae	16.7	4.850	-0.18
Procellariiformes			
Pagodroma nivea	37.2	0.268	0.33
Oceanodroma leucorhoa leucorhoa	33.0	0.041	0.38
Oceanites oceanicus	33.3	0.032	0.40
Puffinu spacificus	30.9	0.388	0.23
Puffinus gravis	30.0	0.849	0.17
Pachyptila desolata	29.3	0.147	0.26
Diomedea nigripes/Phoebastria nigripes	28.6	3.195	0.08
Puffinus opisthomelas	29.4	0.408	0.21
Daption capensis/Daption capense	27.5	0.436	0.17
Fulmarus glacialis	27.1	0.613	0.15
Pelecanoides georgicus	17.7	0.121	0.05
Pelecaniformes			
Phalacrocorax niger/Phalacrocorax sulcirostris	15.8	1.000	-0.11
Fregata magnificens	15.0	1.414	-0.15
Phalacrocorax carbolucidus	14.5	2.669	-0.20
Phalancrocorax auritus/Phalacrocrax auritus floridanus	10.3	1.674	-0.32
Sula bassana/Morus bassanus	9.6	3.000	-0.39
Pelecanus occidentalis	9.7	3.438	-0.39
Phalacrocorax urile	9.5	2.138	-0.37
Phalacrocorax pelagicus	8.0	1.857	-0.44
Nycticorax nycticorax	20.2	0.810	0.01

Charadriiformes			
Turnix suscitator/Turnix suscitator leggei	12.5	0.051	-0.05
Vanellus indicus	22.0	0.181	0.12
Hydrophasianus chirurgus	20.0	0.164	0.09
Philohela minor/Scolopax minor	16.7	0.198	0.00
Larus argentatus	15.8	1.085	-0.12
Charadrius semipalmatus	15.0	0.047	0.03
Limnodromus griseus/Limnodromus griseus griseus	15.4	0.113	-0.01
Uria lomvia	15.0	0.964	-0.13
Capella gallinago/Gallina godelicata	14.3	0.122	-0.04
Fratercula artica	13.9	0.932	-0.16
Accipitriformes			
Milvus migrans/Milvus migrans lineatus (Accipitridae)	15.0	0.836	-0.13
Pandion haliaetus (Accipitridae)	14.3	1.486	-0.18
Haliastur indus (Accipitridae)	12.5	0.529	-0.18
Coragyps atratus/Coragyps atratus atratus (Cathartidae)	16.7	2.159	-0.13
Cathartes aura/Cathartes aura septentrionalis (Cathartidae)	28.7	2.006	0.11
Coliiformes			
Colius macrourus/Urocolius macrourus	9.7	0.046	-0.16
Strigiformes			
Asio flammeus	19.4	0.347	0.04
Bubo virginianus/Bubo virginianus virginianus	18.0	1.355	-0.07
Otus asio/Megascops asio naevius	15.0	0.181	-0.04
Coraciiformes			
Merops orientalis	18.8	0.015	0.19
Megaceryle alcyon/Ceryle alcyon	17.0	0.148	0.02
Upupa epops	14.7	0.061	0.01
Coracias benghalensis	14.3	0.158	-0.06
Bicanistes subcylidricus/Ceratogymna subcylindricus	7.7	1.201	-0.44
Megalaima asiatica	15.4	0.091	0.01
Micropternus brachyurus/Celeus brachyurus phaioceps	14.3	0.108	-0.04
Dendrocopos pubescens/Picoides pubescens	10.0	0.028	-0.12
Megalaima haemocephala/Megalaima haemacephala haemacephala	9.3	0.047	-0.18
Colaptes auratus/Colaptes auratus auratus	8.3	0.127	-0.28
Falconiformes			
Falco peregrinus/Falco peregrinus anatum	20.0	0.815	0.00
Psittaciformes			
Melopsittacus undulata	6.2	0.029	-0.33
Psittacula krameri	10.0	0.117	-0.19

Strigops habroptila	30.2**	1.750	0.14
Passeriformes			
Pitta brachyurus (Suboscine)	18.2	0.056	0.11
Tephrodornis pondicerianus (Corvida)	17.9	0.020	0.15
Dicrurus adsimilis (Corvida)	16.5	0.040	0.08
Lanius schach (Corvida)	16.0	0.052	0.05
Pteruthius rufiventer (Corvida)	14.3	0.045	0.01
Oriolus xanthornus (Corvida)	13.3	0.056	-0.03
Coracina melanoptera (Corvida)	12.0	0.030	-0.04
Dendrocitta vagabunda/Dendrocitta vagabunda pallida (Corvida)	7.2	0.100	-0.33
Cyanocitta cristata (Corvida)	6.3	0.088	-0.38
Corvus brachyrhynchos (Corvida)	5.0	0.506	-0.88
Motacilla maderaspatensis (Passerida)	16.7	0.031	0.10
Hirundo rustica/Hirundo rustica rustica (Passerida)	15.0	0.018	0.08
Copsychus albospecularis inexpectatus (Passerida)	14.0	0.024	0.04
Motacilla flava/Motacilla flava beema (Passerida)	13.6	0.017	0.05
Sturnus malabaricus (Passerida)	12.7	0.040	-0.03
Nectarinia zeylonica/Leptocoma zeylonica (Passerida)	12.9	0.009	0.06
Cinclus cinclus/Cinclus cinclus aquaticus (Passerida)	10.7	0.060	-0.13
Estrilda amandava/Amandava amandava (Passerida)	10.0	0.010	-0.06
Sturnus vulgaris (Passerida)	9.7	0.086	-0.19
Quiscalus quiscula (Passerida)	9.4	0.106	-0.22
Gracula religiosa (Passerida)	7.7	0.192	-0.34
Turdus migratorius (Passerida)	8.6	0.079	-0.24
Molothrus ater/Molothrus ater artemisiae (Passerida)	7.1	0.043	-0.29
Turdoides caudatus/Turdoides caudatus caudatus (Passerida)	5.9	0.034	-0.36
Serinus canaria (Passerida)	6.0	0.024	-0.33
Passarella iliaca (Passerida)	5.8	0.032	-0.36
Zonotrichia albicollis (Passerida)	4.6	0.024	-0.44
Hesperiphona vespertina (Passerida)	4.0	0.060	-0.56
Passer domesticus (Passerida)	3.8	0.028	-0.53
Carpodacus purpureus (Passerida)	4.2	0.023	-0.48
Parus atricapillus/Poecile atricapillus (Passerida)	3.2	0.011	-0.56

Table S2. Olfactory ratios, body masses, and residuals for non-avian theropod species. Most olfactory ratios and body masses are from Zelenitsky et al. [13], but asterisks denote new data obtained in the course of this research (see Materials and Methods). Residuals were calculated from the phylogenetically-corrected least-squares regression of olfactory ratio against body mass for non-avian theropods (figure 2).

Taxon	Catalogue number	Olfactory ratio (%)	Body mass (kg)	Olfactory ratio residual
Allosauroidea				
Allosaurus fragilis	UUVP 294	51.6		
	UUVP 5961	50		
	UMNH VP 18050*	50.1		
	Allosaurus mean	50.6	1468.77	0
Acrocanthosaurus atokensis	OMNH 10146	58.1	3777.58	0.01
Carcharodontosaurus saharicus	SGM-Din 1	56	7905.47	-0.05
Giganotosaurus carolinii	MUCPv-CH-1	57.7	7559.49	-0.04
Ceratosauria				
Ceratosaurus magnicornis	MWC 1	48.1	538.86	0.03
Majungasaurus crenatissimus	FMNH PR 2100	48.3	1130	-0.01
Tyrannosauroidea				
Dilong paradoxus	IVPP V14243	27	9.69	0
Tarbosaurus bataar	PIN 46104	65.1		
	PIN 553-3/1*	67.4		
	Tarbosaurus mean	65.7	2164.6	0.09
Tyrannosaurus rex	AMNH 5117*	68.3		
	FMNH PR 2081	71		
	T. rex mean	69.7	5855.3	0.06
Ornithomimosauria				
Garudimimus brevipes	GIN 100/13	28.8	97.84	-0.1
Ornithomimus edmontonensis	TMP 95.110.1	31.4	152.74	-0.09

Dromiceiomimus brevitertius	NMC 12228	29.4	206.79	-0.13
Struthiomimus altus	TMP 90.26.1	32.5	277.97	-0.1
Oviraptoridae				
Citipati osmolskae	IGM 100/978	31.5	129.78	-0.08
Dromaeosauridae				
Saurornitholestes langstoni	TMP 74.10.5	34.8	16.62	0.08
Bambiraptor feinbergi	KUVP 129737 (based on AMNH FR 30556)	28.5	2.44	0.1
Velociraptor mongoliensis	GIN 100/24	35.7	13.36	0.1
Deinonychus antirrhopus*	composite of MOR 747 and OMNH 50268	41	56.7	0.08
Tsaagan mangas*	IGM 100/1015	36	13.36	0.11
Troodontidae				
Troodon formosus	TMP 79.8.1	33.2		
	TMP 86.36.4	33.5		
	NMC 12340	32.6		
	AMNH 6174	33		
	Troodon mean	33.1	60.76	-0.02

Table S3. Ancestral state values for nodes in molecular phylogeny (figure S3).

Node	Ancestral state	Node	Ancestral state	Node	Ancestral state
node 2	17.53	node 45	22.00	node 88	16.54
node 3	17.96	node 46	24.67	node 89	17.89
node 4	18.47	node 47	20.40	node 90	13.33
node 5	19.17	node 48	18.48	node 91	12.00
node 6	20.94	node 49	17.05	node 92	14.29
node 7	23.19	node 50	14.89	node 93	10.81
node 8	29.12	node 51	15.12	node 94	10.75
node 9	29.74	node 52	15.79	node 95	11.10
node 10	25.81	node 53	14.67	node 96	12.90
node 11	21.38	node 54	13.89	node 97	9.64
node 12	19.20	node 55	15.00	node 98	10.00
node 13	19.12	node 56	12.50	node 99	7.82
node 14	26.32	node 57	17.79	node 100	5.71
node 15	34.29	node 58	18.26	node 101	4.00
node 16	34.44	node 59	21.99	node 102	5.31
node 17	36.50	node 60	15.00	node 103	4.23
node 18	37.70	node 61	18.07	node 104	6.00
node 19	19.50	node 62	16.41	node 105	12.71
node 20	20.47	node 63	15.38	node 106	13.64
node 21	20.86	node 64	15.79	node 107	16.67
node 22	21.72	node 65	16.67	node 108	3.85
node 23	21.54	node 66	14.29	node 109	7.20
node 24	20.55	node 67	20.00	node 110	5.87
node 25	20.13	node 68	17.98	node 111	5.77
node 26	20.00	node 69	18.90	node 112	4.64
node 27	19.83	node 70	18.72	node 113	7.91
node 28	21.17	node 71	20.36	node 114	9.37
node 29	18.18	node 72	12.17	node 115	7.14
node 30	20.00	node 73	10.00	node 116	10.34
node 31	22.34	node 74	6.15	node 117	9.55
node 32	21.74	node 75	30.18	node 118	7.69
node 33	23.74	node 76	16.91	node 119	10.63
node 34	26.67	node 77	18.18	node 120	9.66
node 35	22.22	node 78	13.83	node 121	12.68
node 36	22.75	node 79	13.75	node 122	10.72
node 37	21.87	node 80	15.32	node 123	10.71
node 38	19.90	node 81	14.33	node 124	11.10
node 39	19.08	node 82	9.49	node 125	14.00
node 40	18.67	node 83	6.91	node 126	8.57
node 41	18.67	node 84	5.00	node 127	7.87
node 42	18.75	node 85	6.25	node 128	3.20
node 43	22.96	node 86	7.22	node 129	9.58
node 44	25.00	node 87	15.97	node 130	5.88

Node	Ancestral state	Node	Ancestral state	Node	Ancestral state
node 131	15.00	node 176	21.11	node 221	29.29
node 132	20.00	node 177	20.15	node 222	30.38
node 133	16.56	node 178	19.37	node 223	27.50
node 134	17.13	node 179	20.69	node 224	27.14
node 135	15.22	node 180	21.95	node 225	37.22
node 136	14.29	node 181	22.46	node 226	33.33
node 137	14.24	node 182	22.29	node 227	28.57
node 138	15.00	node 183	21.05	node 228	33.00
node 139	12.50	node 184	23.35	node 229	16.67
node 140	19.60	node 185	23.15	node 230	16.30
node 141	16.67	node 186	22.48	node 231	14.35
node 142	25.00	node 187	22.66	node 232	11.73
node 143	14.58	node 188	22.93	node 233	11.24
node 144	13.60	node 189	22.35	node 234	11.65
node 145	16.52	node 190	24.13	node 235	13.98
node 146	19.44	node 191	26.14	node 236	15.79
node 147	16.51	node 192	23.89	node 237	14.50
node 148	18.00	node 193	20.00	node 238	9.72
node 149	15.00	node 194	23.77	node 239	9.52
node 150	9.71	node 195	23.53	node 240	8.00
node 151	13.58	node 196	24.86	node 241	10.34
node 152	14.15	node 197	22.58	node 242	9.62
node 153	16.25	node 198	22.81	node 243	15.00
node 154	15.86	node 199	24.21	node 244	15.39
node 155	17.04	node 200	21.76	node 245	20.19
node 156	14.29	node 201	20.00	node 246	9.68
node 157	18.75	node 202	22.45	node 247	24.24
node 158	12.63	node 203	25.60	node 248	19.60
node 159	11.32	node 204	20.00	node 249	16.60
node 160	11.31	node 205	20.04	node 250	15.38
node 161	8.33	node 206	20.00	node 251	14.80
node 162	14.29	node 207	19.18	node 252	14.29
node 163	10.00	node 208	21.19	node 253	13.51
node 164	12.43	node 209	27.72	node 254	21.74
node 165	15.38	node 210	28.98	node 255	24.20
node 166	9.28	node 211	30.65	node 256	21.43
node 167	11.99	node 212	29.65	node 257	22.51
node 168	7.69	node 213	27.90	node 258	20.52
node 169	14.71	node 214	29.11	node 259	20.00
node 170	21.86	node 215	30.00	node 260	19.05
node 171	20.94	node 216	30.00	node 261	25.58
node 172	20.92	node 217	30.90	node 262	20.04
node 173	19.86	node 218	29.41	node 263	23.68
node 174	18.29	node 219	24.96	node 264	15.00
node 175	20.37	node 220	17.70	node 265	18.10

Node	Ancestral state
node 266	18.28
node 267	17.89
node 268	17.10

Table S4. Ancestral state values for nodes in morphological phylogeny (figure S4).

Node	Ancestral state	Node	Ancestral state	Node	Ancestral state
node 2	18.16	node 45	5.00	node 88	7.72
node 3	19.22	node 46	6.25	node 89	3.20
node 4	21.60	node 47	7.22	node 90	9.53
node 5	26.26	node 48	15.97	node 91	5.88
node 6	23.70	node 49	16.54	node 92	15.00
node 7	23.61	node 50	17.89	node 93	14.94
node 8	27.64	node 51	13.33	node 94	14.71
node 9	25.02	node 52	12.00	node 95	16.55
node 10	21.11	node 53	14.29	node 96	15.96
node 11	19.20	node 54	10.42	node 97	17.04
node 12	19.12	node 55	10.57	node 98	14.29
node 13	26.32	node 56	11.03	node 99	18.75
node 14	34.29	node 57	12.90	node 100	10.82
node 15	19.50	node 58	9.61	node 101	11.18
node 16	21.22	node 59	10.00	node 102	10.77
node 17	20.01	node 60	7.81	node 103	11.13
node 18	18.47	node 61	5.71	node 104	8.33
node 19	19.03	node 62	4.00	node 105	14.29
node 20	19.99	node 63	5.31	node 106	10.00
node 21	19.50	node 64	4.23	node 107	11.95
node 22	17.63	node 65	6.00	node 108	15.38
node 23	19.76	node 66	12.71	node 109	9.28
node 24	19.11	node 67	13.64	node 110	7.69
node 25	18.81	node 68	16.67	node 111	20.65
node 26	18.67	node 69	3.85	node 112	12.27
node 27	18.67	node 70	7.20	node 113	10.00
node 28	18.75	node 71	5.87	node 114	6.15
node 29	22.53	node 72	5.77	node 115	30.18
node 30	23.18	node 73	4.64	node 116	19.73
node 31	25.00	node 74	7.90	node 117	20.00
node 32	22.00	node 75	9.37	node 118	19.69
node 33	24.67	node 76	7.14	node 119	21.17
node 34	13.64	node 77	10.26	node 120	18.18
node 35	9.71	node 78	9.52	node 121	21.43
node 36	13.58	node 79	7.69	node 122	20.06
node 37	14.91	node 80	10.62	node 123	18.29
node 38	18.18	node 81	9.66	node 124	20.45
node 39	12.96	node 82	12.68	node 125	21.11
node 40	13.57	node 83	10.69	node 126	20.17
node 41	15.26	node 84	10.71	node 127	19.37
node 42	14.31	node 85	11.09	node 128	20.69
node 43	9.48	node 86	14.00	node 129	24.24
node 44	6.91	node 87	8.57	node 130	18.64

Node	Ancestral state	Node	Ancestral state	Node	Ancestral state
node 131	18.48	node 176	22.32	node 221	19.71
node 132	16.75	node 177	24.12	node 222	18.25
node 133	17.01	node 178	26.14	node 223	15.02
node 134	14.29	node 179	23.89	node 224	11.82
node 135	20.00	node 180	20.00	node 225	10.77
node 136	14.75	node 181	23.74	node 226	10.87
node 137	15.00	node 182	23.53	node 227	11.49
node 138	12.50	node 183	24.86	node 228	13.93
node 139	20.05	node 184	22.58	node 229	15.79
node 140	16.67	node 185	22.60	node 230	14.50
node 141	25.00	node 186	24.21	node 231	9.67
node 142	18.41	node 187	21.67	node 232	9.52
node 143	19.44	node 188	20.00	node 233	8.00
node 144	17.14	node 189	22.42	node 234	10.34
node 145	18.00	node 190	25.60	node 235	9.62
node 146	15.00	node 191	20.00	node 236	9.68
node 147	16.37	node 192	20.35	node 237	15.00
node 148	12.50	node 193	21.32	node 238	20.00
node 149	18.14	node 194	22.01	node 239	20.55
node 150	17.37	node 195	28.04	node 240	21.74
node 151	16.05	node 196	29.10	node 241	20.19
node 152	15.79	node 197	30.70	node 242	19.94
node 153	14.98	node 198	29.67	node 243	16.72
node 154	13.89	node 199	27.91	node 244	15.38
node 155	15.00	node 200	29.11	node 245	14.84
node 156	17.93	node 201	30.00	node 246	14.29
node 157	18.31	node 202	30.00	node 247	13.51
node 158	21.99	node 203	30.90	node 248	21.87
node 159	15.00	node 204	29.41	node 249	24.20
node 160	18.12	node 205	24.97	node 250	21.49
node 161	16.43	node 206	17.70	node 251	22.53
node 162	15.38	node 207	29.29	node 252	20.53
node 163	15.80	node 208	30.38	node 253	20.00
node 164	16.67	node 209	27.50	node 254	19.05
node 165	14.29	node 210	27.14	node 255	25.58
node 166	20.00	node 211	37.22	node 256	20.06
node 167	20.68	node 212	33.33	node 257	23.68
node 168	21.98	node 213	28.57	node 258	15.00
node 169	22.13	node 214	33.00	node 259	33.49
node 170	21.05	node 215	16.67	node 260	36.50
node 171	23.35	node 216	21.61	node 261	37.70
node 172	23.15	node 217	20.00	node 262	19.33
node 173	21.90	node 218	23.50	node 263	18.10
node 174	22.44	node 219	26.67	node 264	18.28
node 175	22.83	node 220	22.22	node 265	17.89

Node	Ancestral state
node 266	17.10

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