

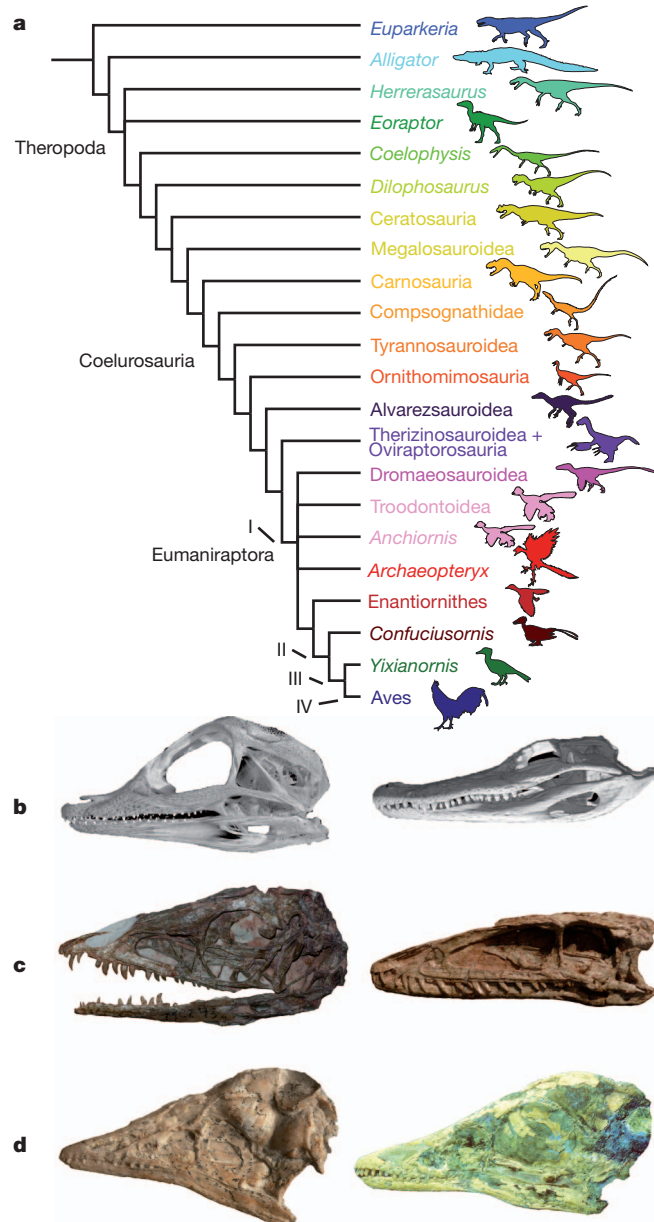
# Birds have paedomorphic dinosaur skulls

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The interplay of evolution and development has been at the heart of evolutionary theory for more than a century<sup>1</sup>. Heterochrony—change in the timing or rate of developmental events—has been implicated in the evolution of major vertebrate lineages such as mammals<sup>2</sup>, including humans<sup>1</sup>. Birds are the most speciose land vertebrates, with more than 10,000 living species<sup>3</sup> representing a bewildering array of ecologies. Their anatomy is radically different from that of other vertebrates. The unique bird skull houses two highly specialized systems: the sophisticated visual and neuromuscular coordination system<sup>4,5</sup> allows flight coordination and exploitation of diverse visual landscapes, and the astonishing variations of the beak enable a wide range of avian lifestyles. Here we use a geometric morphometric approach integrating developmental, neontological and palaeontological data to show that the heterochronic process of paedomorphosis, by which descendants resemble the juveniles of their ancestors, is responsible for several major evolutionary transitions in the origin of birds. We analysed the variability of a series of landmarks on all known theropod dinosaur skull ontogenies as well as outgroups and birds. The first dimension of variability captured ontogeny, indicating a conserved ontogenetic trajectory. The second dimension accounted for phylogenetic change towards more bird-like dinosaurs. Basally branching eumaniraptorans and avialans clustered with embryos of other archosaurs, indicating paedomorphosis. Our results reveal at least four paedomorphic episodes in the history of birds combined with localized peramorphosis (development beyond the adult state of ancestors) in the beak. Paedomorphic enlargement of the eyes and associated brain regions parallels the enlargement of the nasal cavity and olfactory brain in mammals<sup>6</sup>. This study can be a model for investigations of heterochrony in evolutionary transitions, illuminating the origin of adaptive features and inspiring studies of developmental mechanisms.

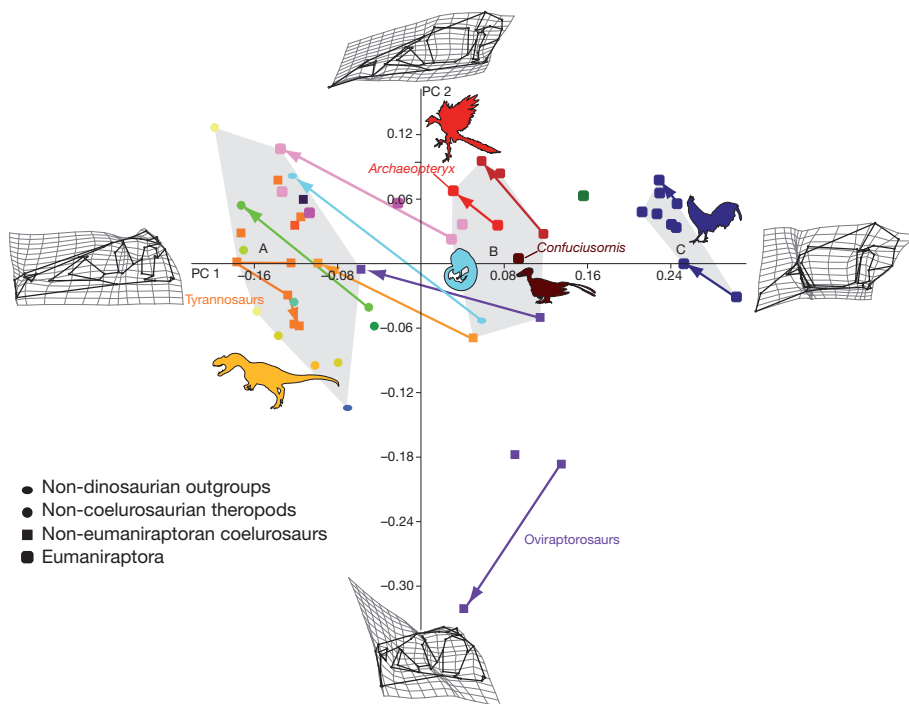
Birds are living theropod dinosaurs and are one branch of Archosauria ('ruling reptiles'), the other major branch of which consists of extant crocodylians and their stem lineage (Fig. 1a)<sup>7</sup>. Archosaurs diversified into several body plans on their divergence from the lizard/snake (lepidosaur) lineage in the Palaeozoic, including many adapted to macropredation<sup>7</sup>. Skulls of crocodylians (Fig. 1b) and early dinosaurs such as *Coelophysis* (Fig. 1c) undergo considerable ontogenetic change, the juveniles displaying the typical juvenile amniote features of relatively short facial (antorbital) regions and large brains and eyes. In contrast, basally branching members of the dinosaur clade Eumaniraptora,

which includes *Archaeopteryx* and modern birds, seem to change little from juvenile to adult. The Eichstätt and Berlin specimens of *Archaeopteryx* (Fig. 1d) are nearly identical cranially despite the fact



**Figure 1 | Archosaur phylogeny and ontogeny.** **a**, Phylogeny of included taxa. Sources are listed in Supplementary Information. Colours serve as keys to data points in Figs 2 and 5. Heterochronic transformations discussed in the text are enumerated as Roman numerals. **b–d**, skulls of selected archosaurs: *Alligator* 46-day embryo (**b**, left) and adult (**b**, right); *Coelophysis* (primitive dinosaur) juvenile (**c**, left) and adult (**c**, right); *Archaeopteryx* (stem-group bird) juvenile (**d**, left) and adult (**d**, right).

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**Figure 2** | PCA plot with outline images of hypothetical extremes along each axis, set on deformation grids from average. Colours correspond to those in Fig. 1a. Arrows indicate ontogenies. Major groupings are outlined, shaded and labelled. Group A are non-eumaniraptoran and secondarily large-bodied eumaniraptoran theropod adults; group B are adults of basal eumaniraptorans and early avialans, and embryos and perinates of other archosaurs; group C are crown-group bird embryos, juveniles and adults.

that the former is half the size of the latter and is ontogenetically the youngest of the known specimens<sup>8,9</sup>. Extant birds show a similar dearth of change<sup>10</sup>. Birds (here referring to the extant radiation) and their close relatives thus seem to be paedomorphic, retaining a morphology as adults that resembles that of the juveniles or embryos of most other archosaurs. This paedomorphosis is most evident in their relatively enormous eyes and enlarged brains, especially those regions correlated with visual function<sup>4,11–13</sup>.

Given these qualitative indications that bird skulls are paedomorphic, we tested this hypothesis with a principal-component analysis (PCA) of shape variation sampled broadly across theropods, using original photographs and computed tomography (CT) scans when possible, and novel or published reconstructions when this was not possible (Supplementary Information). To incorporate ontogeny into the analysis, we included all published juvenile–adult pairs or series of non-avian theropods, as well as selected modern birds and *Alligator*. Note that some of the juvenile–adult pairs—compsognathids and therizinosaurids, part of the tyrannosaur series—use different but closely related taxa. The stem archosaur *Euparkeria* was also included<sup>7</sup>.

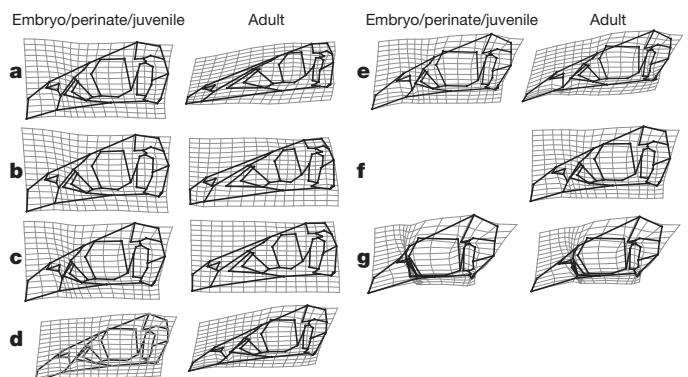
Forty-five landmarks (Supplementary Fig. 1) provided a comprehensive coverage of the lateral view of the cranium, the only view represented in some of the most important specimens, which are two-dimensionally crushed. New data including an undescribed perinate of the oviraptorid *Citipati* and CT scans of birds and crocodylians were employed.

The first two principal components (PCs) of the PCA explained 42.75% and 13.82% of the variation in the sample, respectively; all others explained less than 10% (Fig. 2). The first of these two principal axes (PC 1) largely accounted for ontogenetic change, revealing a conserved pattern of transformation across archosaurs (Supplementary Fig. 2 and Supplementary Information). Note, however, novel ontogenetic transformation related to gigantism in advanced tyrannosaurs; Supplementary Information and Supplementary Fig. 8). The second axis captured transformations between primitive archosaurs and the coelurosaurian theropods. PC 1, in the direction of ontogenetic growth, describes the extension of the face, the relative diminution of orbit and neurocranium, and a constriction in the lower temporal fenestra (Fig. 2 and Supplementary Movie). PC 2, towards coelurosaurian theropods, describes dorsoventral narrowing of the face, alterations in orbital and premaxillary shape, neurocranial

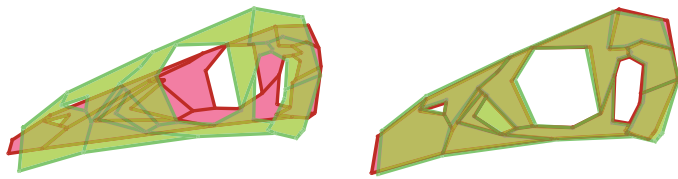
enlargement, and the characteristic posteroventral rotation of the braincase seen during evolution towards birds<sup>14</sup> (Fig. 2 and Supplementary Movie).

Taxonomic and functional groups separate along the axes (Fig. 2 and Supplementary Fig. 5). Early archosaurs cluster away from the more advanced theropods along PC 2. Giant theropods group together (Supplementary Fig. 6), a result consistent with those of a recent morphometric analysis of theropod skulls that excluded avialans and ontogenies, and used 24 landmarks<sup>15</sup>. Basally branching eumaniraptorans and avialans cluster, as do crown-clade birds. The early ornithurine *Yixianornis* spans the gap between these clusters, as might be expected phylogenetically. The morphologically disparate oviraptorosaurs occupy a unique region of the morphospace, separated from the other groups by their position along PC 2. An analysis without oviraptors yielded the same major clusters as the inclusive analysis (Supplementary Information and Supplementary Fig. 9).

Evidence for heterochrony is clear. Whereas adults of taxa distantly related to birds (non-eumaniraptorans) cluster together, basally branching bird relatives (eumaniraptorans) cluster with the embryos and youngest juveniles of other non-avian archosaurs (Figs 2 and 3), with the more crownward avialan *Confuciusornis* nearly identical to



**Figure 3** | Summary of ontogenetic changes in archosaur skulls; outlines on deformation grids from average. a, *Alligator*. b, Compsognathidae. c, Therizinosauridae. d, *Archaeopteryx*. e, Enantiornithes. f, *Confuciusornis*. g, Ostriches (*Struthio*).



**Figure 4 | Similarity of embryonic *Alligator* and adult *Confuciusornis* skulls.** Superimposition of *Alligator* embryo skull (green) onto *Alligator* adult skull (red, left) and onto *Confuciusornis* adult skull (red, right), showing the nearly identical skull configuration of the latter two and indicating paedomorphic cranial morphology in *Confuciusornis*.

embryos and particularly close to the perinate enantiornithine (Figs 3d and 4). The cluster of eumaniraptorans and non-avian embryos is widely separated from the adult cluster. Only a few specimens, all juvenile, intervene (Supplementary Fig. 6 and Supplementary Information). Groupings are confirmed by minimum-spanning-tree analysis (Supplementary Information and Supplementary Fig. 4). The clustering of adult early bird relatives with the youngest individuals of more basal archosaurs (Figs 2–4) supports the hypothesis of paedomorphosis. Moreover, at least four heterochronic transformations are evident (I–IV in Figs 1 and 5; see also Supplementary Information), although additional sampling along the avian stem might reveal more transitions: I, paedomorphosis between other theropods and Eumaniraptora; II, paedomorphosis between Eumaniraptora and *Confuciusornis*; III, general paedomorphosis plus localized peramorphosis (growth beyond the state in adult ancestors) in the premaxillary beak, between *Confuciusornis* and *Yixianornis*; and IV, paedomorphosis between *Yixianornis* and Aves. Before transformation I, a phylogenetic sequence moves largely along PC2, before taking an abrupt 90° turn to move in the reverse-ontogenetic direction along PC1 (Fig. 5). Extant birds are truly extreme, falling farther in that direction than late embryos and perinates of more conservative archosaurs (Fig. 3f, g).

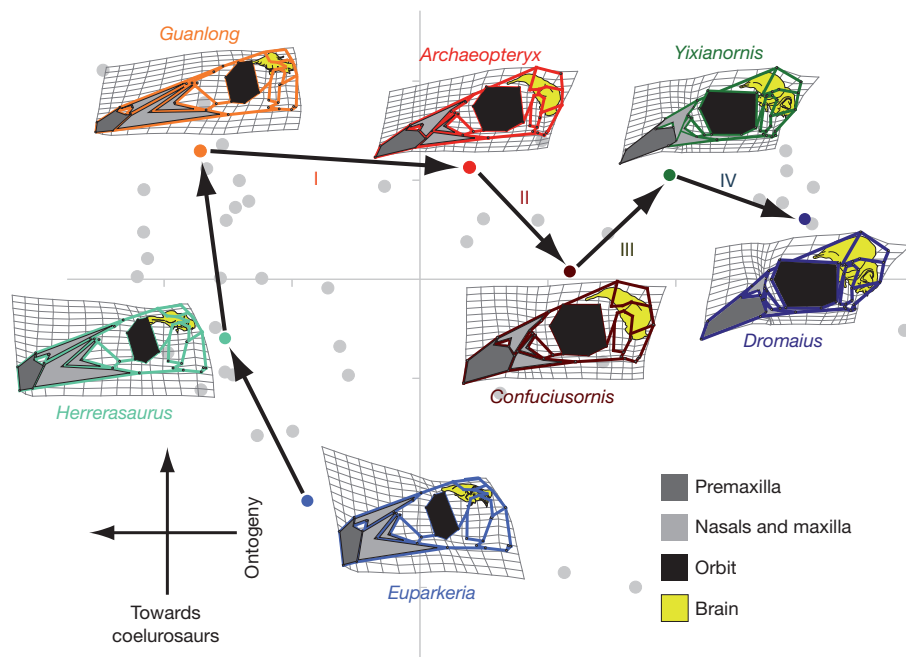
The paedomorphic trend holds even after size and phylogeny are statistically accounted for (Supplementary Information and Supplementary Figs 3–5). *Compsognathus* is tiny, yet as a non-eumaniraptoran it falls within the ancestral adult cluster; small size alone does not result in paedomorphic morphology. *Struthio* and

*Dromaius* are large but group with other birds. Transformations II–IV occurred among animals that were roughly the same size. Transformation I, however, was accompanied by a marked reduction in size.

A regression of shape change on centroid size as a proxy for ontogenetic time (Fig. 6 and Supplementary Information) demonstrates that birds and their close relatives (eumaniraptorans) have shorter ontogenetic trajectories along the PC axes (see also Supplementary Table 1 and the similarity of ontogenetic trajectories indicated by Supplementary Tables 3 and 4) than all other included archosaurs. These short trajectories are consistent with histological data that suggest that sexual and somatic maturation times were truncated during each heterochronic transformation (Supplementary Fig. 10 and Supplementary Table 2)<sup>16</sup>. As expected, compsognathids show an ancestral magnitude of shape change (along the  $y$  axis) despite their small adult size, whereas *Struthio* shows a bird-like magnitude despite its giant size. The aggregate of evidence suggests paedomorphosis by progenesis, early somatic maturation resulting in a truncated ontogeny<sup>17</sup>. Paedomorphosis by truncation is also supported by the position of secondarily larger-bodied eumaniraptorans—*Byronosaurus*, *Zanabazar* and *Velociraptor*—in the PCA. These animals were derived from much smaller, possibly volant, ancestors<sup>18</sup>. They have (secondarily) long ontogenetic trajectories and their adults cluster with advanced maniraptorans that diverged from the bird lineage before transformation I.

Strong support for a progenetic paedomorphic origin of the bird skull seemingly contradicts early work suggesting that simple paedomorphosis in the form of having “retained a juvenile shape” was not involved in the origin of the bird skeleton<sup>16</sup>. That work, however, discussed the postcranial skeleton. Birds do show several peramorphic features in their postcranial skeletons; however, direct comparison with fossil taxa is difficult because substantially complete embryonic postcrania are even rarer than skulls. Cranial evolution is modular with respect to the rest of the body and it is not unusual to find divergent rates of transformation between crania and postcrania, for instance in the origins of pterodactyloid pterosaurs<sup>19</sup> and the origin of mammals<sup>20,21</sup>.

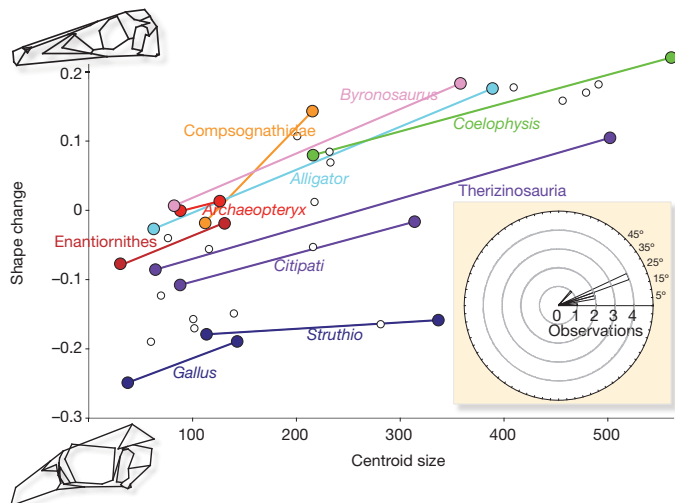
Despite the overwhelming imprint of paedomorphosis on the evolution of the bird skull in the collapse of the face and the enlargement of the brain, peramorphosis also occurs to form the distinctive elongate



**Figure 5 | Summary of heterochrony and phylogeny in bird skull evolution.** A phylogenetic sequence with skull outlines set on deformation grids is depicted from the primitive stem-group archosaur *Euparkeria* to the modern

emu *Dromaius*. Heterochronic transformations referred to in the text are enumerated with Roman numerals. Major anatomical regions involved in heterochronic transformations are labelled.





**Figure 6 | Regression of centroid size (as an indicator of skull size) on shape change, and distribution of vector angles.**

avian beak during transformation III (Figs 3 and 5)<sup>17,22</sup>. In addition, birds do not have embryonic brains. Instead, the neuronal complexity of their brains is elaborated relative to that of ancestral archosaurs<sup>23</sup>. Whereas the larger relative brain size is a pedomorphic feature, the elaboration of the neural tissue, in particular the optic regions, represents a more complex heterometric change<sup>14</sup>.

The brain emerges in this analysis as a major driver of theropod cranial anatomy (Fig. 5)<sup>23,24</sup>. Cranial transformations driven by optic elaboration during the origin of birds parallel olfactory elaboration during mammalian origins<sup>25</sup>. The brain is an early signalling centre during facial development<sup>25</sup> and it is possible that the posteroventral rotation of the brain is in part responsible for the collapse of the facial region in birds. *Archaeopteryx*-like elaboration of visually associated brain regions also appears in Eumaniraptora and may be correlated with some degree of volancy<sup>26</sup>. Although it has been suggested that reduction in body size, which we show accompanied heterochronic transformation I, was associated with the advent of dinosaurian flight<sup>16</sup>, our results agree with work suggesting that size reduction preceded powered flight<sup>18</sup>. This reduction may, however, have been a necessary precursor to flight exapted in its service. The origin of flight was a multistep process and it remains unclear precisely when volancy and powered flight respectively originated<sup>18</sup>. Finally, the peramorphic enlargement of the premaxilla to form a long, pointed beak (Fig. 5 and Supplementary Movie) is coupled with progressive loss of manual grasping ability as digits became bound into the wing<sup>27</sup>. Modern birds are known to perform fine manipulations with the precision tips of their beaks<sup>28</sup>. It may be that the beak evolved in part as a replacement for the eponymous raptorial hands of maniraptoran dinosaurs.

We have provided a powerful new example of how heterochronic changes, pedomorphic and peramorphic, were crucial in the origin and evolution of birds<sup>29</sup>. We further demonstrate that these changes were driven by an extreme degree of elaboration in vision-associated areas of the brain that parallels the olfactory elaboration of mammals, and possibly by the evolution of the face into a precision grasping mechanism as the hands were co-opted for flight.

## METHODS SUMMARY

Skull images were obtained from published literature. Original CT scans performed at the University of Texas High-Resolution X-Ray Scanning Facility (UTCT) and at the Harvard Center for Nanoscale Systems, photographs and novel reconstructions are detailed in the Supplementary Information. Scaling and digitization of landmarks used tpsDIG, and PCA was performed with the software packages TPSRelW, MorphoJ and PAST (see Supplementary Information for full citations). Size regression was performed and evolutionary data were obtained using MorphoJ. Full methods are provided in Supplementary Methods.

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**Supplementary Information** is linked to the online version of the paper at [www.nature.com/nature](http://www.nature.com/nature).

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**Author Contributions** B.-A.S.B. and A.A. designed the study. B.-A.S.B. wrote the paper and performed CT scans, data entry and analytical work. J.M.-L. performed analytical work and assisted with writing and figures. F.R. performed data entry and analytical work. G.B. helped conceive the project and performed data processing on new CT data. T.B.R. contributed CT data and assisted in data interpretation and writing the paper. M.A.N. contributed the major hypotheses to be tested, provided CT data and assisted in writing the paper. A.A. co-wrote the paper.

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