nature

https://doi.org/10.1038/s41586-020-2096-0

Supplementary information

Late Cretaceous neornithine from Europe illuminates the origins of crown birds

In the format provided by the authors and unedited

Daniel J. Field✉, Juan Benito, Albert Chen, John W. M. Jagt & Daniel T. Ksepka

Supplementary Information for:

Late Cretaceous neornithine from Europe illuminates crown bird origins

Daniel J. Field[1]*, Juan Benito[1,2], Albert Chen[1,2], John W.M. Jagt[3], Daniel T. Ksepka[4]

CONTENTS:

I: Museum Abbreviations

The following abbreviations denote the museum collections where fossil material discussed in this supplement is accessioned.

NHMM: Natuurhistorisch Museum Maastricht, The Netherlands

NHMUK: Natural History Museum, London and Tring, United Kingdom

USNM: United States National Museum, Washington D.C., U.S.A.

UMNH: Utah Museum of Natural History, Salt Lake City, UT, U.S.A.

UMZC: University Museum of Zoology, Cambridge, U.K.

UW: University of Wyoming Geological Museum, Laramie, WY, U.S.A.

II: Scan Parameters

NHMM 2013 008, UW *Presbyornis* specimens, and all extant taxa were scanned at the Cambridge Biotomography Centre (CBC). *Presbyornis* UMNH.VP.29030 and UMNH.VP.29031 were scanned at the University of Utah Health Science Cores small animal imaging core research facilities. *Anatalavis oxfordi* was scanned at the Natural History Museum London. Scanning parameters were as follows. All scanned material was digitally segmented and rendered using VGStudio Max 3.3.0.

NHMM 2013 008.1a (femur, tibiotarsus and skull block): Nikon Metrology XT H 225 ST High Resolution CT Scanner at CBC. 150 kV, 155 µA, 1080 projections, 2 frames per projection, copper filter.

NHMM 2013 008.2 (block containing partial tarsometatarsus and partial femur): Nikon Metrology XT H 225 ST High Resolution CT Scanner at CBC. 180 kV, 160 µA, 1080 projections, 2 frames per projection, copper filter.

NHMM 2013 008.3 (block containing partial tibiotarsus): Nikon Metrology XT H 225 ST High Resolution CT Scanner at CBC. 180 kV, 160 µA, 1080 projections, 2 frames per projection, copper filter.

NHMM 2013 008.4 (radius, skull roof, and unidentified element block): Nikon Metrology XT H 225 ST High Resolution CT Scanner at CBC. 180 kV, 160 µA, 1080 projections, 2 frames per projection, copper filter.

NHMM 2013 008.1b (femur, tibiotarsus and skull block): Nikon Metrology XT H 225 ST High Resolution CT Scanner at CBC. 180 kV, 235 µA, 3142 projections, 8 frames per projection, copper filter.

UW *Presbyornis* 2159 (partial femur): Nikon Metrology XT H 225 ST High Resolution CT Scanner at CBC. 125 kV, 175 µA, 2160 projections, 2 frames per projection, no filter.

UMZC extant specimens (UMZC 211.A *Anhima cornuta*, UMZC 395 *Meleagris gallopavo*, UMZC 225 *Anas platyrhynchos*): Nikon Metrology XT H 225 ST High Resolution CT Scanner at CBC. 130 kV, 120 µA, 1080 projections, 2 frames per projection, no filter.

NHMUK extant specimens (NHMUK S-2012.31.1 *Chauna torquata*, NHMUK S-2010.1.31 *Alectura lathami*): Nikon Metrology XT H 225 ST High Resolution CT Scanner at CBC. 130 kV, 165 µA, 3142 projections, 2 frames per projection, no filter.

NHMUK PV A5922 (*Anatalavis oxfordi*): Nikon Metrology XT H 225 ST High resolution CT Scanner the Natural History Museum (London) CT Facility. 110 kV, 136 µA, 3142 projections, 2 frames per projection, copper filter.

UMNH.VP. 29030 and UMNH.VP. 29031 (*Presbyornis pervetus*): Siemens Inveon Multi-modality microPET/SPECT/CT at the Preclinical Imaging Core Facility at the University of Utah. 2048 projections. 80 kV, 200 µA, 540 projections, no filter.

III: Supplementary Video Descriptions

Supplementary Video 01: NHMM 2013 008, Skull of *Asteriornis maastrichtensis* holotype, yaw video

Supplementary Video 02: NHMM 2013 008, Skull of *Asteriornis maastrichtensis* holotype, roll video

IV: Phylogenetic Analyses

We added the following new characters to the character list:

291. Retroarticular process: 0, absent; 1, present.

292: Retroarticular process, shape: 0, unhooked, projects caudally; 1, unhooked, tip directed dorsally (like in *Vegavis*); 2, hooked, tip directed dorsally (e.g., *Anas*, *Asteriornis*, *Anatalavis*).

293: Mandible, processus medialis, orientation in dorsal in view: 0, medially directed; 1, caudally deflected.

294: Interorbital region of frontals in dorsal view: 0, constricted at midpoint of orbit forming hourglass-like shape; 1, unconstricted at midpoint.

295: Nasal-premaxilla contact at tomial margin, degree of fusion: 0, unfused, suture visible; 1, sutures obliterated; 2, no contact.

296: Mesethmoid, rostral extent: 0, restricted to region caudal of antorbital fenestra; 1, extends rostral to caudal margin of antorbital fenestra; 2 extends almost to rostral tip of beak.

297: Shape of occipital condyle: 0, not as follows; 1, heart-shaped, with pronounced incisure in dorsal margin of condyle.

The states for character 1 originally described whether or not the premaxilla was “longer than the cranium”. Given that the premaxilla is part of the cranium, we reworded the character states as follows:

1: Premaxilla, length relative to cranium: 0, more than 50% total cranium length; 1, approximately 50% total cranium length; 2, less than 50% total cranium length.

We deleted state 3 (pterygoid fused to palatine) for character 43, because this state is already characterized by character 41 (os palatinum and os pterygoideum fused). Taxa originally scored with this state were rescored as inapplicable.

We deleted state 0 (absence of the basipterygoid facet on the pterygoid) for character 44 because this character state is correlated with the absence of basipterygoid processes, which is already characterized by character 27 (presence of basipterygoid processes). Taxa originally scored with this state were rescored as inapplicable.

Character 46 originally described whether or not the postorbital process was robust and projected rostrally. Given that this describes two uncorrelated character states (the robusticity and orientation of the postorbital process), we reworded character 46 as follows:

46: Postorbital process, primarily rostrally oriented, forming ventral margin of orbit: 0, no; 1, yes.

Character 64 originally characterized both the presence and proportions of the retroarticular process. To discretize these different character components and avoid redundancy with our new character 291, we modified character 64 as follows:

64: Retroarticular process, shape: 0, narrow (low dorsal-ventral height); 1, blade-like (dorsoventrally tall) but with short caudal projection (subequal to height at rostral base); 2, blade-like and long, length (about twice height of blade at rostral base); 3, short and rounded in lateral view (*Struthio*).

We changed character 260 (number of hypotarsal canals) from ordered to unordered to accommodate the fact that two hypotarsal canals are present in *Pelagornis* but entirely lacking in Eocene pelagornithid specimens[1], which we considered too fragmentary to be included in our analysis. The state of this character is unknown in *Protodontopteryx*.

We scored new characters and reassessed character scores for the pre-existing taxon sample through personal observation of extant taxa and consultation of the literature on fossil taxa. We removed three extant species (*Malacorhynchus membranaceus*, *Talegalla fuscirostris*, and *Eulipoa wallacei*) that we were not able to examine in person and represented clades that were already extensively sampled in our dataset (Anatidae and Megapodiidae).

The original taxon sampling for this dataset included a wide variety of extinct flightless neognaths (*Gastornis*, dromornithids, *Megavitiornis*, *Sylviornis*, *Brontornis*, and *Patagornis*). Preliminary analyses including these taxa resulted in a highly unstable topology that found little resolution within crown-birds and recovered likely spurious results that were

probably driven by convergent acquisition of flightlessness-related characters (such as gastornithiforms, usually found as galloanserans, instead forming a clade within Neoaves with the phorusrhacid *Patagornis*). Similar artefacts were also observed in some analyses of a previous version of this dataset[2]. Given that the phylogenetic affinities of these flightless birds were not a focal point of our study, we chose to remove these taxa from the dataset. The final version of our matrix contains 39 taxa and 297 characters.

The matrix was analysed under both maximum parsimony and Bayesian optimality criteria. For topologically constrained analyses, a molecular scaffold was implemented to enforce the relationships of extant and recently extinct taxa based on recent molecular phylogenetic studies[3-9]. Given that the internal topology of Neoaves remains contentious[8,10], the relationships among Gruiformes (*Antigone* + *Porphyrio*), *Burhinus*, and *Cariama* were left as an unresolved polytomy in our scaffold. The positions of fossil taxa were left unconstrained.

Phylogenetic results

Under a molecular scaffold, parsimony analysis recovered a single most parsimonious tree (MPT) of 1540 steps. *Asteriornis* was recovered as a member of Pangalloanserae with low bootstrap support (16%), weakly excluded from crown-Galloanserae (5%). *Vegavis* was recovered as the sister taxon to crown birds, weakly excluded from Neornithes (22%). Lithornithids were found as stem-palaeognaths, excluded from crown-Palaeognathae with moderate bootstrap support (55%). Pelagornithids and a clade uniting *Anatalavis* and *Conflicto* were found to be successively crownward stem-anseriforms (placed in total-group Anseriformes with bootstrap supports of 9% and 29% respectively). Presbyornithids were recovered as crown-anseriforms, weakly supported as the sister group to *Anseranas* (13%).

Given this topology, constraining *Asteriornis* to the stem of Anseriformes increases tree length by only a single step, and constraining it to the stem of Galliformes increases tree length by 2 steps, emphasising its probable phylogenetic position proximal to the galloanseran root divergence. *Vegavis* can be recovered as a stem-neognath with +2 steps. Only +2 steps are required for presbyornithids to be recovered as stem-anseriforms crownward of *Conflicto* as previously found[11]. The low bootstrap values across deeply diverging nodes in this tree are likely attributable to the unstable positions of these fossil taxa. Less parsimonious alternatives that we tested included *Vegavis* as a stem-galloanseran (+7 steps), stem-anseriform (minimally +8 steps), or crown-anseriform (minimally +12 steps), as well as pelagornithids as stem-galliforms (+5 steps), stem-galloanserans (minimally +6 steps), stem-neognaths (+7 steps), or total-group neoavians (minimally +7 steps).

A molecular scaffold was deemed necessary due to a number of pathological results obtained under unconstrained analyses employing both parsimony and Bayesian optimality criteria. The importance of incorporating molecular scaffolds in combination with this dataset has been previously noted[2] and attributed in part to homoplastic characters shared between flighted pan-palaeognaths (lithornithids and tinamous) and galliforms, which is consistent with our results. The unconstrained parsimony analysis recovered a single MPT of 1488 steps with *Asteriornis* as a crown-galliform on the stem of Megapodiidae with low bootstrap support (16%). This analysis returned numerous results in conflict with robust phylogenetic consensus, including ratite monophyly, a sister group relationship between Palaeognathae and Galliformes, a sister group relationship between Anseriformes and Neoaves, and internal relationships within Galliformes that were strongly incongruent with recent phylogenetic studies. As such, we focus on the results of analyses performed under molecular scaffolds.

Under Bayesian tip-dating with a soft maximum of 86.5 Ma for Neornithes, *Asteriornis* was recovered as the most stemward pan-galliform. The clade uniting

198 *Gallinuloides* and crown-Galliformes was supported by PP=0.87 and *Asteriornis* was
199 supported as the sister group to this clade by PP=0.93. *Vegavis* was part of a polytomy at the
200 base of Neognathae along with total-group Neoaves and Galloanserae (PP=0.69).
201 Pelagornithids were weakly recovered as total-group neoavians (PP=0.61), whereas
202 (*Anatalavis* + *Conflicto*) and presbyornithids were found as successively crownward stem-
203 anseriforms (PP=0.97 and PP=0.91 respectively). Bayesian tip-dating under the more
204 restrictive soft maximum of 72.72 Ma for Neornithes recovered a nearly identical topology
205 with comparable nodal support values to the other tip-dating analysis, though a small number
206 of nodes were more poorly resolved. For example, lithornithids collapsed into a polytomy at
207 the base of total-group Palaeognathae instead of forming a monophyletic group. The
208 *Anatalavis-Conflicto* clade also collapsed into a polytomy at the base of the anseriform total-
209 group (Anserimorphae).
210 Undated Bayesian analysis recovered *Asteriornis* as a stem-galliform one node
211 crownward of *Gallinuloides*, an inferred position we consider improbable. This result likely
212 stems from idiosyncratic preservation of character states optimising as synapomorphies for
213 *Asteriornis* and megapodes (i.e. unfused splenial) that cannot be coded for *Gallinuloides*, and
214 the lack of postcranial skeletal elements for *Asteriornis*, such as the pectoral girdle, which
215 bear plesiomorphic character states in *Gallinulloides*. The clade uniting *Asteriornis* and
216 crown-galliforms to the exclusion of *Gallinuloides* was weakly supported (PP=0.68), but
217 statistical support for uniting *Gallinuloides*, *Asteriornis*, and crown-Galliformes was strong
218 (PP=1). In this analysis lithornithids were recovered as a grade leading up to crown-
219 palaeognaths (excluded from the crown by PP=0.87). *Vegavis* formed a polytomy in
220 Neognathae along with Neoaves, Anseriformes, and Pangalliformes (PP=0.81).
221 Presbyornithids and (*Anatalavis* + *Conflicto*) formed a clade (PP=0.71) of crown-anseriforms,

sister to Anseres (PP=0.74). Pelagornithids were recovered as stem-galliforms stemward of *Gallinuloides* (PP=0.82).

We compared alternative phylogenetic positions for *Asteriornis* within a Bayesian framework using the stepping-stone sampling method[12], implemented in MrBayes. Three alternative topologies were tested: *Asteriornis* as a stem-galliform, *Asteriornis* as a stem-anseriform, and *Asteriornis* as a stem-galloanseran. For each alternative topology, a stepping-stone analysis was run for 30,000,000 generations (divided into 50 steps with convergence being attained in each step). In contrast to our results from tree length comparisons under parsimony, the stepping-stone analyses assigned the highest marginal likelihood to a stem-galliform position for *Asteriornis* [ln(mean marginal likelihood) of -5171.80, compared with -5179.39 for a position as a stem-anseriform and -5181.61 for a position as a stem-galloanseran]. When subjected to a standard Bayes factor (BF) test ($2\times\log_e BF$)[13], the difference in marginal likelihood of a stem-galliform position and that of a stem-anseriform position results in a value of 15.18, whereas this value is 19.62 when stem-galliform and stem-galloanseran hypotheses are compared. $2\times\log_e BF > 10$ has been considered "very strong" support for a specific hypothesis[14]. Thus, our stepping-stone analyses favour a stem-galliform position for *Asteriornis*, consistent with its placement in Bayesian phylogenetic analyses. Despite this, we found that few or no unambiguous synapomorphies can be optimized in support of an *Asteriornis* + Galliformes clade to the exclusion of anseriforms, with the few potential synapomorphies observable in *Asteriornis* also known to be present in early pan-anseriforms such as *Conflicto* (see Supplementary Information section VIII). Considering this, along with ongoing debates about the suitability of standard Bayesian models for approximating morphological evolution[15], we recommend caution in the interpretation of *Asteriornis* as a stem-galliform. Moreover, inconsistency in the phylogenetic placement of *Asteriornis* across different optimality criteria may be consistent with the fossil

247 occupying a short phylogenetic branch proximal to the ancestral node for Galloanserae, one
248 of the deepest phylogenetic bifurcations in the neornithine tree of life[16].

249 To provide a metric of comparison between our parsimony and Bayesian results, we
250 reconstructed the topologies recovered by our Bayesian analyses in TNT and compared their
251 tree lengths to that of the MPT recovered in our constrained parsimony analysis. The shortest
252 tree that is both compatible with the undated Bayesian topology and does not violate the
253 molecular scaffold is 13 steps longer than the MPT, whereas the shortest tree compatible with
254 the tip-dated topologies is +8 steps. Although some recent studies have argued that Bayesian
255 analyses of morphological data provide more accurate estimates of phylogenetic relationships
256 than parsimony[17,18], others have considered a +12-14 step difference in tree length to be
257 sufficient to reject alternative phylogenetic hypotheses[19]. Evaluating the relative merits of
258 parsimony and Bayesian phylogenetic methods is beyond the scope of this study; however, if
259 Bayesian phylogenetic methods do indeed produce more accurate results than parsimony,
260 perhaps the acceptable threshold of plausibility for alternate topologies based on tree length
261 should be reassessed in future studies. It is also noteworthy that our tip-dated topology was
262 found to be more parsimonious than its undated counterpart. Whether this is a consistent
263 pattern across different phylogenetic datasets and study taxa remains to be seen.

264 Although we urge caution in the interpretation of divergence time results from our
265 Bayesian tip-dating analyses, especially in light of research that suggests tip-dating under the
266 fossilized-birth death model is likely to overestimate divergence times when taxon sampling
267 is selective[20] (a hypothesis our findings appear to corroborate), we present these results for
268 completeness. The tip-dating analysis using the older soft maximum estimated a mean origin
269 date for crown-birds at 107.23 Ma. Under the younger soft maximum, we found a slightly
270 younger origin date of 89.85 Ma. These values bracket the ~100 Ma origin date estimated by
271 some molecular divergence time studies[5]. We estimated the Neoaves-Galloanserae split at

101.59 Ma under the older soft maximum and 86.83 Ma under the younger soft maximum, also bracketing some molecular divergence time estimates of ~88 Ma[5]. The split between Anseriformes and Galliformes was estimated at 93.56 Ma under the older soft maximum and 81.73 Ma under the younger soft maximum, which are both considerably older than the estimates from two recent and influential molecular divergence time studies: Jarvis et al. (2014) (~65 Ma)[5] and Prum et al. (2015) (~54 Ma)[6]. However, it should be noted that both of those studies predated the description of the Paleocene total-group anseriform *Conflicto*[11]. As a result, both studies calibrated the root galloanseran divergence using Eocene-aged fossils much younger than the oldest fossil pan-galloanserans included in our study. Nonetheless, these tip-dating analyses do not accommodate the potential for accelerated rates of evolutionary change in the lowermost Cenozoic, which may lead to pronounced overestimates of phylogenetic divergence times[21,22].

Comparisons with previously published phylogenetic results

Vegavis was originally described as a crown-anseriform closely related to Anatidae[23] and has been recommended as a fossil calibration for the divergence between Anatidae and *Anseranas*[24]. However, it has also recently been recovered as a stem-anseriform[2], and some authors have considered a position outside of crown-Galloanserae[25] or even Neornithes[26,27] to be plausible. Although our study does not conclusively resolve the affinities of *Vegavis*, our phylogenetic analyses place it alternatively as a stem-bird or in an unresolved position within Neognathae. A position for *Vegavis* within crown-Anseriformes was found to be poorly supported by our dataset, supporting the general hypothesis of a limited degree of crown bird diversification in the Mesozoic.

Recent studies have generally recovered presbyornithids as members of crown-Anseriformes, often closely allied to Anatidae[2,23,28,29]. However, Tambussi et al. (2019)[11]

297 instead found them as stem-anseriforms. Our parsimony and undated Bayesian analyses
298 favoured the traditional placement of presbyornithids within the anseriform crown group, but
299 we also found that a stem-anseriform position was only slightly less parsimonious and
300 recovered them on the anseriform stem in our tip-dating analyses. Furthermore, in our tree
301 topologies that recovered presbyornithids as crown-anseriforms, we found that
302 presbyornithids often exhibited reversals of character states that were optimized as crown-
303 anseriform synapomorphies (see Supplementary Information section VIII), which may reflect
304 either a phylogenetic position on the anseriform stem or secondary acquisition of
305 plesiomorphic characters. Thus, a thorough reassessment of how presbyornithids relate to
306 extant anseriforms awaits investigation by future studies, with implications for questions such
307 as whether some distinctively 'galliform-like' features of screamers (Anhimidae) represent
308 galloanseran plesiomorphies or autapomorphic reversals[11,30,31]. Given the abundance of
309 presbyornithid fossils in Paleogene deposits as well as their purported presence in
310 Cretaceous-aged sediments[31], a robust understanding of presbyornithid affinities will likely
311 be critical for elucidating the evolutionary history of anseriforms and calibrating divergence
312 times for crown-birds.

313 Our parsimony and tip-dating analyses corroborate the results of Tambussi et al.
314 (2019)[11] in placing *Anatalavis* and *Conflicto* in a monophyletic group along the anseriform
315 stem lineage, though our undated Bayesian analysis suggests that a position within the
316 anseriform crown may still be plausible. In none of our analyses do we recover a close
317 relationship between *Anatalavis* and *Anseranas*, as was proposed in the original description
318 of *Anatalavis oxfordi*[32], emphasising the importance of a thorough re-evaluation of the
319 morphology and phylogenetic position of this fossil taxon.

320 Despite being potential early-diverging pan-galloanserans or pan-neognaths of
321 controversial phylogenetic position[33], pelagornithids had not been included in previous

iterations of this phylogenetic dataset. Our analyses do not recover a consistent position for pelagornithids within Neognathae, variably positioning them as stem-anseriforms, stem-galliforms, or stem-neoavians. Although a detailed assessment of pelagornithid affinities was not the focus of this study, we consider it noteworthy that we find a stem-anseriform position to be the most parsimonious hypothesis, as suggested in one of the earliest studies of the phylogenetic affinities of these birds[34].

All of our phylogenetic analyses were consistent in allying *Asteriornis* with members of Galloanserae. The most parsimonious topology recovered *Asteriornis* as the only known stem galloanseran. All of our analyses employing molecular scaffolds, regardless of optimality criterion, recovered it as an early-diverging member of Pangalloanserae, either as a stem-galloanseran or an early stem-galliform. Furthermore, evaluation of alternative tree topologies by comparing tree length found positions for *Asteriornis* as a stem-galloanseran, an early stem-galliform, or an early stem-anseriform to be almost equally parsimonious, presumably reflecting its phylogenetic and temporal proximity to the ancestral divergence of the anseriform and galliform total groups. In contrast, our Bayesian stepping-stone analyses recovered strong support for stem-galliform affinities. However, we stress that we could identify little unambiguous anatomical evidence to support that position. As such, we refrain from confidently rejecting any of those three alternative placements for *Asteriornis*, but it appears clear that it represents a pan-galloanseran close to the origin of crown Galloanserae regardless of its precise position within the galloanseran total group.

V: Provenance Data for New Fossil Material

NHMM 2013 008 was recovered from just above the contact between the uppermost portion of the Lanaye Member of the Gulpen Formation and the overlying Valkenburg Member of the Maastricht Formation at the Cimenterie Belge Réunie (CBR)-Romontbos

quarry (outcrop 61H-45), west of Eben Emael, province of Liège, Belgium. It is preserved in a matrix composed of comparatively fine-grained, poorly indurated, pale yellow biocalcarenite with a limited macrofossil content, matching the typical lithology of the lower part of the Maastricht Formation (Valkenburg and Gronsveld members)[35-37].

The specimen was collected in 2000 by Maarten van Dinther (Leiden, The Netherlands). At this locality, the uppermost portion of the Lanaye Member (flint levels 20, 21, 22 and 23) is well exposed, although no fossil hash level (known as the Lichtenberg Horizon) separates the Gulpen and Maastricht Formations, unlike in adjacent quarries. Consequently, the position of the Lichtenberg Horizon is inferred from thickness of the Valkenburg and Gronsveld members of the Maastricht Formation[38-40]. The upper Maastricht Formation is truncated at this locality, with the highest portion corresponding to the Kanne Horizon of the Nekum Member. In the adjoining Dutch province of Limburg the overlying Meerssen Member preserves the K-Pg boundary corresponding to the Berg en Terblijt Horizon, as well as the overlying lower Paleocene (lower-middle Danian) Geulhem Member (Houthem Formation).

Based on the most recent cyclostratigraphic and chronostratigraphic age models for the type Maastrichtian[40], the base of the Valkenburg Member (i.e., the contact between the Gulpen and Maastricht formations) is dated to 66.8 Ma, and the base of the overlying Gronsveld Member (St Pieter Horizon) is dated to 66.7 Ma. An unnamed putative ichthyornithine avialan (NHMM RD 271) was recovered from a roughly equivalent level in the basal Valkenburg Member[41,42], and, based on estimated sedimentation rates (~6.4m per 100 kyr)[37,40] their temporal separation cannot amount to more than tens of thousands of years. This horizon is interpreted to represent the early stages of a transgression from a relative lowstand during a tectonic inversion phase, while the overlying Gronsveld Member

represents a relative highstand during tectonic relaxation[43], with the maximum flooding surface situated around the middle of this unit.

In the western part of southern Limburg (the Netherlands) and adjoining Belgian territory (province of Liège), the Valkenburg Member comprises poorly indurated, white-yellowish to yellowish-grey, fine- to coarse-grained biocalcarenites, with greyish brown flint nodules of varying sizes. The overlying Gronsveld Member consists of poorly indurated, white-yellowish to yellowish-grey, fine- to coarse-grained biocalcarenites, with small, light to dark greyish-brown flint nodules of varying sizes and shapes occurring in the lower part. In the higher portion they are arranged in more or less regular beds of light-grey to greyish blue nodules. The lower Maastricht Formation has been considered to represent a gravelly intrabiomicrosparite, with regional currents constant enough to horizontally displace sediment particles over the entire platform, at depths of 20 to 40m and free from oceanic influence[44]. Sediment reworking resulted in their homogenisation over depths of a few decimetres, resulting in a relatively firm sea floor and clear waters. This setting has been interpreted as middle sublittoral, with subtropical temperatures and seagrass communities[45].

VI: Phylogenetic Definitions of Relevant Clade Names

Taxon	Phylogenetic definition
Avialae Gauthier, 1986[46]	The most inclusive clade including *Passer domesticus* but not *Deinonychus antirrhopus* or *Stenonychosaurus inequalis*.
Notes: Definition modified from Maryańska et al. (2002)[47]. Several competing phylogenetic definitions of Avialae have been proposed, but this one is consistent with widespread usage by recent studies (e.g.: Godefroit et al., 2013[48]; Hendrickx et al., 2015[49]).	
Neornithes Gadow, 1892[50]	The least inclusive clade including *Struthio camelus* and *Passer domesticus*.

Notes: Definition following Sereno (1998)[51]. This clade corresponds to the bird crown group. As used here, this name is equivalent to Aves *sensu* Gauthier and de Queiroz (2001)[52].	
Panpalaeognathae Gauthier and de Queiroz, 2001[52]	The most inclusive clade including *Struthio camelus* and *Tinamus major* but not *Gallus gallus* or *Vultur gryphus*.
Notes: Definition following Gauthier and de Queiroz (2001)[52]. This clade corresponds to the palaeognath total group.	
Palaeognathae Pycraft, 1900[53]	The least inclusive clade including *Struthio camelus* and *Tinamus major*.
Notes: Definition following Gauthier and de Queiroz (2001)[52]. This clade corresponds to the palaeognath crown group. Gauthier and de Queiroz[52] originally defined this clade under the assumption that tinamous and "ratites" form mutually exclusive clades, but recent molecular phylogenetic and developmental studies have provided a strong and consistent signal that the latter are paraphyletic with respect to the former[6,7,54-60], which raises the question of whether the addition of further internal specifiers may be necessary for taxonomic stability. However, these studies uniformly recover *Struthio* as the extant sister group of all other palaeognaths, thus the definition of Gauthier and de Queiroz[52] maintains the intended taxonomic scope of this name without additional internal specifiers.	
Notopalaeognathae Yuri et al., 2013[61]	The least inclusive clade including *Tinamus major*, *Rhea americana*, *Casuarius casuarius*, and *Apteryx australis*.
Notes: Yuri et al. (2013)[61] coined this name for the group uniting all extant palaeognaths other than *Struthio*, which is strongly supported as a clade by recent phylogenetic studies (see notes for Palaeognathae). Our proposed definition reflects their intended taxonomic scope.	
Panneognathae Gauthier and de Queiroz, 2001[52]	The most inclusive clade including *Pluvialis apricaria* but not *Struthio camelus* or *Tinamus major*.
Notes: Definition following Gauthier and de Queiroz (2001)[52]. This clade corresponds to the neognath total group.	

Neognathae Pycraft, 1900[53]	The least inclusive clade including *Anser anser* and *Pluvialis apricaria*.
Notes: Definition modified from Gauthier and de Queiroz (2001)[52]. This clade corresponds to the neognath crown group.	
Panneoaves Gauthier and de Queiroz, 2001[52]	The most inclusive clade including *Passer domesticus* but not *Anser anser* or *Gallus gallus*.
Notes: Definition following Gauthier and de Queiroz (2001)[52]. This clade corresponds to the neoavian total group.	
Neoaves Sibley et al., 1988[62]	The least inclusive clade including *Phoenicopterus ruber*, *Columba oenas*, *Otis tarda*, *Musophaga violacea*, *Caprimulgus europaeus*, *Opisthocomus hoazin*, *Grus grus*, *Charadrius hiaticula*, *Phaethon aethereus*, *Procellaria aequinoctialis*, and *Passer domesticus*.
Notes: Definition modified from Gauthier and de Queiroz (2001)[52]. This clade corresponds to the neoavian crown group. The precise interrelationships of neoavian birds remain unsettled, thus the internal specifiers here include representatives from all major subgroups consistently recovered as monophyletic by recent studies[5,6,8]: Mirandornithes (*Phoenicopterus ruber*), Columbimorphae (*Columba oenas*), Otidimorphae (*Otis tarda* and *Musophaga violacea*), Strisores (*Caprimulgus europaeus*), Opisthocomiformes (*Opisthocomus hoazin*), Gruiformes (*Grus grus*), Charadriiformes (*Charadrius hiaticula*), Phaethontimorphae (*Phaethon aethereus*), Aequornithes (*Procellaria aequinoctialis*), and Telluraves (*Passer domesticus*).	
Pangalloanserae Gauthier and de Queiroz, 2001[52]	The most inclusive clade including *Anser anser* and *Gallus gallus* but not *Passer domesticus*.
Notes: Definition following Gauthier and de Queiroz (2001)[52]. This clade corresponds to the galloanseran total group.	
Galloanserae Sibley et al., 1988[62]	The least inclusive clade including *Anser anser* and *Gallus gallus*.
Notes: Definition following Gauthier and de Queiroz (2001)[52]. This clade corresponds to the	

galloanseran crown group. Mayr (2011a)[63] advocated for the use of Galloanseres Weber, 1993[64] for this group because it shares the same suffix as Neoaves, which is strongly supported as the extant sister group of this clade. However, here we favour the earlier-named Galloanserae based on nomenclatural priority. Moreover, given perpetual shifts in the understanding of phylogenetic relationships and the absence of formal regulation on suffix formation of higher-order clades, amending the names of all taxa to reflect sister-group relationships across the tree of life is likely impractical.	
Anserimorphae Sibley et al., 1988[62]	The most inclusive clade including *Anser anser* but not *Gallus gallus*.
Notes: This name has been used to encompass both crown-anseriforms and putative stem-anseriforms, including distinctive taxa such as *Gastornis* (Andors, 1992)[65]. As such, here we define it such that it corresponds to the anseriform total group (pan-Anseriformes). A branch-based phylogenetic definition is also consistent with those of other taxon names in the bird total group that end in "-morpha" or "-morphae", such as Dinosauromorpha (Nesbitt, 2011)[66], Maniraptoromorpha (Cau, 2018)[67], and Caprimulgimorphae (Chen et al., 2019)[68].	
Odontoanserae Bourdon, 2005[34]	The most inclusive clade including *Pelagornis miocaenus* and *Anser anser* but not *Gallus gallus* or *Passer domesticus*.
Notes: Bourdon (2005)[34] coined this name in accordance with a specific phylogenetic hypothesis, that pelagornithids and anseriforms form a clade exclusive of galliforms or neoavians. As such, our proposed definition reflects this topology. Under studies that do not recover this grouping as a clade (e.g.: Mayr, 2011b[33]), this name would not be formally recognized.	
Anseriformes (Wagler, 1831)[69]	The least inclusive clade including *Anhima cornuta*, *Anseranas semipalmata*, and *Anser anser*.
Notes: Definition modified from Martyniuk (2012)[70]. This corresponds to the anseriform crown group, following the recommendation by Gauthier and de Queiroz (2001)[52] that widely used and long-established taxon names originally based on extant taxa should be assigned crown-group phylogenetic definitions.	

Anseres Linnaeus, 1758[71]	The least inclusive clade including *Anseranas semipalmata* and *Anser anser*.
Notes: Our proposed definition follows the intended taxonomic scope of this name outlined by Livezey (1997)[29]. As used here, this name is equivalent to Anatoidea *sensu* Worthy et al. (2017)[2].	
Anatoidea Leach, 1820[72]	The most inclusive clade including *Anas platyrhynchos* but not *Anseranas semipalmata*.
Notes: Definition modified from Martyniuk (2012)[70]. This definition follows the intended taxonomic scope of this name outlined by Livezey (1997)[29].	
Pangalliformes Clarke, 2004[73]	The most inclusive clade including *Gallus gallus* but not *Anser anser*.
Notes: Definition following Clarke (2004)[73]. This clade corresponds to the galliform total group.	
Galliformes (Temminck, 1820)[74]	The least inclusive clade including *Megapodius freycinet*, *Crax rubra*, *Numida meleagris*, *Odontophorus gujanensis*, and *Gallus gallus*.
Notes: This corresponds to the galliform crown group. Our proposed definition follows similar reasoning to that presented under notes for Anseriformes. As used here, this name is equivalent to Galli *sensu* Worthy et al. (2017)[2].	
Phasianoidea Vigors, 1825[75]	The least inclusive clade including *Numida meleagris*, *Odontophorus gujanensis*, and *Phasianus colchicus*.
Notes: This name is widely used in recent literature[76,77] to unite the galliform clades Numididae, Odontophoridae, and Phasianidae. As such, our proposed definition reflects this usage.	

VII: Additional Anatomical Observations

NHMM 2013 008 represents the first figured and described skull of a crown bird from the Mesozoic. The specimen comprises a near-complete, three-dimensional skull lacking the occipital region, lacrimals, pterygoids, and vomer. In addition to the skull it also comprises complete lower jaws and several incomplete long bone shafts, identified as parts of both

femora, both tibiotarsi, one tarsometatarsus, one unidentified long bone shaft, and a distal radius.

Measurements of holotype

Measurements are in mm.

Maximum skull width in dorsal view, 15.4 ; *skull width at midpoint of orbits,* 6.0 ; *maximum length of right naris,* 12.7 ; *maximum length of left naris,* 14.1 ; *maximum width of internarial bar,* 3.2 ; *midpoint width of internarial bar,* 2.3 ; *maximum length of postorbital process,* 7.1 ; *bill length (tip of premaxilla to nasofrontal hinge),* 26.9 ; *maximum width of bill in dorsal view,* 6.6 ; *maximum length of left mandible,* 35.3, *maximum depth of left mandible,* 7.9 ; *midpoint depth of left mandible,* 4.1 ; *maximum length of right mandible,* 42.4 ; *maximum depth of right mandible,* 9.1 ; *midpoint depth of right mandible,* 3.7 ; *maximum length of left retroarticular process,* 5.1 ; *maximum width of left retroarticular process,* 2.9 ; *maximum length of medial process of right mandible,* 6.5 ; *minimum mediolateral width of tarsometatarsus shaft,* 3.3 ; *maximum length of right femur,* 53.14* ; *maximum length of tarsometatarsus fragment and contiguous impression,* 60.08 ; *maximum length of longest tarsometatarsus fragment and contiguous impression,* 60.84.

*This measurement spans two blocks, and is likely a slight overestimate

Description and comparisons

Much of the skull, including the premaxillae and nasals, are preserved in life position in their entireties, as are both lower jaws. The frontal and the right circumorbital elements are similarly undisplaced, although the caudal end of the frontal, caudal to the postorbital process, is fractured where the specimen was broken into two blocks during collection. The left quadrate is virtually complete and undistorted, and additional cranial elements at least

419 partially preserved include the jugals, palatines, maxillae, basisphenoid and mesethmoid. The
420 block containing the majority of the skull includes a well-preserved distal femur and a partial
421 shaft of a tibiotarsus. The specimen comprises three additional blocks which contain a
422 number of partial postcranial elements and a fragment of the skull roof.

423 Most major cranial components are largely in their original anatomical positions in
424 NHMM 2013 008. Major distortion and breakage of the skull is limited to its caudal end,
425 with a portion of skull roof near the frontoparietal suture preserved in a separate block, and
426 the temporal and occipital regions unpreserved. The pterygoids and vomer appear to be
427 absent, most likely displaced taphonomically by the dorsal displacement of the mandibles
428 into the buccal cavity (Extended Data Figs.1-3). Part of the processus maxillaris of the left
429 palatine appears to be present in its original orientation. This element is narrow and elongate,
430 comparable in width to the jugal as in extant galliforms such as *Meleagris gallopavo*. The
431 element is flattened and slightly ventrally concave in cross-section, similar to the condition in
432 extant Galliformes and unlike the more complex, subtriangular cross-sectional shape of the
433 processus maxillaris in *Anas platyrhynchos*. Although the vomer is unpreserved, the
434 morphology of the palatine would seem to be consistent with a schizognathous palate for
435 *Asteriornis*, as in extant galliforms. The right femur has been preserved in contact with the
436 postorbital process along the right surface of the skull. Some breakage of the right lateral
437 surface of the frontal and the right os laterosphenoidale appears to be caused by displacement
438 from the femur. Smooth bone surfaces indicate that the individual was skeletally mature[78].

439 The left and right maxillae are present as poorly ossified elements in life position,
440 medial to the nasals and the maxillary processes of the premaxillae. Both maxillae exhibit
441 vertically oriented plate-like nasal processes and do not appear to contribute substantially to
442 the palatal surface of the beak. The right maxilla is in better condition than the left, and is
443 preserved in association with the right palatine, with a short, sheet-like maxillopalatine

process overlying the rostral end of the palatine. An opening perforates the main body of both maxillae, similar to the ventral foramen that has been identified in some extant neoavian clades but seems to be absent in extant galloanserans[79].

The ethmoid complex and the septum interorbitale are largely intact; however, the left quadrate is medially displaced, with the orbital process and pars mandibularis medialis partially penetrating the septum interorbitale. Correspondingly the rostral terminus of the quadrate's orbital process is poorly preserved, though the remainder of the quadrate is well preserved in three dimensions.

The dorsally positioned fonticulus orbitocranialis (*sensu*[80]) is large and subtriangular in shape. The proportions are reminiscent of those in extant Mirandornithes such as *Phoenicopterus ruber* and *Podiceps cristatus*. The proportions of this fonticulus are larger than those in examined Galloanserae, where the fonticulus is completely absent in *Chauna*, and smaller in *Anas platyrhynchos*, which exhibits a similar subtriangular shape. In *Meleagris* this fonticulus is a narrow, horizontally elongated gap running between the midpoint of the mesethmoid and the ventral surface of the frontals, and is more open at earlier ontogenetic stages.

The caudally positioned foramen nervi optici is also relatively large, somewhat larger than but otherwise comparable in shape and position to that in examined galliforms and anseriforms.

A large element of uncertain identity lies along the left lateral margin of the skull, partially crushing the left postorbital region. This element appears to have caused the medial displacement of the left quadrate as noted above, and may have also displaced the jugals from the left side of the skull. The texture of this element's cortical bone in cross section differs from that of the remainder of the skull in NHMM 2013 008, suggesting that the element likely derives from another source, possibly representing a partial actinopterygian jaw.

469 The zona flexoria craniofacialis exhibits limited breakage, and there has been minor
470 lateral displacement of the rostral portion of the facial region relative to the rest of the skull.
471 Measurement of the frontal processes of the premaxillae suggests that the rostral portion of
472 the skull has been displaced ~1.5mm to the right. The rostral cranial elements of galliforms
473 often separate from the rest of the skull in osteological preparations due to limited fusion of
474 these elements[30], and the slight displacement of the rostral cranial elements in NHMM 2013
475 008 may be related to a similar lack of joint fusion in this region of the skull. The well
476 preserved and largely undisplaced elements in this region allow characterization of the zona
477 flexoria craniofacialis as lacking the distinct nasofrontal hinge that is present in most
478 Anseriformes; as such the architecture of this region more closely resembles that of crown
479 Galliformes where the zona flexoria exhibits a slight depression. The absence of a distinct
480 nasofrontal hinge in NHMM 2013 008 suggests the well-defined hinge of Anseriformes is
481 apomorphic for this clade.
482 A substantial portion of the left jugal, ~4.5mm in length, is preserved in its original
483 position. The jugal is subtriangular in cross-section, and is less mediolaterally flattened than
484 that of *Meleagris gallopavo*, and substantially less so than the extreme mediolaterally
485 compressed morphology of *Anas platyrhynchos*. Caudal to that element, a displaced fragment
486 of either the jugal or quadratojugal has rotated into a position perpendicular to the main
487 portion of the jugal. This element exhibits a similar subtriangular cross-sectional shape as the
488 main jugal fragment. The zygoma is rarely preserved in Mesozoic Avialae[81], and the origin of
489 the crown bird kinetic system is only gradually being elucidated[82]. As such, the preservation
490 of kinetic system components such as the jugal and the quadrate in NHMM 2013 008 is
491 notable.
492 The basicranium is relatively poorly preserved. This region of the skull is rarely
493 preserved in avialan fossils of any age owing to its delicate nature. The basisphenoid is

494 partially preserved, and its caudal end extends along the posteroventral surface of the
495 mesethmoid before terminating due to breakage. This breakage occurs caudal to the
496 parasphenoid rostrum, and assessment of the basipterygoid processes and detailed
497 basisphenoid morphology is precluded due to poor preservation. The internal canal of the
498 tuba auditiva appears visible in certain views, but is too poorly preserved to draw any firm
499 conclusions regarding its morphology. Fragmentary components of the prootic and
500 laterosphenoid may also be present in this region but are challenging to distinguish
501 unambiguously due to distortion and breakage.
502 The right lateral surface of the cranium is more complete than the left lateral surface,
503 and exhibits a well-preserved postorbital region. However, the postorbital process and
504 surrounding components of the frontal and laterosphenoid appear to be slightly rostrally
505 displaced (~1-2mm) due to contact with the femur. By contrast, the left lateral surface of the
506 cranium has not been displaced from its original position, although it does not preserve a
507 complete postorbital process—a component that is rarely preserved intact in Mesozoic
508 Avialae[82]. In dorsolateral view, the right postorbital process sweeps strongly ventrally before
509 deflecting rostrally to define part of the ventral margin of the orbit. In Anseres (the crown
510 clade uniting non-anhimid Anseriformes) the postorbital process extends far rostrally, up to
511 or exceeding the mid-point of the orbit. In Galliformes and Anhimidae, the postorbital
512 process is rostro-ventrally oriented and does not define the orbit's ventral surface, with its
513 rostral terminus not reaching the midpoint of the orbit. In NHMM 2013 008, the postorbital
514 process protrudes further rostrally than in Galliformes and Anhimidae, but less so than in
515 most Anseres (especially considering its inferred rostral displacement), extending along
516 slightly less than 50% of the ventral margin of the orbit. The postorbital process itself is
517 broad and its distal terminus is blunt, comparable to the shape in the anhimid *Chauna*
518 *torquata*, though not rounded as in *Meleagris gallopavo*, and differing substantially from the

519 comparatively narrow, acute terminus in Anseres. In contrast to the condition in many
520 Galliformes, there does not appear to have been an aponeurosis zygomaticus osseus (ossified
521 tendons of the temporal musculature). In cross section, the internal structure of the bone at its
522 distal terminus does not differ from that positioned more proximally along the postorbital
523 process, unlike that of the aponeurosis zygomaticus osseus of galliforms such as *Meleagris*
524 *gallopavo*.

525 In Anseres, a massive lacrimal fused to the rostrolateral face of the frontal defines a
526 discrete antorbital fenestra rostrally, and in lateral view, the rostroventral surface of the
527 orbit[83]. This condition differs substantially from that seen in Anhimidae and Galliformes,
528 where a much smaller lacrimal is weakly fused or unfused, and does not contribute markedly
529 to the lateral shape of the orbit[83]. No lacrimal appears to be preserved in NHMM 2013 008,
530 although a small element ventromedial to the right nasals may represent a fragment of the
531 lacrimal. Alternatively, this small, flat element may represent a fragment of the palatines, a
532 flat, unexpanded ectethmoid, or a displaced fragment of the rostral terminus of the
533 parasphenoid rostrum. Across the nasofrontal contact, a faintly defined facet suggests a ~7
534 mm area of attachment of an incompletely fused lacrimal, comparable to the dimensions of
535 the lacrimal contact across the nasofrontal hinge in *Chauna torquata* (NHMUK S/2012.31.1).
536 The position of the lacrimal facet appears distinctly similar to the condition in *C. torquata*,
537 where the facet overlies the dorsolateral surface of the rostral end of the frontal, continuing
538 across the nasofrontal hinge onto the nasal where the nasals overlie a ventrolateral facet, with
539 the facet's rostral terminus lying just caudal to the maxillary process of the nasal. However,
540 the majority of this facet lies along the nasal in Anhimidae, whereas the majority of the facet
541 appears to be positioned on the frontal in NHMM 2013 008. In crown galliforms like
542 *Meleagris gallopavo*, the lacrimal facet lies primarily along the caudolateral surface of the
543 nasals, whereas it lies along the rostrolateral surface of the frontals in Anseres. In addition to

544 anhimids, this suture crosses the nasofrontal hinge in certain crown galliforms, such as
545 Numididae and Cracidae[83]. The texture of this bone surface in NHMM 2013 008 shows no
546 sign that a large, fused lacrimal has been broken off, indicative of an unfused lacrimal. In this
547 respect and in combination with the galliform-like nasals in NHMM 2013 008, the
548 morphology of the rostral end of the orbit closely resembles that of most Galliformes.
549 The rostral portion of the cranial roof is well preserved in three-dimensions. The
550 frontals are fractured transversely slightly rostral to the frontoparietal suture, and a small
551 portion of the caudal skull roof is preserved in a separate block adjacent to the distal radius.
552 This portion comes from an area proximal to or encompassing the frontoparietal suture,
553 although no distinct suture is visible. This precludes assessment of whether the element
554 derives from the caudal end of the frontals, the rostral end of the parietals, or the boundary
555 between these elements. The dorsal surfaces of the orbits are both preserved in their entireties,
556 with the left side entirely undisplaced, and the postorbital region of the right side slightly
557 displaced by the femur as described above. In dorsal view, the width of the frontals is
558 constricted at the midpoint of the orbits, resulting in an hourglass-shaped cranial roof with
559 wider rostral and caudal ends, strikingly similar to the shape of the frontals in *Anas*
560 *platyrhynchos*. By contrast, the shape of the interorbital region of the crania of some
561 Galliformes and Anhimidae is considerably more expanded with the width at the midpoint
562 greater or equal to that at the rostral end. The lateral surfaces of the frontals are distinctly
563 deep dorsoventrally, with the bone surface in this region relatively thicker than in
564 Galliformes or Anseriformes including Anhimidae. Fossae for salt glands are not clearly
565 visible along the dorsolateral margins of the frontals, with no clear emarginations or
566 associated pitting, unlike in other Late Cretaceous avialans from marine sediments such as
567 *Ichthyornis dispar* and numerous marine representatives of Anseriformes and other major
568 neornithine clades[84]. However, slight depressions along the dorsolateral margin of the

frontals may correspond to weakly developed salt gland fossae, which would not be unexpected given the fossil's depositional setting in a nearshore marine environment.

In contrast to the condition of non-tinamiform palaeognaths, the mesethmoid does not form part of the roof of the skull, and is restricted to the ventral surface of the cranial roof where it fuses with the ventral surface of the frontals. The mesethmoid and frontals are completely fused, with the boundary between frontals and mesethmoid difficult to discern in cross section.

The left quadrate is well preserved in three dimensions and bears distinct similarities to the quadrate of *Presbyornis*[85,86]. The prootic and squamosal heads are clearly divided by a well-developed incisure as in Neognathae. This bicondylar condition is observed in almost all Neognathae and contrasts with the condition seen in crownward avialans such as *Ichthyornis* where the division between these condyles is poorly marked, and Palaeognathae where the condyles are merged into a single head. Two pneumatic foramina pierce the quadrate. The foramen pneumaticum rostromediale has a variable distribution across Galloanserae; it is present in all galliforms but absent in most anseriforms (present in the pan-anseriform *Conflicto* and a few extant taxa such as *Cereopsis*), and also occurs in taxa such as *Pelagornis* and certain Neoaves. The foramen basiorbitale is present in *Ichthyornis*, *Presbyornis*, *Conflicto*, *Pelagornis*, and Galliformes, although it is absent in Palaeognathae. The optimisation of this feature is unclear within Neornithes, but it may represent a plesiomorphy for crown birds based on its presence in *Ichthyornis*. The tuberculum subcapitulare is moderately developed, on the lateral face of the otic process. This character has been considered a derived feature of Galloanserae[86]; however, it is present in many Neoaves, and given its absence in Palaeognathae and *Ichthyornis* it may instead represent a synapomorphy of Neognathae. Further study will be necessary to clarify whether this feature represents an unambiguous synapomorphy of Galloanserae. The foramen caudomediale does

not open on the surface of the quadrate. This feature is present in most Anseriformes and certain Palaeognathae. Importantly, this foramen is only clearly absent in renderings of the quadrate that maximize the opacity of the bone surface, due to a deep invagination in the region of the foramen caudomediale that does not pierce the surface of the bone. This condition is remarkably similar to that of *Presbyornis* UMNH.VP.29030[87].

The cotyla jugalis of the quadrate is fairly deep and socket-like with a complete rim. This rim is notched in Phasianidae, Numididae and is notched in some Anseriformes. The pterygoid articulation is more widely separated dorsally from the mandibular condyle than in some Galloanserae such as *Alectura*, and is very similar to that of *Presbyornis*.

An important feature of Galloanserae is the presence of a bicondylar articulation between the quadrate and mandible through two quadrate condyles and two corresponding mandibular cotyles[25,28,88]. However, because *Ichthyornis* and some neoavians (e.g., Columbidae) also exhibit a bicondylar condition the ancestral condition for Neornithes is not unambiguous, and the status of this feature as a galloanseran synapomorphy is unclear[25].

The quadrate's pterygoid articulations (condylus pterygoideus and facies articularis pterygoidea of the processus orbitalis) are widely separated from one-another, forming a gently arcing margin of the quadrate very similar to the condition in megapodiids such as *Alectura lathami*, *Presbyornis* and extant Phasianoidea. On the basis that the articulations are not widely separated and are instead adjacent to one another in many extant taxa, including *Anseranas*, anhimids, anatids and cracids, this condition has been proposed to be the plesiomorphic neognath condition[86]. Widely separated articulations characterize *Presbyornis*, megapodiids, and all phasianoid families. The dorsolateral margin of the quadrate (from the processus oticus to the dorsal tip of the crista orbitalis) is strongly concave, almost indistinguishable from the shape of this margin in *Presbyornis*.

Like all known Galloanserae, the mandible of NHMM 2013 008 exhibits two cotylae for articulation with the quadrate and a blade-like retroarticular process. This process is strongly hooked in a comma-like shape, and in its shape and proportions it bears a very strong resemblance to *Anatalavis oxfordi.* As in Anseriformes and some megapodes (e.g., *Alectura lathami*) the process is dorsoventrally tall, but the process is shorter in caudal extent than in Anseriformes and more similar to Megapodiidae. The caudal terminus is strongly dorsally deflected, resulting in its comma-like shape. The recessus conicalis is absent, whereas it is present in Anseres, *Conflicto*, Presbyornithidae, and *Anatalavis*. An elongate, narrow, slightly dorsally oriented processus medialis is preserved on the right jaw, as in all Galloanserae. The splenial is incompletely fused to the dentary, as in Megapodiidae and Palaeognathae. The splenial of the left jaw is separated and medially displaced from the dentary. In cross-section, the splenial of the right jaw is in its original position but remains unfused along its entire rostrocaudal length.

Although the caudal extremity of the cranium is missing in NHMM 2013 008, the proportions of the mandible indicate that it must have been shorter than the total length of the skull. This conforms to the proportions in Galliformes and Anhimidae, whereas in *Anseranas* and Anatidae the length of the mandible is approximately equal to the total length of the skull. The coronoid region of the mandible is not markedly deeper than the caudal end of the mandible, similar to the condition in Anhimidae and Galliformes but in contrast to the condition in Anseres. The rostral end of the mandible is flattened but maintains a broad, shallowly concave palatal surface. It is strongly pitted with neurovascular foramina as in many extant galloanserans. The rostrocaudal extent of the mandibular symphysis is comparable to that of Anhimidae and Megapodiidae (e.g., *Alectura lathami*).

The general appearance of the premaxillary beak resembles that of extant Galliformes, in particular with regard to its gently downcurved tip and delicate construction, lacking

643 ossified joints among the rostral components[30]. The contralateral frontal processes of the
644 premaxillae remain unfused along their entire length. Likewise, the premaxilla and nasal are
645 unfused at both their tomial and narial contacts. A notable distinction between NHMM 2013
646 008 and most extant Galloanserae is that the beak tip is unhooked, distinguishing it from
647 extant galliforms, *Anseranas*, Anhimidae, many Anseres, as well as fossil taxa such as
648 *Anatalavis oxfordi*. The tip of the bill is unhooked in some Anseres such as *Alopochen*
649 *aegyptiacus* and the fossil pan-anseriform *Presbyornis*.
650 The majority of the left femur, including a largely intact distal end, is preserved in
651 cranial view above the main portion of the skull; the remains of its proximal end are
652 preserved in a separate, continuous block alongside a portion of the cranial roof close to the
653 frontoparietal suture. The femur is broken sagitally, with most of its cranial surface missing,
654 but the distal articular region is well-preserved in three dimensions. The femur is elongate
655 and the lateral and medial margins of the shaft are parallel along the length of the element. In
656 caudal view, the condylus medialis is approximately aligned with the condylus lateralis, as in
657 *Anseranas* and unlike most other Galloanserae where it is distinctly less projected. The
658 condylus medialis exhibits a subangular profile between the condyle's articular surface and
659 its cranial margin as in most Anseriformes, whereas it is evenly rounded in most Galliformes.
660 The sulcus patellaris is narrow and deep, and the popliteal fossa is shallow with no pneumatic
661 foramina. The impressio ligamenti cruciati cranialis is poorly defined as in most anseriforms
662 and some Megapodiidae (more marked in *Anseranas*, *Presbyornis*, and many galliforms).
663 Intermuscular lines are fairly well marked on the caudal surface of the distal femur, although
664 their original orientations are difficult to assess due to some crushing of the femoral shaft.
665 Part of the shaft of the right femur is also preserved in a separate block with a partial
666 tibiotarsus. The diameter and bone thickness of this femur are similar to those of the left
667 femur, but few additional morphological details of this fragmentary element are notable. A

668 flattened surface may correspond to the patellar sulcus and a flattened medial condyle may
669 also be present.
670 Additional fragmentary remains of the postcranium include a distal radius, and bone
671 shafts deriving from both tibiotarsi, a tarsometatarsus, and an unidentified element that may
672 represent a fragment of a humerus shaft.
673 The distal radius resembles that of *Lophura swinhoii* (UMZC 397.A) in shape. The
674 caudal surface is flattened suggesting a shallow depression ligamentosa (unlike *Anas*
675 *castanea* UMZC 222.g). A tendinal groove in the radiocarpal articular facet may correspond
676 to an attachment point for the lig. radiocarpale dorsale, or an articulation point for the
677 distoventral projection of the radiale. A tubercle on the cranial surface is more centrally
678 positioned than the more dorsally positioned tubercle in *Anas castanea*. In distal view the
679 radius is craniocaudally compressed, yielding an hourglass-like profile similar to that of *Anas*
680 *castanea* and *Podiceps cristatus* (UMZC 208.A), and less like that of *Lophura swinhoii*. A
681 dorsal projection of the distal radius is moderately projected from the main axis of the radius,
682 similar to the degree of projection in *Anas castanea* but less so than in *L. swinhoii*, which also
683 exhibits a more strongly hooked morphology. This projection is very robust, strongly
684 projected, and hooked in *Presbyornis*.
685 In the same block as the main portion of the skull, a partial shaft of a tibiotarsus is
686 preserved. This widens slightly towards one end of the bone, presumably the proximal end,
687 and the cranial surface becomes progressively flatter distally yielding a subtriangular cross-
688 section. This general form corresponds with the tibiotarsi of extant Galloanserae. A second
689 tibiotarsus is preserved in a block on its own; this shaft narrows somewhat near the midpoint
690 of the preserved portion of the shaft, though it is possible that at least part of this narrowing is
691 due to taphonomic flattening. The bone diameter, thickness, and length are comparable to the

other tibiotarsus shaft fragment, and the mediolateral cross-sectional diameters of the narrowest points on both shafts are nearly identical (3.6mm and 3.7mm).

A final fragmentary element represents a probable portion of a tarsometatarsus; the shaft is widest towards its proximal end, and narrowest at its midpoint before widening distally. This is congruent with the preserved portion corresponding to the central portion of the shaft, indicating that the element was quite elongate. This element is smaller in diameter than the tibiotarsus fragments, suggestive of a relatively narrow, elongate tarsometatarsus. Two marked ridges (plantar crests) bound both the lateral and medial side of the plantar surface of the element. Two additional shallow ridges extend along the cranial surface of the bone. These are subparallel for most of the length of the preserved fragment, but approach each other at the narrowest point of the midshaft before diverging again distally. These are congruent with the ridges extending from the cranial end of the unpreserved proximal lateral and medial cotylae. The narrower tarsometatarsus (minimum mediolateral diameter 3.3mm) relative to the tibiotarsus (minimum mediolateral diameter 3.6mm-3.7mm) compares with the approximate relative proportions of many extant ground-dwelling birds (e.g., *Burhinus grallarius*). Additionally, the preserved proportions of the postcranium of NHMM 2013 008 indicate relatively elongate hindlimbs. The maximum possible length of the right femur is 53.14mm, although this may be an overestimate as the measurement length includes a gap between two blocks of the holotype. The length of the longest tibiotarsus fragment is 65.38mm (its absolute length and that of its contiguous impression), and the length of the tarsometatarsus fragment (its absolute length and that of its contiguous impression) is 62.54mm. This yields a minimum "hindlimb index" [(length of tibiotarsus+length of tarsometatarsus)/(length of femur)][89] of 2.41, exceeding that of most tree-dwelling birds. The preserved portions of the tarsometatarsus and tibiotarsus show no indications of the proximal or distal articular regions, suggesting that the elements were substantially longer than the

717 preserved fragments and, therefore, that the hindlimb index of *Asteriornis* would comfortably
718 fall within the range of variation of long-limbed ground-dwelling birds (>~2.6)[89].
719
720 **VIII: Synapomorphies Diagnosing Key Neornithine Clades**
721 **Autapomorphic character combinations for *Asteriornis***
722 Inferred under the results of constrained parsimony analysis
723 • Postorbital process rostrally oriented (char. 46: 0 > 1, also evolved independently in
724 *Anseranas* and Anatidae)
725 • Splenial not fused to dentary in adults (char. 67: 0 > 1, also evolved independently in
726 Panpalaeognathae and Megapodiidae)
727 • Distal extent of medial condyle on femur in caudal view approximately equal to that
728 of lateral condyle (char. 210: 1 > 0, also evolved independently in *Ichthyornis*,
729 *Lithornis promiscuus*, *Tinamus*, Gruiformes, [*Anatalavis* + *Conflicto*], and *Coturnix*)
730 • Medial and lateral plantar crests on tarsometatarsus poorly developed (char. 268: 1 >
731 0, also evolved independently in *Dinornis*, *Pelagornis*, and *Presbyornis*)
732 • Medial processes of mandible caudally deflected in dorsal view (char. 293: 0 > 1, also
733 evolved independently in *Anhima*, *Anseranas*, and Anatidae)
734 Inferred under the results of constrained, undated Bayesian analysis
735 • Postorbital process rostrally oriented (char. 46: 0 > 1, also evolved independently in
736 Anseres)
737 • Distal extent of medial condyle on femur in caudal view approximately equal to that
738 of lateral condyle (char. 210: 1 > 0, also evolved independently in *Ichthyornis*,
739 *Lithornis promiscuus*, *Tinamus*, Gruiformes, [*Anatalavis* + *Conflicto*], and *Coturnix*)
740 • Medial processes of mandible caudally deflected in dorsal view (char. 293: 0 > 1, also
741 evolved independently in *Anhima* and Anseres)

Inferred under the results of Bayesian tip-dating analysis

- Postorbital process rostrally oriented (char. 46: 0 > 1, also evolved independently in Anseres)
- Distal extent of medial condyle on femur in caudal view approximately equal to that of lateral condyle (char. 210: 1 > 0, also evolved independently in *Ichthyornis*, *Lithornis promiscuus*, *Tinamus*, Gruiformes, *Anatalavis*, *Conflicto*, and *Coturnix*)
- Internal edge of distal femoral shaft interrupted by caudally prominent medial supracondylar crest (char. 218: 0 > 1, also evolved independently in Gruiformes, *Burhinus*, *Presbyornis*, *Chauna*, [*Tadorna* + *Anser*], *Crax*, and [*Coturnix* + *Gallus*])
- Medial and lateral plantar crests on tarsometatarsus poorly developed (char. 268: 1 > 0, also evolved independently in *Dinornis*, *Pelagornis*, and *Presbyornis*)

Inferred synapomorphies under the results of constrained maximum parsimony analysis (characters in bold are exhibited by *Asteriornis*)

Neornithes

- Sulcus m. supracocracoidei of coracoid not excavated under facies articulating with humerus (char. 102: 1 > 0, reversed in *Lithornis plebius*, *Burhinus*, Presbyornithidae, and [*Tadorna* + *Anser*])
- Capital shaft ridge on humerus absent (char. 115: 0 > 1, reversed in *Porphyrio*, *Burhinus*, [*Conflicto* + *Anatalavis*], and Anseres)
- Infratrochlear fossa of carpometacarpus shallow (char. 160: 2 > 1, reversed in [*Lithornis plebius* + *Paracathartes*], *Porphyrio*, *Burhinus*, *Chauna*, *Presbyornis*, and *Dendrocygna*)
- **Most prominent part of medial crest on femur centered on shaft** (char. 204: 1 > 0, reversed in *Cariama*, Anhimidae, *Presbyornis*, *Tadorna*, and *Anser*)

- **Fibular trochlea on femur lacking distinct depression immediately proximal of articular surface in caudal view** (char. 209: 1 > 0, reversed in Gruiformes, *Pelagornis*, *Wilaru*, *Dendrocygna*, *Phasianus*, and *Gallus*)
- Proximal projection of cranial cnemial crest on tibiotarsus equal with or slightly proximal of patellar crest (char. 222: 1 > 0, reversed in *Antigone*, *Chauna*, and Anseres)
- Distal extent of cranial cnemial crest on tibiotarsus ends level with or just proximal to proximal end of fibular crest (char. 229: 2 > 1, reversed in [*Burhinus* + *Cariama*] and *Presbyornis*)

Panpalaeognathae

- Palatine and pterygoid fused (char. 41: 1 > 0)
- Basipterygoid facet on pterygoid close to caudal end of bone (char. 44: 0 > 2)
- Capitulum squamosum and capitulum oticum on quadrate form single elongate dumbbell-shaped head (char. 49: 1 > 0, also evolved independently in *Conflicto*)
- **Splenial and dentary unfused in adults** (char. 67: 0 > 1, also evolved independently in *Asteriornis* and Megapodiidae)
- Ulnar bicipital tubercle forms single scar (char. 148: 0 > 3, reversed in *Paracathartes*, also evolved independently in Presbyornithidae)
- Distal rim of carpal trochlea on carpometacarpus ends considerably short of ventral rim in caudal view (char. 156: 1 > 0, reversed in *Paracathartes*, also evolved independently in *Porphyrio*, *Burhinus*, and Galliformes)
- Craniocaudal length of extensor process on carpometacarpus near or less than half the length of the carpal trochlea in ventral view (char. 163: 1 > 0, reversed in *Paracathartes*, also evolved independently in *Pelagornis*, Megapodiidae, and Phasianoidea)

- Medial condyle of femur evenly rounded in medial aspect (char. 212: 1 > 0, also evolved independently in Galliformes)
- Fibular crest on tibiotarsus 20-25% of tibiotarsus length (char. 230: 0 > 1, also evolved independently in *Cereopsis*, *Tadorna*, [*Alectura* + *Leipoa*], *Megapodius reinwardt*, *Ortalis*, and *Phasianus*)
- Deep ligamental pit on cranial external facies of medial condyle on tibiotarsus (char. 233: 0 > 1, reversed in *Tinamus*, also evolved independently in *Cereopsis*)
- Short, conspicuous scar for medial collateral ligament proximocaudal to medial epicondyle on tibiotarsus (char. 236: 0 > 1, also evolved independently in *Burhinus*, *Anseranas*, and *Presbyornis*)
- Distal opening of extensor canal on tibiotarsus directed towards and broadly overlaps in lateromedial plane with medial condyle (char. 243: 1 > 0)
- No flange-like process on plantarmedial edge of medial cotyle on tarsometatarsus (char. 252: 1 > 0, reversed in *Lithornis plebius* and *Tinamus*, also evolved independently in *Burhinus*, *Cariama*, *Anseranas*, Presbyornithidae, *Tadorna*, *Cereopsis*, *Alectura*, and *Macrocephalon*)
- No nasal-premaxilla contact (char. 295: 0 > 2, reversed in *Tinamus*)

Palaeognathae

- Pila otica with pneumatic openings lateral or caudolateral to it (char. 26: 0 > 1, also evolved independently in *Antigone*, *Ortalis*, and [*Coturnix* + *Gallus*])
- Coracoid fused to scapula (char. 109: 0 > 1, reversed in *Tinamus*)
- Preacetabular region of synsacrum less than 40% synsacral length (char. 173: 0 > 1, reversed in *Tinamus*, also evolved independently in *Vegavis* and *Anatalavis*)
- Lateral condyle on femur markedly divergent from axis (char. 205: 0 > 1, reversed in *Tinamus*, also evolved independently in *Cariama* and *Cereopsis*)

- Pneumatic popliteal fossa on femur (char. 216: 0 > 1, reversed in *Tinamus*, also evolved independently in *Vegavis*, *Cariama*, *Anhima* [variably present], Anatidae, and *Phasianus*)
- Internal edge of distal femoral shaft smoothly curving continuous to condyle in medial view (char. 218: 2 > 0, reversed in *Tinamus*, also evolved independently in *Cariama* and Galloanserae)
- Elongate, conspicuous scar for medial collateral ligament proximocaudal to medial epicondyle on tibiotarsus (char. 236: 1 > 2, reversed in *Tinamus*, also evolved independently in *Cariama*)
- Junction of cartilaginous trochlea crest and rim of medial condyle on tibiotarsus not marked by a distinct shallow notch (char. 237: 1 > 0, also evolved independently in *Porphyrio*, *Burhinus*, *Cariama*, *Anseranas*, *Dendrocygna*, and *Cereopsis*)
- Intercondylar ligament impression on tibiotarsus absent (char. 239: 1 > 0, reversed in *Tinamus*)
- Intercondylar incisure on tibiotarsus absent (char. 245: 0 > 2, reversed in *Tinamus*)
- Sulcus m. fibularis on tibiotarsus faces laterally (char. 246: 0 > 1, also evolved independently in *Burhinus* and Galliformes)
- Medial cotyle of tarsometatarsus laps dorsally onto dorsal facies (char. 251: 0 > 1, reversed in *Tinamus*, also evolved independently in *Pelagornis*)
- Fossa for metatarsal I on tarsometatarsus absent (char. 271: 0 > 1, also evolved independently in *Antigone*, *Burhinus*, *Cariama*, *Wilaru*, Anatidae, and *Coturnix*)
- Distal vascular foramen on tarsometatarsus small but distinct (char. 279: 0 > 1, also evolved independently in *Burhinus*, *Cariama*, *Leipoa*, Cracidae, *Macrocephalon*, and *Gallus*)

- Intermediate phalanges on pedal digit IV gradually shorten towards ungual (char. 281: 0 > 1, reversed in *Tinamus*)
- Ungual on pedal digit III wider than deep at midlength (char. 283: 0 > 2, also evolved independently in Megapodiidae)

Neognathae

- **Tuberculum subcapitulare on otic process of quadrate** (char. 50: 0 > 1, reversed in *Burhinus*, *Pelagornis*, and *Anseranas*)
- Metacarpal III extends dorsal of ventral rim of carpal trochlea on carpometacarpus (char. 159: 1 > 0, reversed in Galliformes)
- Synostosis of metacarpals II and III longer than wide (char. 171: 0 > 1, reversed in *Cariama*, *Anseranas*, *Wilaru*, and Galliformes)
- Recessus caudalis fossae shallow and pneumatic (char. 180: 2 > 1, reversed in *Burhinus* and Anatidae)
- Ilioischiadic foramen approximately half the length of the ischium from the acetabular foramen (char. 182: 2 > 1, reversed in *Conflicto*, *Tadorna*, and *Anser*)
- Ilioischiadic foramen caudally closed (char. 183: 0 > 1)
- Tuberculum m. gastrocnemialis lateralis a round scar, close to or abutting fibular trochlea on caudal facies of femur (char. 207: 1 or 4 > 0, reversed in *Porphyrio*, Anseres, and Phasianidae, also evolved independently in Lithornithidae)
- Internal edge of distal femoral shaft interrupted by caudally prominent medial supracondylar crest (char. 218: 2 > 1, reversed in *Phasianus*)

Neoaves

- Basipterygoid processes absent (char. 27: 0 > 1)

- Angulus caudolateralis of palatine present (char. 34: 0 > 1, also evolved independently in Anseriformes)
- Ventral crest on palatine strongly developed (char. 35: 0 > 1)
- Strongly-developed fossa on dorsal facies of pterygoid (char. 42: 0 > 1)
- Pterygoid condyle and pterygoid articulation facies of the orbital process on quadrate adjacent or fused to each other (char. 56: 1 > 0, also evolved independently in Anserimorphae)
- Scapulotriciptal sulcus on humerus present on caudal face but does not extend around distal end of dorsal epicondyle (char. 140: 0 > 1, also evolved independently in *Conflicto*, *Wilaru*, Anatidae, *Crax*, *Phasianus*, and *Gallus*)
- Ilioischiadic foramen less than half the length of the ischium from the acetabular foramen (char. 182: 1 > 0, also evolved independently in Anhimidae, *Presbyornis*, and Galliformes)
- Long axis of extensor canal distal opening aligned across tibiotarsal shaft (char. 248: 1 > 0, also evolved independently in *Dinornis*, [*Conflicto* + Anseriformes], and *Acryllium* [variably present])
- Femoral neck narrower than ball in caudal view (char. 187: 0 > 1, also evolved independently in Lithornithidae, *Tinamus*, *Wilaru*, *Dendrocygna*, and Galliformes)
- Tarsometatarsus more than 105% femur length (char. 249: 0 or 1 > 2, also evolved independently in *Struthio*, *Dromaius*, *Dinornis*, and [*Conflicto* + Anseriformes])
- Dorsal facies of distal tarsometatarsus shaft flat or concave (char. 270: 0 > 1, also evolved independently in *Struthio*, *Dromaius*, *Presbyornis*, Anatidae, and Phasianidae)

Pangalloanserae

- **Pneumatic foramen on anteromesial surface of otic process of quadrate** (char. 52: 0 > 1, reversed in Anseriformes, also evolved independently in *Porphyrio*)

- **Medial processes of mandible long, narrow, and dorsally oriented** (char. 68: 0 > 1, reversed in *Pelagornis*)

Galloanserae

- Nasal aperture of premaxilla shorter than width of craniofacial hinge (char. 2: 0 > 2, reversed in *Anatalavis*, *Presbyornis*, *Ortalis* and *Gallus*, also evolved independently in *Dinornis*)
- Internal edge of distal femoral shaft smoothly curving continuous to condyle in medial view (char. 218: 2 > 0, reversed in *Phasianus*, also evolved independently in Palaeognathae and *Cariama*)

Anserimorphae

- Well developed zona flexoria (char. 8: 0 > 1, reversed in *Anhima*, also evolved independently in *Porphyrio*, *Cariama*, and *Macrocephalon*)
- Pterygoid condyle and pterygoid articulation facies of the orbital process on quadrate adjacent or fused to each other (char. 56: 1 > 0, reversed in *Presbyornis*, also evolved independently in Neoaves)
- Significant lateromedial curvature of clavicles (char. 111: 0 > 1, also evolved independently in *Tinamus*, *Burhinus*, and *Macrocephalon*)
- Robust, U-shaped furcular hypocleideum (char. 114: 2 > 1)
- Width across the ventral pneumtricipital fossa on humerus from crus dorsale fossae to crus ventrale fossae distinctly less than the length from ventral tubercle to the junction of the bicipital crest and shaft (char. 131: 1 > 0, reversed in *Presbyornis*, also evolved independently in Gruiformes)

- Length of metacarpal II from alular process to start of intermetacarpal space relative to craniocaudal width of fused metacarpals II and III (char. 165: 1 > 0, reversed in Anhimidae, Presbyornithidae, and *Anser*, also evolved independently in Gruiformes)
- Distal opening of extensor canal on tibiotarsus has no overlap in lateromedial plane with medial condyle (char. 243: 1 > 2, also evolved independently in *Ichthyornis* and *Porphyrio*)
- Depth of medial crest on hypotarsus greater than or equal to depth of medial cotyle on tarsometatarsus (char. 256: 1 > 0, reversed in *Anhima*, *Presbyornis*, and *Anser*, also evolved independently in *Porphyrio*)
- Nasal-premaxilla suture at tomial margin obliterated (char. 295: 0 > 1, also evolved independently in *Antigone*, *Cariama*, and *Macrocephalon*)

Anseriformes

- Mamillar tuberosities large and prominent on caudalateral corner of parasphenoid lamina (char. 25: 0 > 1, reversed in *Cereopsis*, also evolved independently in *Dinornis*, *Cariama*, and *Macrocephalon*)
- Angulus caudolateralis of palatine present (char. 34: 0 > 1, reversed in *Presbyornis*, also evolved independently in Neoaves)
- Palatines completely fused along midline (char. 36: 0 > 1, reversed in *Presbyornis*)
- Pneumatic foramen on anteromesial surface of otic process of quadrate absent (char. 52: 1 > 0, reversal to plesiomorphic state for Neornithes, reversed in *Cereopsis*)
- Orbital crest prominent and on lateral bulge of orbital process on quadrate (char. 53: 0 > 1, also evolved independently in *Crax*)
- Basiorbital pneumatic foramen on medial surface of otic process of quadrate absent (char. 54: 1 > 0, reversed in *Presbyornis*, also evolved independently in Panpalaeognathae, Neoaves, and *Phasianus*)

- Dorsolateral margin extending from otic process to dorsal tip of orbital process of quadrate forms straight line or slightly concave (char. 58: 1 > 0, reversed in *Presbyornis* and *Tadorna*)
- Retroarticular process tall and long (char. 64: 1 > 2, reversed in *Presbyornis*)
- Pneumatic pores on pars cardiaca of sternum widely scattered (char. 80: 2 > 0, also evolved independently in *Antigone* and Cracidae)
- Pneumatic foramen at cranial end of scapula (char. 90: 1 > 0, reversed in Presbyornithidae, also evolved independently in *Macrocephalon*)
- Ventral tubercle on humerus directed proximally in caudal view (char. 128: 1 > 0, reversal to plesiomorphic state for Neornithes, reversed in *Wilaru*)
- Femoral trochanter elongate, extending distally past the level of the femoral head a distance exceeding the proximodistal width of the femoral head (char. 197: 1 > 0, also evolved independently in *Vegavis*, Lithornithidae, *Struthio*, *Dromaius*, *Antigone*, *Macrocephalon*, and [Cracidae + Phasianidae])
- Breadth of intercondylar ligamental impression on tibiotarsus extends medially caudally to medial condyle (char. 0 > 1, also evolved independently in Lithornithidae and *Burhinus*)

Anseres

- Premaxillae spatulate (char. 3: 0 > 1, convergent with *Anatalavis*)
- Well-developed lamellae in upper beak (char. 6: 1 > 2)
- Basipterygoid processes on sides of the parasphenoid rostrum, rostral to the caudal end of rostrum (char. 1 > 2)
- Pterygoid articulation with palatine a ball and socket joint with a prominent additional dorsal condyle (char. 0 > 2, reversed in *Cereopsis*)

- Basipterygoid facet on pterygoid close to the rostral end of bone (char. 44: 0 > 1, also evolved independently in Galliformes)
- Deep groove in ventral surface of rostral portion of mandibular rami (char. 62: 0 > 1, also evolved independently in *Lithornis promiscuus*)
- Transverse foramina on atlas (char. 72: 0 > 1, reversed in *Cereopsis*, also evolved independently in *Dromaius* and *Dinornis*)
- Carpal tubercle on ulna large, projecting more than half the craniocaudal width of dorsal and ventral condyles (char. 154: 1 > 0, also evolved independently in *Burhinus*)
- Corpus of first synsacro-thoracic vertebra considerably more compressed than following vertebra (char. 174: 0 > 1, reversed in [*Cereopsis* + *Anser*], also evolved independently in *Ichthyornis*)
- Tuberculum m. gastrocnemialis lateralis a round scar well separated from fibular trochlea on caudal facies of femur (char. 207: 0 > 1, reversal to plesiomorphic state for Neornithes)
- Webbing between toes semipalmate or palmate (char. 285: 1 > 2 or 3)

Presbyornithidae + *Anseranas*

- Distalmost costal process on sternum in distal half of sternal basin (char. 86: 2 > 0, also evolved independently in *Dromaius*, *Antigone*, *Chauna*, and *Anser*)
- Dorsal and ventral lobes of acrocoracoid process on coracoid overhang supracocracoidal sulcus (char. 98: 1 > 2 or 3, reversal to plesiomorphic state for Neornithes)
- Line linking acrocoracoid process of coracoid and angulus medialis forms > 90-100° angle with line linking lateral and medial extremes of sternal facet (char. 108: 1 > 0, also evolved independently in *Ichthyornis*, *Antigone*, *Anhima*, *Anser*, [*Alectura* + *Leipoa*], and Phasianoidea)

- Caudal carpal fovea deep and not pneumatic (char. 158: 2 > 1, also evolved independently in *Vegavis* and Gruiformes)
- Cranial facies of trochanteric crest on femur deeply concave (char. 190: 0 > 1)
- Impression for medial collateral ligament on tibiotarsus low and not prominent (char. 223: 1 > 0, reversal to plesiomorphic state for Neornithes)
- Impression for meniscotibial ligament on tibiotarsus forms low facet abutting intercondylar fossa (char. 240: 2 > 1, also evolved independently in Panpalaeognathae, *Antigone*, *Burhinus*, *Cariama*, *Phasianus*, and *Gallus*)
- Distal end of major hypotarsal ridge is markedly hooked caudodistally, forming notch (char. 258: 2 > 0, also evolved independently in *Porphyrio* and Galliformes)

Pangalliformes

- Premaxilla less than 50% total cranium length (char. 1: 0 > 2, also evolved independently in [*Dinornis* + *Tinamus*], Anhimidae, *Dendrocygna*, and *Cereopsis*)
- Three or four costal processes on sternum (char. 81: 1 > 2, reversed in *Alectura*, also evolved independently in Notopalaeognathae)
- Four notches or fenestrae in sternum (char. 87: 1 > 0, also evolved independently in *Ichthyornis*, *Burhinus*, and *Presbyornis*)
- Supracoracoid nerve foramen absent (char. 93: 0 > 2, also evolved independently in *Cariama*, *Conflicto*, *Chauna*, *Dendrocygna*, and *Anser*)
- Procoracoid absent or with minimal medial projection (char. 94: 1 > 0)
- Acrocoracoid process on coracoid directed primarily medially, forming near right angle with medial margin of humeral facet (char. 99: 0 > 1, also evolved independently in *Tinamus*)
- Coracoid facies articulating with humerus flat or convex (char. 100: 0 > 1, also evolved independently in *Ichthyornis*, *Tinamus*, and *Anatalavis*)

- Furcular hypocleideum present as prominent ridge or lobe (char. 112: 0 or 1 > 2)
- Dorsal pneumotricipital fossa on humerus is wide and shallow, greater than or equal to width of ventral pneumotricipital fossa (char. 118: 0 > 2, also evolved independently in *Conflicto*)
- Insertion of m. supracoracoideus tendon on humerus forms elongate scar extending distal to dorsal tubercle (char. 126: 0 > 1, also evolved independently in *Tinamus*)
- Moderate dorsoventral curvature of distal third of femur (char. 200: 0 > 1, reversed in *Macrocephalon* and *Crax*, also evolved independently in Lithornithidae and *Tinamus*)
- Intercondylar incisure on tibiotarsus narrow, width subequal to extensor canal (char. 245: 0 > 1, also evolved independently in *Burhinus*, *Cariama*, and *Pelagornis*)

Galliformes

- Scapula increases distally in dorsoventral height (char. 88: 0 > 1, reversed in *Coturnix*, also evolved independently in *Tinamus* and *Dendrocygna*)
- Facies articulating with scapula forms a subplanar to convex articulation on coracoid (char. 95: 0 > 2, also evolved independently in *Tinamus* and *Antigone*)
- Pneumatic foramen in impressio m. sternocoracoidei on coracoid (char. 104: 1 > 0, reversed in *Acryllium* and *Coturnix*, also evolved independently in *Antigone*, *Anatalavis*, Anhimidae, and *Anseranas*)
- Deltopectoral crest on humerus caudally flat or convex with angular profile (char. 121: 0 > 1, also evolved independently in *Ichthyornis*, *Tinamus*, and Pelagornithidae)
- Radial depression on distal ulna not marked (char. 153: 1 > 0, also evolved independently in *Tinamus*, *Antigone*, *Burhinus*, *Pelagornis*, *Wilaru*, and *Dendrocygna*)
- Distal rim of carpal trochlea on carpometacarpus ends considerably short of ventral rim in caudal view (char. 156: 1 > 0, also evolved independently in Panpalaeognathae, *Porphyrio*, and *Burhinus*)

- Metacarpal III entirely ventral to ventral rim of carpal trochlea on carpometacarpus (char. 159: 0 > 1, reversal to plesiomorphic state for Neornithes)
- Infratrochlear fossa on carpometacarpus absent (char. 160: 1 > 0, reversed in *Phasianus*, also evolved independently in *Tinamus*)
- Synostosis of metacarpals II and III shorter than wide (char. 171: 1 > 0, reversal to plesiomorphic state for Neornithes, reversed in *Megapodius reinwardt*)
- Facet for manual digit III extends more distally than that for digit II (char. 172: 1 > 0, also evolved independently in *Tinamus*, *Cariama*, *Anhima*, and *Anseranas*)
- Ilioischiadic foramen less than half the length of the ischium from the acetabular foramen (char. 182: 1 > 0, also evolved independently in Neoaves, Anhimidae, and *Presbyornis*)

Inferred synapomorphies under the results of constrained, undated Bayesian analysis (characters in bold are exhibited by *Asteriornis*)

Panpalaeognathae

- Capitulum squamosum overhangs lateral surface of otic process on quadrate (char. 57: 1 > 0, reversed in *Tinamus*, also evolved independently in Gruiformes, *Cariama*, *Chauna*, and *Anseranas*)
- Three mandibular cotyles (char. 60: 1 > 0, also evolved independently in Neoaves)
- **Splenial and dentary unfused in adults** (char. 67: 0 > 1, also evolved independently in *Asteriornis* and Megapodiidae)
- Well-developed tubercle on scapula for attachment of acrocoraco-procracoid ligament (char. 92: 0 > 1, reversed in *Tinamus*, also evolved independently in Galliformes)
- Bicipital crest on humerus distinctly wider than long in caudal view (char. 131: 1 > 2, also evolved independently in *Vegavis*, *Anhima*, *Anatalavis*, *Wilaru*, *Ortalis*, *Phasianus*, and *Gallus*)

- Distal extent of flexor process on humerus roughly equal to that of ventral and dorsal condyles in cranial view (char. 137: 0 > 1, reversed in *Lithornis promiscuus*, also evolved independently in *Porphyrio*, *Cariama*, *Dendrocygna*, and *Tadorna*)
- Insertion for dorsal ulnocarpo-metacarpal ligament on carpometacarpus relatively distal (char. 167: 0 > 1, reversed in *Lithornis promiscuus*, also evolved independently in *Cariama* and Galliformes)
- Femoral neck narrower than ball in caudal view (char. 187: 0 > 1, reversed in *Struthio*, *Dromaius*, and *Dinornis*, also evolved independently in Neoaves, *Wilaru*, *Dendrocygna*, and Galliformes)
- Facies on femur articulating with antitrochanter convex in lateromedial plane (char. 188: 0 > 1, reversed in *Dinornis*, also evolved independently in *Conflicto*, *Wilaru*, Anatidae, and Pangalliformes)
- Moderate dorsoventral curvature of distal third of femur (char. 200: 0 > 1, reversed in *Struthio*, *Dromaius*, and *Dinornis*, also evolved independently in [*Gallinuloides* + Galliformes])
- Impressio ansa m. iliofibularis caudalis on femur present on lateral facies but also wraps around caudolateral margin at proximal side of fibular trochlea (char. 208: 0 > 1, reversed in *Struthio* and *Dromaius*, also evolved independently in *Porphyrio*, *Cariama*, *Macrocephalon*, *Phasianus*, and *Coturnix*)
- Medial condyle of femur evenly rounded in medial aspect (char. 212: 1 > 0, also evolved independently in Galliformes)
- Medial supracondylar crest on femur absent (char. 217: 1 > 2, reversed in *Struthio*, *Dromaius*, and *Dinornis*)

- Fibular trochlea of femur short in caudal view, merging distally with lateral condyle and forming a notch (char. 219: 0 > 1, reversed in *Struthio*, *Dinornis*, and *Tinamus*, also evolved independently in *Burhinus*)
- Cranial cnemial crest of tibiotarsus deflected laterally from axis at base (char. 225: 0 > 1, also evolved independently in Pangalliformes)
- Short, conspicuous scar for medial collateral ligament proximocaudal to medial epicondyle on tibiotarsus (char. 236: 0 > 1, also evolved independently in *Burhinus*, *Anseranas*, and *Presbyornis*)
- Distal opening of extensor canal on tibiotarsus directed towards and broadly overlaps in lateromedial plane with medial condyle (char. 243: 1 > 0)
- No flange-like process on plantarmedial edge of medial cotyle on tarsometatarsus (char. 252: 1 > 0, reversed in *Lithornis plebius* and *Tinamus*, also evolved independently in *Burhinus*, *Cariama*, [Presbyornithidae + Anseres], *Alectura*, and *Macrocephalon*)
- Intercotylar eminence on tarsometatarsus not prominent proximally in lateral view (char. 255: 0 > 1, reversed in *Struthio* and *Tinamus*, also evolved independently in Megapodiidae, *Crax*, and *Coturnix*)
- Tuberositas m. tibialis cranialis is two distinct tuberosities fused as one at the base of the extensor sulcus of the tarsometatarsus (char. 263: 1 > 2, reversed in *Struthio* and *Tinamus*, also evolved independently in *Cariama* and *Wilaru*)

Palaeognathae

- Closed frontoparietal suture (char. 15: 0 > 1, reversed in *Tinamus*, also evolved independently in *Ichthyornis* [variably present] and Neognathae)
- Pila otica with pneumatic openings lateral or caudolateral to it (char. 26: 0 > 1, also evolved independently in *Antigone*, *Ortalis*, and [*Coturnix* + *Gallus*])

- Well-developed haemal processes on posterior caudal vertebrae absent (char. 77: 1 > 0, also evolved independently in Neoaves, Megapodiidae, *Phasianus*, and *Gallus*)
- Pneumatic foramina absent on sternal midline (char. 79: 0 > 2, also evolved independently in Gruiformes, *Anatalavis*, *Gallus*, and *Coturnix* [variably present])
- Coracoid fused to scapula (char. 109: 0 > 1, reversed in *Tinamus*)
- Preacetabular region of synsacrum less than 40% synsacral length (char. 173: 0 > 1, reversed in *Tinamus*, also evolved independently in *Vegavis* and *Anatalavis*)
- Ilia extensively fused to synsacrum in adults (char. 175: 0 > 1, reversed in *Tinamus*, also evolved independently in Gruiformes, *Cariama*, Anhimidae, *Anatalavis*, Anatidae, and *Phasianus*)
- Femoral neck not or slightly constricted in caudal view (char. 187: 1 > 0, reversal to plesiomorphic state for Neornithes, reversed in *Tinamus*)
- Lateral condyle on femur markedly divergent from axis (char. 205: 0 > 1, reversed in *Tinamus*, also evolved independently in *Cariama* and *Cereopsis*)
- Pneumatic popliteal fossa on femur (char. 216: 0 > 1, reversed in *Tinamus*, also evolved independently in *Vegavis*, *Cariama*, *Anhima* [variably present], Anatidae, and *Phasianus*)
- Medial supracondylar crest on femur shorter than width of medial condyle (char. 217: 2 > 1, reversal to plesiomorphic state for Neornithes, reversed in *Tinamus*)
- Internal edge of distal femoral shaft smoothly curving continuous to condyle in medial view (char. 218: 2 > 0, reversed in *Tinamus*, also evolved independently in *Cariama* and Galloanserae)
- Elongate, conspicuous scar for medial collateral ligament proximocaudal to medial epicondyle on tibiotarsus (char. 236: 1 > 2, reversed in *Tinamus*, also evolved independently in *Cariama*)

- Junction of cartilaginous trochlea crest and rim of medial condyle on tibiotarsus not marked by a distinct shallow notch (char. 237: 1 > 0, also evolved independently in *Porphyrio*, *Burhinus*, *Cariama*, *Anseranas*, *Dendrocygna*, and *Cereopsis*)
- Intercondylar ligament impression on tibiotarsus absent (char. 239: 1 > 0, reversed in *Tinamus*)
- Intercondylar incisure on tibiotarsus absent (char. 245: 0 > 2, reversed in *Tinamus*)
- Sulcus m. fibularis on tibiotarsus faces laterally (char. 246: 0 > 1, also evolved independently in *Burhinus* and Galliformes)
- Tarsometatarsus more than 105% femur length (char. 249: 0 or 1 > 2, reversed in *Tinamus*, also evolved independently in Neoaves and Anseriformes)
- Medial cotyle of tarsometatarsus dorsoplantarly elongated, protruding dorsal to lateral cotyle (char. 250: 0 > 1, reversed in *Tinamus*, also evolved independently in *Ichthyornis*)
- Medial cotyle of tarsometatarsus laps dorsally onto dorsal facies (char. 251: 0 > 1, reversed in *Tinamus*, also evolved independently in *Pelagornis*)
- Medial parahypotarsal fossa of tarsometatarsus shallow, with concave surface from medial calcaneal ridge to cranial margin of medial shaft (char. 261: 1 > 2, reversed in *Dinornis*, also evolved independently in *Antigone*, *Cariama*, Anhimidae, *Cereopsis*, *Pelagornis*, *Phasianus*, and *Coturnix*)
- Fossa for metatarsal I on tarsometatarsus absent (char. 271: 0 > 1, also evolved independently in *Antigone*, *Burhinus*, *Cariama*, *Wilaru*, Anatidae, and *Coturnix*)
- Distal vascular foramen on tarsometatarsus small but distinct (char. 279: 0 > 1, also evolved independently in *Burhinus*, *Cariama*, *Leipoa*, Cracidae, *Macrocephalon*, and *Gallus*)

Neognathae

- **Tuberculum subcapitulare on otic process of quadrate** (char. 50: 0 > 1, reversed in *Burhinus*, *Pelagornis*, and *Anseranas*)
- Pterygoid condyle and pterygoid articulation facies of the orbital process on quadrate adjacent or fused to each other (char. 56: 1 > 0, reversed in *Presbyornis* and [*Asteriornis* + Galliformes])
- Dorsal and ventral lobes of acrocoracoid process on coracoid do not overhang supracoracoidal sulcus (char. 98: 3 > 0, reversed in *Burhinus*, *Cariama*, Presbyornithidae, *Crax*, *Acryllium*, and *Coturnix*)
- Cranial end of acrocoracoid process on coracoid not projected over medial margin of supracoracoidal sulcus (char. 101: 1 > 0, reversed in *Burhinus*, *Cariama*, [*Anatalavis* + *Conflicto*], *Wilaru*, *Cereopsis*, and [*Gallinuloides* + Galliformes])
- Humerus with essentially parallel sides in caudal or cranial view (char. 135: 2 > 0, reversed in *Cariama*, *Conflicto*, and Galliformes, also evolved independently in *Dromaius*)
- Ventral supracondylar tubercle on humerus parallel to shaft and not buttressed proximally (char. 139: 1 > 0, reversed in *Porphyrio*, *Burhinus*, *Chauna* [variably present], *Conflicto*, Presbyornithidae, Anatidae, Megapodiidae, *Phasianus*, and *Coturnix*)
- External rim of carpal trochlea on carpometacarpus extensive with even convex profile extending caudally to caudal carpal fovea (char. 155: 1 > 0, reversed in [*Tadorna* + *Anser*], *Pelagornis*, and *Macrocephalon*, also evolved independently in *Tinamus*)
- Synostosis of metacarpals II and III longer than wide (char. 171: 0 > 1, reversed in *Vegavis*, *Cariama*, *Wilaru*, *Anseranas*, and Galliformes)

- Recessus caudalis fossae shallow and pneumatic (char. 180: 2 > 1, reversed in *Vegavis*, *Burhinus*, and Anatidae)
- Ilioischiadic foramen approximately half the length of the ischium from the acetabular foramen (char. 182: 2 > 1, reversed in *Conflicto*, *Tadorna*, and *Anser*)
- Ilioischiadic foramen caudally closed (char. 183: 0 > 1)
- Tuberculum m. gastrocnemialis lateralis a round scar, close to or abutting fibular trochlea on caudal facies of femur (char. 207: 1 > 0, reversed in *Porphyrio*, [Presbyornithidae + Anseres], and Phasianidae, also evolved independently in Lithornithidae)
- **Impression for cranial cruciate ligament on femur poorly defined and not extending onto lateral condyle** (char. 221: 0 > 1, reversed in *Porphyrio*, *Burhinus*, *Chauna*, *Anseranas*, *Tadorna*, and Galliformes)
- Supratendinal bridge on tibiotarsus present (char. 242: 1 > 0, also evolved independently in [*Dinornis* + *Tinamus*])
- Intercontylar eminence on tarsometatarsus prominent dorsally in proximal view (char. 254: 1 > 0, reversed in [*Gallinuloides* + Galliformes], also evolved independently in *Ichthyornis*)
- Medial parahypotarsal fossa of tarsometatarsus shallow, with concave surface from medial calcaneal ridge to cranial margin of medial shaft (char. 261: 1 > 2, reversed in *Presbyornis*, *Anseranas*, *Macrocephalon*, *Acryllium*, and *Gallus*, also evolved independently in *Struthio* and *Dromaius*)

Neoaves

- Basipterygoid processes absent (char. 27: 0 > 1)
- Ventral crest on palatine strongly developed (char. 35: 0 > 1)
- Strongly-developed fossa on dorsal facies of pterygoid (char. 42: 0 > 1)

- Three mandibular cotyles (char. 60: 1 > 0, also evolved independently in Panpalaeognathae)
- Well-developed haemal processes on posterior caudal vertebrae absent (char. 77: 1 > 0, also evolved independently in Palaeognathae, Megapodiidae, *Phasianus*, and *Gallus*)
- Scapulotriciptal sulcus on humerus present on caudal face but does not extend around distal end of dorsal epicondyle (char. 140: 0 > 1, also evolved independently in *Conflicto*, *Wilaru*, Anatidae, *Crax*, *Phasianus*, and *Gallus*)
- Ilioischiadic foramen less than half the length of the ischium from the acetabular foramen (char. 182: 1 > 0, also evolved independently in Anhimidae, *Presbyornis*, and Galliformes)
- Femoral neck narrower than ball in caudal view (char. 187: 0 > 1, also evolved independently in Lithornithidae, *Tinamus*, *Wilaru*, *Dendrocygna*, and Galliformes)
- Distinct trochanteric fossa on femur (char. 189: 1 > 0, also evolved independently in *Tinamus*, Anhimidae, Presbyornithidae, and Galliformes)
- Dorsal facies of distal tarsometatarsus shaft flat or concave (char. 270: 0 > 1, also evolved independently in *Struthio*, *Dromaius*, *Presbyornis*, Anatidae, and Phasianidae)

Anseriformes

- Rudimentary lamellae on upper beak (char. 6: 0 > 1)
- Maxillopalatine processes of premaxilla incompletely fused (char. 7: 0 > 1)
- Impression of only pars articularis of m. adductor mandibulae externus present laterally on cranium, with pars coronoidea restricted to medial surface of postorbital process (char. 19: 0 > 1, also evolved independently in *Burhinus*)
- Caudal end of vomer not deeply cleft (char. 37: 0 > 1)
- Caudal end of vomer does not wrap around parasphenoid rostrum (char. 38: 0 > 1)

- Pneumatic foramen caudal to medial crest on otic process of quadrate (char. 51: 0 > 1, reversed in *Cereopsis*, also evolved independently in *Lithornis promiscuus*, *Dromaius*, and *Dinornis*)
- Orbital crest prominent and on lateral bulge of orbital process on quadrate (char. 53: 0 > 1, reversed in *Conflicto*, also evolved independently in *Crax*)
- Retroarticular process tall and long (char. 64: 0 or 3 > 2)
- **Medial processes of mandible long, narrow, and dorsally oriented** (char. 68: 0 > 1, also evolved independently in [*Asteriornis* + Galliformes])
- Acromial process of furcula pointed (char. 110: 0 > 1, reversed in *Wilaru*, also evolved independently in *Lithornis promiscuus* and *Burhinus*)
- Robust, U-shaped furcular hypocleideum (char. 114: 2 > 1, also evolved independently in Pelagornithidae)
- Proximal profile of humerus not or barely interrupted by capital incisure (char. 130: 1 > 0, reversed in *Tadorna*, also evolved independently in *Ichthyornis*, Gruiformes, *Leipoa*, *Megapodius*, *Phasianus*, and *Coturnix*)
- Attachment of m. flexor carpi ulnaris on flexor process of humerus forms two scars of approximately equal depth (char. 143: 0 or 2 > 1, also evolved independently in *Cariama*)
- Insertion of m. iliotrochnatericus caudalis on femur in dorsal half of femur depth, but separated from dorsal margin (char. 202: 0 > 1, also evolved independently in *Tinamus* and Galliformes)
- Medial supracondylar crest on femur shorter than width of medial condyle (char. 217: 1 > 0, reversed in Presbyornithidae, also evolved independently in *Ichthyornis*)

- Medial condyle of tibiotarsus projects markedly cranially relative to lateral condyle (char. 235: 1 > 0, reversed in *Presbyornis*, also evolved independently in *Dinornis* and *Antigone*)
- Impression for intercondylar ligament on tibiotarsus extends medially by excavation caudal to medial condyle (char. 241: 0 > 1, reversed in *Conflicto*, also evolved independently in *Paracathartes*, *Lithornis*, and *Burhinus*)
- Distal opening of extensor canal on tibiotarsus has no overlap in lateromedial plane with medial condyle (char. 243: 1 > 2, also evolved independently in *Ichthyornis*, *Porphyrio*, and Pelagornithidae)
- Medial displacement of medial condyle on tibiotarsus pronounced relative to medial facies of shaft (char. 244: 0 > 1, also evolved independently in *Ichthyornis*, Notopalaeognathae, and Gruiformes)
- Trochlea for metatarsal II with flattened medial facies (char. 276: 0 > 1, reversed in *Anseranas*, also evolved independently in Notopalaeognathae, *Burhinus*, and *Cariama*)
- Webbing between toes rudimentary (char. 285: 0 > 1, also evolved independently in Cracidae)

Presbyornithidae + Anseres

- Premaxillae spatulate (char. 3: 0 > 1, reversed in *Conflicto*)
- **Frontal depression forms a shallow, elongate groove** (char. 14: 0 > 1, reversed in *Anser*, also evolved independently in *Asteriornis*, Cracidae, *Phasianus*, and *Coturnix*)
- Zygomatic processes absent (char. 17: 0 > 1, also evolved independently in *Pelagornis* and *Gallinuloides*)
- Fontanelles in occipital region (char. 30: 0 > 1, reversed in *Cereopsis*)
- Conical recess in impressio m. depressor mandibulae (char. 65: 0 > 1)

- Lateral compression of mandibular rami defining long, very narrow inter-ramal region (char. 69: 0 > 1)
- Carpal tubercle on ulna large, projecting more than half the craniocaudal width of dorsal and ventral condyles (char. 154: 1 > 0, also evolved independently in *Burhinus*)
- Tuberculum m. gastrocnemialis lateralis a round scar well separated from fibular trochlea on caudal facies of femur (char. 207: 0 > 1, reversal to plesiomorphic state for Neornithes)
- No flange-like process on plantarmedial edge of medial cotyle on tarsometatarsus (char. 252: 1 > 0, reversed in *Dendrocygna* and *Anser*, also evolved independently in Panpalaeognathae, *Burhinus*, *Cariama*, *Alectura*, and *Macrocephalon*)
- Webbing between toes semipalmate or palmate (char. 285: 1 > 2 or 3)

Pangalliformes

- **Pneumatic foramen on anteromesial surface of otic process of quadrate** (char. 52: 0 > 1, also evolved independently in *Porphyrio*, *Conflicto*, and *Cereopsis*)
- **Basiorbital pneumatic foramen on medial surface of otic process of quadrate** (char. 54: 0 > 1, reversed in *Phasianus*, also evolved independently in *Ichthyornis*, *Conflicto*, and *Presbyornis*)
- Pneumatic fossa on ventral facies of scapula under facies articulating with humerus (char. 91: 0 > 1, reversed in *Megapodius eremita* and Phasianoidea, also evolved independently in *Tinamus*)
- Furcular hypocleideum present as low ridge (char. 112: 0 > 1, also evolved independently in *Burhinus*, *Conflicto*, Presbyornithidae, and *Anseranas*)
- Ventral tubercle on humerus directed cranio-caudally in caudal view (char. 128: 0 > 1, reversed in *Acryllium*, also evolved independently in [*Anatalavis* + *Conflicto*] and *Wilaru*)

- Ischiopubic space narrow (char. 181: 0 > 1, reversed in *Megapodius* and *Acryllium*, also evolved independently in *Lithornis promiscuus*, *Tinamus*, Gruiformes, and *Cariama*)
- Facies on femur articulating with antitrochanter convex in lateromedial plane (char. 188: 0 > 1, reversed in *Crax* and *Coturnix*, also evolved independently in Panpalaeognathae, *Conflicto*, *Wilaru*, and Anatidae)
- Cranial cnemial crest of tibiotarsus deflected laterally from axis at base (char. 225: 0 > 1, reversed in *Ortalis*, also evolved independently in Panpalaeognathae)
- Impressions for extensor retinacula form two short crests proximal to proximal vascular foramen (char. 266: 1 > 0, reversed in *Phasianus*, also evolved independently in *Lithornis promiscuus*, *Anseranas*, and *Tadorna*)

Gallinuloides + Galliformes

- Premaxilla less than 50% total cranium length (char. 1: 0 > 2, also evolved independently in [*Dinornis* + *Tinamus*], Anhimidae, *Dendrocygna*, and *Cereopsis*)
- Supracoracoid nerve foramen absent (char. 93: 0 > 2, also evolved independently in *Cariama*, *Chauna*, *Conflicto*, *Dendrocygna*, and *Anser*)
- Procoracoid absent or with minimal medial projection (char. 94: 1 > 0)
- Acrocoracoid process on coracoid directed primarily medially, forming near right angle with medial margin of humeral facet (char. 99: 0 > 1, also evolved independently in *Tinamus*)
- Coracoid facies articulating with humerus flat or convex (char. 100: 0 > 1, also evolved independently in *Ichthyornis*, *Tinamus*, and *Anatalavis*)
- Furcular hypocleideum present as prominent ridge or lobe (char. 112: 1 > 2)

- Dorsal pneumotricipital fossa on humerus is wide and shallow, greater than or equal to width of ventral pneumotricipital fossa (char. 118: 0 > 2, also evolved independently in *Conflicto*)
- Insertion of m. supracoracoideus tendon on humerus forms elongate scar extending distal to dorsal tubercle (char. 126: 0 > 1, also evolved independently in *Tinamus*)
- Moderate dorsoventral curvature of distal third of femur (char. 200: 0 > 1, reversed in *Macrocephalon* and *Crax*, also evolved independently in Lithornithidae and *Tinamus*)
- Intercondylar incisure on tibiotarsus narrow, width subequal to extensor canal (char. 245: 0 > 1, also evolved independently in *Burhinus*, *Cariama*, and *Pelagornis*)

Asteriornis + Galliformes

- No unambiguous synapomorphies

Galliformes

- Impression for cranial cruciate ligament on femur well marked and excavated into caudodistal facies of lateral condyle (char. 221: 1 > 0, reversal to plesiomorphic state for Neornithes, reversed in *Macrocephalon*)

Inferred synapomorphies under Bayesian tip-dating (characters in bold are exhibited by *Asteriornis*)

Panpalaeognathae

- Palatine and pterygoid fused (char. 41: 1 > 0)
- Capitulum squamosum and capitulum oticum on quadrate form single elongate dumbbell-shaped head (char. 49: 1 > 0, also evolved independently in *Conflicto*)
- Basiorbital pneumatic foramen on medial surface of otic process of quadrate absent (char. 54: 1 > 0, also evolved independently in Neoaves, Anseriformes, and *Phasianus*)

- Capitulum squamosum overhangs lateral surface of otic process on quadrate (char. 57: 1 > 0, reversed in *Tinamus*, also evolved independently in Gruiformes, *Cariama*, *Chauna*, and *Anseranas*)
- Three mandibular cotyles (char. 60: 1 > 0, also evolved independently in Neoaves)
- **Splenial and dentary unfused in adults** (char. 67: 0 > 1, also evolved independently in *Asteriornis* and Megapodiidae)
- Cranial extent of acromion distinctly craniad of coracoid tubercle on scapula (char. 89: 0 > 1, also evolved independently in *Pelagornis*, *Cariama*, Presbyornithidae, *Anhima*, Anatidae, and Galliformes)
- Well-developed tubercle on scapula for attachment of acrocoraco-procracoid ligament (char. 92: 0 > 1, reversed in *Tinamus*, also evolved independently in Galliformes)
- Attachment of m. scapulohumeralis cranialis on humerus ventral to crus dorsal fossae (char. 127: 0 > 1, also evolved independently in Galloanserae)
- Bicipital crest on humerus distinctly wider than long in caudal view (char. 131: 1 > 2, also evolved independently in *Vegavis*, *Wilaru*, *Anhima*, *Anatalavis*, *Ortalis*, *Phasianus*, and *Gallus*)
- Distal extent of flexor process on humerus roughly equal to that of ventral and dorsal condyles in cranial view (char. 137: 0 > 1, reversed in *Lithornis promiscuus*, also evolved independently in *Porphyrio*, *Cariama*, *Dendrocygna*, and *Tadorna*)
- Ulnar bicipital tubercle forms single scar (char. 148: 0 > 3, reversed in *Paracathartes*, also evolved independently in Presbyornithidae)
- Distal rim of carpal trochlea on carpometacarpus ends considerably short of ventral rim in caudal view (char. 156: 1 > 0, reversed in *Paracathartes*, also evolved independently in *Porphyrio*, *Burhinus*, and Galliformes)

- Craniocaudal length of extensor process on carpometacarpus near or less than half the length of the carpal trochlea in ventral view (char. 163: 1 > 0, reversed in *Paracathartes*, also evolved independently in *Pelagornis*, Megapodiidae, and Phasianoidea)
- Insertion for dorsal ulnocarpo-metacarpal ligament on carpometacarpus relatively distal (char. 167: 0 > 1, reversed in *Lithornis promiscuus*, also evolved independently in *Cariama* and Galliformes)
- Femoral neck narrower than ball in caudal view (char. 187: 0 > 1, reversed in *Struthio*, *Dromaius*, and *Dinornis*, also evolved independently in Neoaves, *Wilaru*, *Dendrocygna*, and Galliformes)
- Impressio ansa m. iliofibularis caudalis on femur present on lateral facies but also wraps around caudolateral margin at proximal side of fibular trochlea (char. 208: 0 > 1, reversed in *Struthio* and *Dromaius*, also evolved independently in *Porphyrio*, *Cariama*, *Macrocephalon*, *Phasianus*, and *Coturnix*)
- **Fibular trochlea on femur lacking distinct depression immediately proximal of articular surface in caudal view** (char. 209: 1 > 0, also evolved independently in *Burhinus*, *Cariama*, and Galloanserae)
- Medial condyle of femur evenly rounded in medial aspect (char. 212: 1 > 0, also evolved independently in Galliformes)
- Medial supracondylar crest on femur absent (char. 217: 1 > 2, reversed in *Struthio*, *Dromaius*, and *Dinornis*)
- Fibular trochlea of femur short in caudal view, merging distally with lateral condyle and forming a notch (char. 219: 0 > 1, reversed in *Struthio*, *Dinornis*, and *Tinamus*, also evolved independently in *Burhinus*)

- Cranial cnemial crest of tibiotarsus deflected laterally from axis at base (char. 225: 0 > 1, also evolved independently in *Pelagornis* and Galliformes)
- Deep ligamental pit on cranial external facies of medial condyle on tibiotarsus (char. 233: 0 > 1, reversed in *Tinamus*, also evolved independently in *Cereopsis*)
- Short, conspicuous scar for medial collateral ligament proximocaudal to medial epicondyle on tibiotarsus (char. 236: 0 > 1, also evolved independently in *Burhinus*, *Anseranas*, and *Presbyornis*)
- Distal opening of extensor canal on tibiotarsus directed towards and broadly overlaps in lateromedial plane with medial condyle (char. 243: 1 > 0)
- No flange-like process on plantarmedial edge of medial cotyle on tarsometatarsus (char. 252: 1 > 0, reversed in *Lithornis plebius* and *Tinamus*, also evolved independently in *Burhinus*, *Cariama*, Presbyornithidae, *Anseranas*, *Tadorna*, *Cereopsis*, *Alectura*, and *Macrocephalon*)
- Intercotylar eminence on tarsometatarsus not prominent proximally in lateral view (char. 255: 0 > 1, reversed in *Struthio* and *Tinamus*, also evolved independently in Megapodiidae, *Crax*, and *Coturnix*)
- Tuberositas m. tibialis cranialis is two distinct tuberosities fused as one at the base of the extensor sulcus of the tarsometatarsus (char. 263: 1 > 2, reversed in *Struthio* and *Tinamus*, also evolved independently in *Cariama* and *Wilaru*)

Palaeognathae

- Closed frontoparietal suture (char. 15: 0 > 1, reversed in *Tinamus*, also evolved independently in *Ichthyornis* [variably present] and Neognathae)
- Pila otica with pneumatic openings lateral or caudolateral to it (char. 26: 0 > 1, also evolved independently in *Antigone*, *Ortalis*, and [*Coturnix* + *Gallus*])

- Well-developed haemal processes on posterior caudal vertebrae absent (char. 77: 1 > 0, also evolved independently in Neoaves, Megapodiidae, *Phasianus*, and *Gallus*)
- Coracoid fused to scapula (char. 109: 0 > 1, reversed in *Tinamus*)
- Preacetabular region of synsacrum less than 40% synsacral length (char. 173: 0 > 1, reversed in *Tinamus*, also evolved independently in *Vegavis* and *Anatalavis*)
- Ilia extensively fused to synsacrum in adults (char. 175: 0 > 1, reversed in *Tinamus*, also evolved independently in Gruiformes, *Cariama*, *Anatalavis*, Anseriformes, and *Phasianus*)
- Femoral neck not or slightly constricted in caudal view (char. 187: 1 > 0, reversal to plesiomorphic state for Neornithes, reversed in *Tinamus*)
- Straight or slight dorsoventral curvature of femur (char. 200: 1 > 0, reversal to plesiomorphic state for Neornithes, reversed in *Tinamus*)
- Lateral condyle on femur markedly divergent from axis (char. 205: 0 > 1, reversed in *Tinamus*, also evolved independently in *Cariama* and *Cereopsis*)
- Pneumatic popliteal fossa on femur (char. 216: 0 > 1, reversed in *Tinamus*, also evolved independently in *Vegavis*, *Cariama*, *Anhima* [variably present], Anatidae, and *Phasianus*)
- Medial supracondylar crest on femur shorter than width of medial condyle (char. 217: 2 > 1, reversal to plesiomorphic state for Neornithes, reversed in *Tinamus*)
- Internal edge of distal femoral shaft smoothly curving continuous to condyle in medial view (char. 218: 2 > 0, reversed in *Tinamus*, also evolved independently in *Cariama* and Galloanserae)
- Elongate, conspicuous scar for medial collateral ligament proximocaudal to medial epicondyle on tibiotarsus (char. 236: 1 > 2, reversed in *Tinamus*, also evolved independently in *Cariama*)

- Junction of cartilaginous trochlea crest and rim of medial condyle on tibiotarsus not marked by a distinct shallow notch (char. 237: 1 > 0, also evolved independently in *Porphyrio*, *Burhinus*, *Cariama*, *Anseranas*, *Dendrocygna*, and *Cereopsis*)
- Intercondylar ligament impression on tibiotarsus absent (char. 239: 1 > 0, reversed in *Tinamus*)
- Intercondylar incisure on tibiotarsus absent (char. 245: 0 > 2, reversed in *Tinamus*)
- Sulcus m. fibularis on tibiotarsus faces laterally (char. 246: 0 > 1, also evolved independently in *Burhinus* and Galliformes)
- Tarsometatarsus more than 105% femur length (char. 249: 0 or 1 > 2, reversed in *Tinamus*, also evolved independently in Neoaves and Anseriformes)
- Medial cotyle of tarsometatarsus dorsoplantarly elongated, protruding dorsal to lateral cotyle (char. 250: 0 > 1, reversed in *Tinamus*, also evolved independently in *Ichthyornis*)
- Medial cotyle of tarsometatarsus laps dorsally onto dorsal facies (char. 251: 0 > 1, reversed in *Tinamus*, also evolved independently in *Pelagornis*)
- Width of hypotarsus approximately or distinctly less than half the width of proximal tarsometatarsus (char. 257: 2 > 0 or 1, reversed in *Tinamus*, also evolved independently in *Ichthyornis*, *Porphyrio*, *Cariama*, and Galloanserae)
- Medial parahypotarsal fossa of tarsometatarsus shallow, with concave surface from medial calcaneal ridge to cranial margin of medial shaft (char. 261: 1 > 2, reversed in *Dinornis*, also evolved independently in *Pelagornis*, *Antigone*, *Cariama*, Anhimidae, *Cereopsis*, *Phasianus*, and *Coturnix*)
- Fossa for metatarsal I on tarsometatarsus absent (char. 271: 0 > 1, also evolved independently in *Antigone*, *Burhinus*, *Cariama*, *Wilaru*, Anatidae, and *Coturnix*)

- Distal vascular foramen on tarsometatarsus small but distinct (char. 279: 0 > 1, also evolved independently in *Burhinus*, *Cariama*, *Leipoa*, Cracidae, *Macrocephalon*, and *Gallus*)
- Intermediate phalanges on pedal digit IV gradually shorten towards ungual (char. 281: 0 > 1, reversed in *Tinamus*)
- Ungual on pedal digit III wider than deep at midlength (char. 283: 0 > 2, also evolved independently in Megapodiidae)

Neognathae

- Dorsal and ventral lobes of acrocoracoid process on coracoid do not overhang supracoracoidal sulcus (char. 98: 3 > 0, reversed in *Burhinus*, *Cariama*, Presbyornithidae, *Crax*, *Acryllium*, and *Coturnix*)
- Humerus with essentially parallel sides in caudal or cranial view (char. 135: 2 > 0, reversed in *Cariama*, *Conflicto*, and Galliformes, also evolved independently in *Dromaius*)
- Ventral supracondylar tubercle on humerus parallel to shaft and not buttressed proximally (char. 139: 1 > 0, reversed in *Porphyrio*, *Burhinus*, *Conflicto*, Presbyornithidae, *Chauna* [variably present], Anatidae, Megapodiidae, *Phasianus*, and *Coturnix*)
- Ilioischiadic foramen approximately half the length of the ischium from the acetabular foramen (char. 182: 2 > 1, reversed in *Conflicto*, *Tadorna*, and *Anser*)
- Ilioischiadic foramen caudally closed (char. 183: 0 > 1)
- **Impression for cranial cruciate ligament on femur poorly defined and not extending onto lateral condyle** (char. 221: 0 > 1, reversed in *Porphyrio*, *Burhinus*, *Chauna*, *Anseranas*, *Tadorna*, and Galliformes)

- Supratendinal bridge on tibiotarsus present (char. 242: 1 > 0, also evolved independently in [*Dinornis* + *Tinamus*])

Panneoaves

- Mandibular process of quadrate ascends to meet ascending ramus of otic process in wide angle (char. 47: 0 > 1, also evolved independently in *Lithornis promiscuus*, *Struthio*, *Dromaius*, *Tadorna*, and *Ortalis*)
- Pterygoid condyle and pterygoid articulation facies of the orbital process on quadrate adjacent or fused to each other (char. 56: 1 > 0, also evolved independently in Anseriformes)
- Ridge linking ventral rim of carpal trochlea and pisiform process on carpometacarpus has a rounded profile, only slightly elevated over ventral facies of extensor process (char. 161: 1 > 0, reversed in *Antigone*, also evolved independently in *Tinamus*, *Wilaru*, Anhimidae, Anatidae, *Gallinuloides*, *Megapodius eremita*, Cracidae, *Acryllium*)
- Ischiopubic space narrow (char. 181: 0 > 1, reversed in *Burhinus*, also evolved independently in *Lithornis promiscuus*, *Tinamus*, and [*Gallinuloides* + Galliformes])
- Retroarticular process absent (char. 291: 1 > 0, reversed in *Antigone*, also evolved independently in *Ichthyornis*)

Neoaves

- Ossified zygomatic aponeurosis at least partially separated from postorbital process (char. 18: 0 > 1, also evolved independently in *Ichthyornis* and Galliformes)
- Basiorbital pneumatic foramen on medial surface of otic process of quadrate absent (char. 54: 1 > 0, also evolved independently in Panpalaeognathae, Anseriformes, and *Phasianus*)

- Three mandibular cotyles (char. 60: 1 > 0, also evolved independently in Panpalaeognathae)
- Scapulotriciptal sulcus on humerus present on caudal face but does not extend around distal end of dorsal epicondyle (char. 140: 0 > 1, also evolved independently in *Conflicto*, *Wilaru*, Anatidae, *Crax*, *Phasianus*, and *Gallus*)
- Ilioischiadic foramen less than half the length of the ischium from the acetabular foramen (char. 182: 1 > 0, also evolved independently in *Presbyornis*, Anhimidae, and Galliformes)
- Femoral neck narrower than ball in caudal view (char. 187: 0 > 1, also evolved independently in *Lithornis*, *Paracathartes*, *Tinamus*, *Wilaru*, *Dendrocygna*, and Galliformes)
- Distinct trochanteric fossa on femur (char. 189: 1 > 0, also evolved independently in *Tinamus*, Presbyornithidae, Anhimidae, and Galliformes)
- Long axis of extensor canal distal opening aligned across tibiotarsal shaft (char. 248: 1 > 0, also evolved independently in *Dinornis*, [*Conflicto* + Anseriformes], and *Acryllium* [variably present])
- Tarsometatarsus more than 105% femur length (char. 249: 0 or 1 > 2, also evolved independently in *Struthio*, *Dromaius*, *Dinornis*, and [*Conflicto* + Anseriformes])

Galloanserae

- **Frontal depression forms a shallow, elongate groove** (char. 14: 0 > 1, reversed in Anhimidae, *Anser*, *Alectura*, [*Macrocephalon* + *Megapodius*], and *Acryllium*)
- Tympanic recess bound ventrally by laterally projecting parasphenoid wings (char. 20: 0 > 1)
- **Retroarticular process tall but short in length** (char. 64: 0 or 3 > 1, reversed in [Cracidae + Phasianoidea])

- **Medial processes of mandible long, narrow, and dorsally oriented** (char. 68: 0 > 1)
- Attachment of m. scapulohumeralis cranialis on humerus ventral to crus dorsal fossae (char. 127: 0 > 1, reversed in *Anseranas*, also evolved independently in Panpalaeognathae)
- Insertion of m. iliotrochnatericus caudalis on femur in dorsal half of femur depth, but separated from dorsal margin (char. 202: 0 > 1, also evolved independently in *Tinamus*)
- **Fibular trochlea on femur lacking distinct depression immediately proximal of articular surface in caudal view** (char. 209: 1 > 0, reversed in *Wilaru*, *Dendrocygna*, *Phasianus*, and *Gallus*, also evolved independently in Panpalaeognathae, *Burhinus*, and *Cariama*)
- Internal edge of distal femoral shaft smoothly curving continuous to condyle in medial view (char. 218: 2 > 0, reversed in *Phasianus*, also evolved independently in Palaeognathae and *Cariama*)
- Width of hypotarsus approximately half the width of proximal tarsometatarsus (char. 257: 2 > 1, reversed in *Presbyornis*, Anatidae, and *Crax*, also evolved independently in *Dinornis*, *Porphyrio*, and *Cariama*)
- **Retroarticular process hooked** (char. 292: 0 or 1 > 2)

Anserimorphae

- Maxillopalatine processes of premaxilla incompletely fused (char. 7: 0 > 1)
- Impression of only pars articularis of m. adductor mandibulae externus present laterally on cranium, with pars coronoidea restricted to medial surface of postorbital process (char. 19: 0 > 1, also evolved independently in *Burhinus*)
- Fontanelles in occipital region (char. 30: 0 > 1, reversed in Anhimidae and *Cereopsis*)

- Pneumatic foramen caudal to medial crest on otic process of quadrate (char. 51: 0 > 1, reversed in *Cereopsis*, also evolved independently in *Lithornis promiscuus*, *Dromaius*, and *Dinornis*)
- Conical recess in impressio m. depressor mandibulae (char. 65: 0 > 1, reversed in Anhimidae)
- Lateral compression of mandibular rami defining long, very narrow inter-ramal region (char. 69: 0 > 1, reversed in Anhimidae)
- Dorsal and ventral lobes of acrocoracoid process on coracoid overhang supracocracoidal sulcus (char. 98: 1 > 2 or 3, reversal to plesiomorphic state for Neornithes, reversed in *Anhima* and Anatidae)
- Acromial process of furcula pointed (char. 110: 0 > 1, reversed in *Wilaru*, also evolved independently in *Lithornis promiscuus* and *Burhinus*)
- Medial condyle of tibiotarsus projects markedly cranially relative to lateral condyle (char. 235: 1 > 0, reversed in *Presbyornis*, also evolved independently in *Dinornis* and *Antigone*)
- Distal opening of extensor canal on tibiotarsus has no overlap in lateromedial plane with medial condyle (char. 243: 1 > 2, also evolved independently in *Ichthyornis* and *Porphyrio*)
- Medial displacement of medial condyle on tibiotarsus pronounced relative to medial facies of shaft (char. 244: 0 > 1, also evolved independently in *Ichthyornis*, Notopalaeognathae, and Gruiformes)
- Fossa at dorsal side of capital incisure on humerus bound distally by transverse crus dorsal fossa and dorsally by capital shaft ridge (char. 290: 0 > 1, reversed in Anatidae, also evolved independently in *Vegavis* and *Protodontopteryx*)

Anseriformes

- Angulus caudolateralis of palatine present (char. 34: 0 > 1, also evolved independently in Neoaves)
- Palatines completely fused along midline (char. 36: 0 > 1)
- Prominent submeatica on caudomedial facies of lateral and quadratojugal processes of quadrate (char. 48: 0 > 1, also evolved independently in Cracidae)
- Basiorbital pneumatic foramen on medial surface of otic process of quadrate absent (char. 54: 1 > 0, also evolved independently in Panpalaeognathae, Neoaves, and *Phasianus*)
- Pterygoid condyle and pterygoid articulation facies of the orbital process on quadrate adjacent or fused to each other (char. 56: 1 > 0, also evolved independently in Neoaves)
- Dorsolateral margin extending from otic process to dorsal tip of orbital process of quadrate forms straight line or slightly concave (char. 58: 1 > 0, reversed in *Tadorna*)
- Retroarticular process tall and long (char. 64: 1 > 2)
- Pneumatic foramen at cranial end of scapula (char. 90: 1 > 0, also evolved independently in *Macrocephalon*)
- Ventral pneumotricipital fossa on humerus open and highly pneumatic (char. 129: 1 > 0, reversal to plesiomorphic state for Neornithes)
- Ilia extensively fused to synsacrum in adults (char. 175: 0 > 1, reversed in *Tinamus*, also evolved independently in Palaeognathae, Gruiformes, *Cariama*, *Anatalavis*, and *Phasianus*)
- Interorbital region flat or convex in dorsal view (char. 294: 0 > 1, reversed in [*Tadorna* + *Anser*], also evolved independently in Gruiformes, *Cariama*, *Macrocephalon*, and *Crax*)

Pangalliformes

- No unambiguous synapomorphies

Galliformes

- Ossified zygomatic aponeurosis at least partially separated from postorbital process (char. 18: 0 > 1, also evolved independently in *Ichthyornis* and Neoaves)
- Scapula increases distally in dorsoventral height (char. 88: 0 > 1, reversed in *Coturnix*, also evolved independently in *Tinamus* and *Dendrocygna*)
- Facies articulating with scapula forms a subplanar to convex articulation on coracoid (char. 95: 0 > 2, also evolved independently in *Tinamus* and *Antigone*)
- Deltopectoral crest on humerus caudally flat or convex with angular profile (char. 121: 0 > 1, also evolved independently in *Ichthyornis*, *Tinamus*, and Pelagornithidae)
- Radial depression on distal ulna not marked (char. 153: 1 > 0, also evolved independently in *Tinamus*, *Antigone*, *Burhinus*, *Pelagornis*, *Wilaru*, and *Dendrocygna*)
- Distal rim of carpal trochlea on carpometacarpus ends considerably short of ventral rim in caudal view (char. 156: 1 > 0, also evolved independently in Panpalaeognathae, *Porphyrio*, and *Burhinus*)
- Infratrochlear fossa on carpometacarpus absent (char. 160: 1 > 0, reversed in *Phasianus*, also evolved independently in *Tinamus*)
- Facet for manual digit III extends more distally than that for digit II (char. 172: 1 > 0, also evolved independently in *Tinamus*, *Cariama*, *Anhima*, and *Anseranas*)
- Ilioischiadic foramen less than half the length of the ischium from the acetabular foramen (char. 182: 1 > 0, also evolved independently in Neoaves, *Presbyornis*, and Anhimidae)

IX: Morphological Character Descriptions

This matrix is based primarily on the matrix of Worthy et al. (2017)[2] and subsequent modifications by Tambussi et al. (2019)[11]. Any changes to the original character descriptions and codings are noted following the description of character states. Characters marked with a star were treated as ordered in the analysis. Newly added characters are listed at the end.

Skull

*1. Premaxilla, length relative to total length of cranium: 0, more than 50% total cranium length; 1, approximately 50% total cranium length; 2, less than 50% total cranium length. We added codings of (0) for both *Conflicto* and *Anatalavis*, and changed the scoring for *Burhinus* to (1).

*2. Premaxilla, length facies apertura nasalis compared to width craniofacial hinge, which in palaeognaths is interpreted as the rostral side of lacrymal: 0, long, greater than width of craniofacial hinge; 1, intermediate, approximately equal to width craniofacial hinge; 2, short, much less than width craniofacial hinge. See Worthy and Lee[90] (2008, char. 3), not Livezey (1996a[91], char. 3), which is related to highly autapomorphic taxa. We modified the coding for *Conflicto* to (0) as the nares appear much longer than the nasofrontal hinge in published images, and also made this character ordered as it describes a morphocline.

3. Premaxilla: 0, sides divergent caudally; 1, spatulate; 2, not spatulate, dorsoventrally deep, with steep culmen, nares reduced.

4. Premaxilla, rostral section curved ventrally so ventral profile curved down: 0, Yes, (e.g. *Anseranas*); 1, No, straight ventral margin. Note, this is not the character of Livezey (1986[92]: char. 12; 1996a: char. 10) & Worthy and Lee (2008[90], char. 16), which referred to the rostral tip of the median terminus of the premaxilla, which in e.g. *Malacorhynchus* is depressed ventrally. We coded *Anatalavis* (0) based on examination of the material.

5. Premaxilla, with culmen forming a distinct broad flattened ridge extending to tip defined by grooves laterally, with parallel structure ventrally on mandible: 0, yes; 1, no. From Parkes and Clark (1966)[93], overlaps Ericson (1997[28], char set A: 21), (Worthy and Scofield 2012[94], char. 57) with state 0 a synapomorphy of palaeognaths.

*6. Upper beak, lamellae for filter feeding: 0, absent; 1, vestigial, 2, well developed. See Olson and Feduccia (1980[30], fig. 6) concerning the presence of vestigial lamellae in the Anhimidae. Mayr and Clarke (2003[95], char. 3). We edited the coding for all fossil taxa (e.g. *Lithornis*, *Presbyornis*) to (?) as this character cannot be evaluated without soft tissue preservation.

*7. Premaxilla, palatal surface, fusion of proc. maxillopalatini: 0, not fused medially, fenestra ventromedialis open caudally (e.g. galliforms); 1, fused medially but incompletely, i.e., palate directly desmognathous, caudally enclosing elongate fenestra ventromedialis (e.g. *Anseranas*, anatids); 2, fused medially and completely and entire palate lacking fenestrae. Modified from Mayr and Clarke (2003[95]: Fig. 5B, char. 11) and Worthy and Lee (2008[90], char 18), relates to Ksepka (2009[96], char. 9). Dinornithiforms have the processus maxillopalatini connected by the intervening vomer in perfect specimens so enclosing a fenestra ventromedialis but as the processus themselves are not fused medially are here coded 0.

*8. Skull, zona flexoria craniofacialis: 0, zona absent or indistinct, no transverse sulcus, overlap of processus frontalis of premaxilla and frontals and os nasales continuous over zona, e.g. palaeognaths; 1, well developed zona present marked by transverse sulcus, nasals and processus frontalis cross zona, e.g. *Anseranas*; 2, zona flexoria essentially a hinge, e.g. *Sylviornis*, *Dromornis*.

9. Cranium, os prefrontale (lacrimal), synostosis with os frontale and or os nasale: 0, lacking; 1, present but restricted to area caudal of craniofacial hinge; 2, present adjacent to nasal

rostral to craniofacial hinge, and synostosed caudal to hinge. See Livezey (1986[92], char. 10; 1996a[91], char. 6), Ericson (1997[28], char set A: 5), Worthy and Lee (2008[90], char. 4).

10. Cranium, lacrimal, presence proc. supraorbitalis, enclosing notch caudally: 0, process absent or small, variably laterally oriented; 1, large, encloses marked notch. Modified from Livezey (1986[92], char. 11 in part; 1996a, char. 7); Mayr and Clarke (2003[95], char. 13), Worthy and Lee (2008[90], char 5), Ksepka (2009[96], char. 6). Taxa with unfused or vestigial os prefrontales are coded 0. *Cereopsis* is coded 1 as the lateral margins of the lacrimal protrude markedly laterad and enclose a foramen caudally, even though caudally they are linked to osseous struts created from the autapomorphically deep salt gland impressions.

11. Cranium, os frontale, facies dorsalis, sulcus glandulae nasalis (salt gland impressions): 0, absent; 1, present, typically lateral. See Livezey (1996a[91], char. 9 part), Mayr and Clarke (2003[95], char. 25), Worthy and Lee (2008[90], char. 7).

*12. Cranium, lacrimal, processus orbitalis lacrimale: 0, absent, e.g. *Leipoa*; 1, dorsoventrally short, tapering markedly ventrally (e.g. *Anseranas*); 2, dorsoventrally elongate. Here the process is coded the same despite whether is narrow, e.g. *Aythya australis*, or broad e.g. *Malacorhynchus*. Modified from Worthy and Lee (2008[90], char 10).

*13. Cranium, lacrimal – os ectethmoidale (ectethmoid) complex: 0, ectethmoid not ossified, or just an incipient ridge dorsally below the nasals; 1, ectethmoid ossified and small, not fused to lacrimal; 2, ectethmoid ossified and large, fused to or abuts lacrimal forming lacrimal-ectethmoid complex (e.g. *Malacorhynchus*). Worthy and Lee (2008, char 11), Ksepka (2009, char. 8). The os ectethmoidale complex is that which encloses the capsula nasalis osseae and thus state 2 overlaps Bourdon's (2011[97], char. 61) in which a well-developed mesethmoidale was found to be an apomorphy of Odontoanserae. We coded *Asteriornis* (1) because the presence of a small intact ecethmoid as well as a facet for the articulation of the lacrimal to skull roof indicate these elements were separate.

*14. Cranium, facies interorbitalis, depression frontalis: 0, absent; 1, shallow, elongate groove, variably extending to area between lacrimals or through the interorbital area; 2, marked concavity extending from between lacrimals through interorbital area. Modified from Worthy and Lee (2008[90], char 9). We coded this character (?) for *Anatalavis* as we consider the skull roof too badly crushed to accurately code it.

15. Cranium, fronto-parietal suture: 0, open; 1, closed. Mayr and Clarke (2003, char. 32).

16. Cranium, projection of os squamosum lateroventrally links with an outgrowth of the ala parasphenoidalis rostrally enclosing the recessus tympanicus rostralis: 0, absent; 1, present. See Worthy et al. (1997[98]: char. 124), Worthy and Lee (2008[90], char 17).

17. Cranium, processus zygomaticus: 0, present; 1, absent or obsolete e.g. *Anseranas*, *Cereopsis*, See Zusi and Livezey (2000[99]). The zygomatic process is present in most birds and is small in galliforms. Modified from Mayr and Clarke (2003, char. 33).

*18. Cranium, proc. zygomaticus, aponeurosis zygomatica : 0, unossified, e.g. *Dromaius*; 1. ossified, and often extends towards or converges with proc. postorbitalis but separated at its base by the impressio musculi adductoris mandibulae externus pars coronoidea on the lateral cranium in adults, e.g. *Alectura*; 2, ossified, and merges with proc. postorbitalis over whole length, e.g. anhimids. See Zusi and Livezey (2000) and Ksepka (2009, char. 12 and 13) here combined.

19. Cranium, impressio musculi adductoris mandibulae externus pars coronoidea et pars articularis (see, Zusi and Livezey (2000), both present laterally on cranium, small: 0, yes, e.g. *Leipoa*; 1, no, only pars articularis present laterally on cranium with pars coronoidea restricted to medial surface of proc. postorbitalis, e.g. anseriforms. In those taxa with a crista adductoris mandibulae externus articularis (see Zusi and Livezey 2000), e.g. anhimids, the pars coronoidea forms a sulcus medially at the junction of the processus postorbitalis and aponeurosis zygomatica, so are coded 1.This character is essentially the same as Ericson

(1997, char. set A: 4) and overlaps Bourdon (2011, char. 59). We re-coded this character as (1) for *Anatalavis* based on examination of CT scans.

20. Cranium, recessus tympanicus (=tympanic cavity), lateral flange of the ala parasphenoidalis or a lateral projection of the lamina parasphenoidalis, and caudal connections with the proc. paroccipitalis of os exoccipitale: 0, recessus tympanicus not bound ventrally by laterally projecting ala parasphenoidalis, e.g. *Dromaius*; 1, recessus tympanicus bound ventrally by laterally projecting ala parasphenoidalis which links caudally to the proc. paroccipitalis lateral to fossa parabasalis. Modified from Worthy and Lee (2008[90], char. 12). We re-coded this character as (1) for *Anatalavis* based on examination of CT scans.

21. Cranium, lacrimal, facies articularis frontonasalis, length relative to anterocaudal orbit diameter: 0, shorter than or equal to; 1, longer than. Worthy and Lee (2008, char. 13). We re-coded this character as (?) for *Anatalavis* based on examination of CT scans.

22. Cranium, tuba auditiva communis, separation of ostia (Livezey and Zusi 2006[80]: char. 126): 0, widely separated; 1, closely approach mid line of cranium opening into ostium pharyngeale or tuba auditiva communis. Mayr and Clarke (2003, char. 29), Worthy and Scofield (2012, char. 23). In *Anhima*, the tuba auditiva communis open rostrally in a single broad foramen, so is coded as 1.

23. Cranium, caudal part os basisphenoidale, ostium canalis opthalmici externa (for tubae auditivae, eustachian tubes) completely ossified ventrally: 0, yes; 1, no. Modified from Mayr and Clarke (2003, char. 28), Worthy and Scofield (2012, char. 22).

24. Cranium, basiparasphenoid plate (= lamina parasphenoidalis) inflated ventrally below the tuba auditiva communis and the ostium pharyngeale and associated foramina rami palatinus et sphenomaxillaris, rounded, and broad: 0, no; 1, yes. In part Mayr and Clarke (2003, char. 26) and Worthy and Lee (2008, char. 19). With the inflation defined as relative to the tuba auditiva communis, *Anhima* is markedly inflated although it has a flat ventral surface.

Anseranas and *Alectura* are coded 0, and *Gallus* is coded 1. We note that *Alectura* was coded (1) in the Tambussi et al. (2019) matrix but explicitly described as coded (0) in the text of the character description. We have thus edited the coding to (0) which conforms the morphology observed in available specimens.

25. Cranium, lamina parasphenoidalis, caudolateral corner, development of tuberculum basilare (mamillar tuberosities), proc. mediales parasphenoidales (Livezey and Zusi 2006): 0, obsolete; 1, large and prominent. From Parker (1895[100]), Pycraft (1900[53]: 172), Livezey & Zusi (2006: char. 123), Mayr and Clarke (2003: char. 30), Worthy and Scofield (2012: char 18). We re-coded *Anhima* (1) as the processes in this taxon are arguably larger than in *Chauna* (which is coded 1 in the orginal matrix).

26. Cranium, os opisthoticum/prooticum, pila otica with pneumatic openings lateral or caudolateral to it: 0, no; 1, yes. From Mayr and Clarke (2003, char. 31). Foramina anterolateral to the pila are not considered in this character. *Coturnix* differs from other galliforms examined with a taller and more rostrally located pila otica and an extra foramen caudolaterally.

27. Cranium, os basisphenoidale (os parasphenoidale), presence of proc. basipterygoidei: 0, yes; 1, no.

*28. Cranium, os basisphenoidale (os parasphenoidale), position of proc. basipterygoidei: 0, on anterolateral corner of basitemporal platform caudal to rostrum parasphenoidale; 1, rostral to basitemporal platform on caudal end of caudally broad rostrum parasphenoidale; 2, on sides of rostrum parasphenoidale anterior to caudal end of rostrum, usually narrowly separated, e.g. Anatidae. Worthy and Scofield (2012, char. 12). We coded this character as (1) for *Anatalavis* based on examination of CT scans.

*29. Cranium, basipterygoid process, facet for articulation with pterygoid pedicellate (stalked): 0, yes, and elongate; 1, yes, short, ie facet is well raised above facies; 2, no.

30. Cranium, occipital region, fontanelles: 0, absent; 1, present. See Livezey (1986, char. 9), in part Ericson (1997, char. set A: 1), Mayr and Clarke (2003, char. 27), and Worthy and Lee (2008, char. 8 and notes). Taxa where fontanelles are variably present are coded 1.

31. Cranium, ventral view, paroccipital notch, i.e. between proc. paroccipitalis and the mamillar tuberosity, location of foramen n. vagi (vagus foramen for IX^{th} and X^{th} nerves): 0, in the notch; 1, caudad or mesad of the notch. From Parker (1895) and Pycraft (1900); Worthy and Scofield (2012, char. 10). We re-coded *Conflicto* as (?) since we found it impossible to distinguish this foramen in published images.

*32. Cranium, ventral view, location of external aperture of carotid canal: 0, caudal to paroccipital notch; 1, in paroccipital notch, e.g. *Leipoa*; 2, rostral to paroccipital notch. From Parker (1895) and Pycraft (1900). Modified from Worthy and Scofield (2012, char. 11).

33. Cranium, ventral view, position of proc. jugale of os maxillare relative to processus maxillopalatini (=processus palatus maxillaris Livezey and Zusi 2006) of maxilla: 0, dorsal or on same plane; 1, ventral. From Ericson (1997: char. 11).

34. Cranium, os palatinum, angulus caudolateralis: 0, absent or very small; 1, present and prominent. Modified from Mayr and Clarke (2003, char. 16).

35. Cranium, ossa palatina, development of crista ventralis: 0, poorly developed or absent; 1, strongly developed ventrally. See Ericson (1997, char. set A: 9), Mayr and Clarke (2003, char. 15).

36. Cranium, ossa palatina completely fused along midline caudally, with or without vomer: 0, no; 1, yes. See Ericson (1997, char. set A: 8), Mayr and Clarke (2003, char. 17). In dinornithiforms the palatines are separated by and fused to the vomer, but not to each other.

37. Cranium, vomer, caudal ends not fused, more or less deeply cleft: 0, yes; 1, no. From Mayr and Clarke (2003, fig. 5C, char. 19).

38. Cranium, vomer, caudal end sleeves over (wraps around) rostrum parasphenoidale: 0, yes; 1, no, may or may not fuse to processus rostralis of ossa palatina.

39. Cranium, vomer mediolaterally wide: 0, yes; 1, no. From Mayr and Clarke (2003, fig. 5A), char. 20).

40. Cranium, vomer forms a narrow and dorsoventrally high lamella on the midline: 0, no; 1, yes. From Mayr and Clarke (2003, char. 21).

41. Cranium, os palatinum and os pterygoideum fused: 0, yes; 1, no. From Mayr and Clarke (2003, char. 22) and Ksepka (2009, char. 10). We edited the coding for *Anatalavis* from (0) to (1).

42. Cranium, os pterygoideum: presence of a fossa on the dorsal facies caudal to the basipterygoid process: 0, absent or weakly developed; 1, strongly developed fossa. We coded *Anatalavis* (0) for this character based on examination of the specimen.

43. Cranium, os pterygoideum, articulation with palatine: 0, a simple abutment; 1, a ball and socket joint with 1 main condyle; 2, a ball and socket joint with prominent additional dorsal condyle.

44. Cranium, os pterygoideum, location of basipterygoid facet: 0, facet separated from rostral end by c. 1/2 length facet; 1, facet closer to rostral end than (1) and may abut palatine articulation; 2, facet close to the caudal end. We coded *Anatalavis* (1) for this character based on examination of the specimen. We also eliminated the original state (0) indicating absence of a facet as that condition is correlated to the absence of basipterygoid processes which is already represented by character 27.

45. Cranium, os exoccipitale, processus paroccipitalis, strongly protruding caudoventrally, caudally convex: 0, no; 1, yes. From Bourdon (2011, char. 56). We re-coded *Anatalavis* and *Conflicto* (0) for this character as the condition in both is strongly similar to that in anatoids.

46: Postorbital process, primarily rostrally oriented, forming ventral margin of orbit: 0, no; 1, yes. We modified this character from the original description.

Quadrate (Os quadratum)

47. Quadrate, proc. mandibularis in lateral view, profile above cotyla quadratojugalis: 0, subparallel to plane across ventral margins of condyli lateralis et medialis, meeting ascending ramus of proc. oticus at about right angles (e.g. *Malacorhynchus*); 1, ascends to meet ascending ramus of proc. oticus in wide angle (e.g. *Anas*). Worthy and Lee (2008, char. 20).

48. Quadrate, pars mandibularis, processus lateralis pars quadratojugalis, prominentia submeatica on caudomedial facies: 0, absent; 1, present. Present in anseriforms but absent in most neornithines including Presbyornithidae (Ericson 1997, char. set A: 17).

*49. Quadrate, capitulum squamosum and capitulum oticum: 0, form single elongate dumbbell shaped head, capituli with articular facets indistinct or essentially abutting each other; 1, have distinct articular facets widely separated by incisura intercapitulum; 2, one articular surface forming an oval head. Note: Overlaps with Ericson (1997, char. set A: 16), Mayr and Clarke (2003, char. 34), and Worthy and Scofield (2012, char. 51).

50. Quadrate, proc. oticus, tuberculum subcapitulare (=eminentia articularis): 0, absent; 1, present. Mayr and Clarke (2003: char. 35), with terminology of Elzanowski and Stidham (2010[86]). In *Anseranas*, there is no sign of the tuberculum: the feature labelled ‘proximal expansion of the subcapitular tubercle’ by Elzanowski and Stidham (2010) is part of the articular facet of capitulum oticum.

51. Quadrate, pneumatic foramen caudal to crista medialis on proc. oticus, foramen pneumaticum caudomediale, sensu Elzanowski and Stidham (2010): 0, no; 1, yes. Note: this character solely concerns presence or absence of a distinct foramen on the shaft, not whether there are foramina adjacent to the head. In *Anhima*, lateromedial compression of the quadrate

results in this fossa lying on the medial facies, but as it is caudal to the crista medialis descending from the capitulum oticum, it is homologous with state (1). However, in *Cereopsis*, the only foramen is on the medial facies, which in the absence of a crista medialis, is interpreted as the foramen pneumaticum rostromediale and that the caudomedial foramen is absent, unlike other Anseriformes. Overlaps Mayr and Clarke (2003, char. 36), Worthy and Scofield (2012, char. 52).

52. Quadrate, pneumatic foramen on anteromesial surface of proc. oticus, equals foramen pneumaticum rostromediale (Elzanowski and Stidham 2010), rostral to the crista medialis: 0, no; 1, yes. Worthy and Scofield (2012, char. 50). Anseriforms are state 0, except for *Cereopsis*, see notes under character 51.

53. Quadrate, crista orbitalis proc. orbitalis (Elzanowski and Stidham 2010): 0, crista orbitalis weak and on bulge laterally on processus orbitalis; 1, crista orbitalis prominent and on bulge laterally on processus orbitalis; 2, crista mainly on tip of processus orbitalis, which has no lateral bulge.

54. Quadrate, foramen pneumaticum basiorbitale (see Elzanowski and Stidham 2010) ventrally on medial surface of processus oticus: 0, no; 1, yes. Elzanowski and Stidham (2010) list this as consistently present in galliforms (except *Phasianus*). Contra Elzanowski and Stidham (2010) a small basiorbital foramen was observed in *Gallus* by Worthy et al. (2017). We re-coded *Conflicto* (1) for this character as the text clearly states the foramen is present and it is visible in the figure in the original description.

55. Quadrate, proc. oticus, capitulum oticum, pneumatic under capitulum: 0, no; 1, yes. Worthy and Scofield (2012, char. 53).

56. Quadrate, pterygoid articulations, condylus pterygoideus and facies artic. pterygoidea of the orbital process: 0, adjacent or fused to each other; 1, widely separated, distinct facet on orbital process. Elzanowski and Stidham (2010) argued on the basis that the articulations are

adjacent in the majority of Neoaves, as well as in *Anseranas*, anhimids, anatids and cracids, that the adjacent condition is likely the plesiomorphic condition. Widely separated articulations characterize *Presbyornis*, megapodiids, and all phasianoid families. We recoded *Conflicto* (?) for this character because the bone surface preservation in the relevant area appears too poor to accurately evaluate the morphology.

57. Quadrate, the capitulum squamosum overhangs the lateral surface of the processus oticus: 0, yes (e.g. *Anseranas*); 1, no. Worthy and Lee (2008, char. 21). We recoded *Conflicto* (1) based on published images, which show no evidence of overhang

58. Quadrate, the dorsolateral margin extending from processus oticus to the dorsal tip of the crista orbitalis: 0, forms straight line (e.g. *Dendrocygna*) or slightly concave; 1, markedly concave. Livezey (1986: char. 15), see also Raikow (1971[101]), Worthy and Lee (2008, char. 22). For non-galloanserans, a line from proc. oticus to tip of the orbital process is used to score this character.

59. Quadrate, pars quadratojugalis, fovea quadratojugalis, incisura caudalis (see Elzanowski and Stidham 2010): 0, absent; 1, present. A distinct caudoventral notch in the rim of the fovea is present in the anatids, most non-megapode galliforms (except Odontophoridae), and *Anhima*. The rim is complete in *Anseranas*, *Presbyornis* and most neornithines. This rim is complete, albeit thin caudally, in *Leipoa*, contra Elzanowski and Stidham (2010) who reported it was half open in this genus and *Alectura*.

Mandible

60. Mandible – cotylae fossae articularis: 0, three cotylae, with cotyla medialis and cotyla lateralis separated by a shallow groove (sulcus intercotylaris), the crista intercotylaris restricted to the rostral part of the articulation area, caudal cotyla either separated from or merged with lateral cotyla; 1, two cotylae, cotyla medialis and cotyla lateralis large and

separated by an rostrocaudally oriented crista intercotylaris. Ericson (1997, char. set A: 18), overlaps Mayr and Clarke (2003: char. 38).

61. Mandible, convex ventrally: 0, essentially lacking, < ½ depth dentary extends below middle of line linking the mandible tip and the cranial end of the dentary: 1, pronounced, > ½ depth below such line. Livezey (1996a: char. 4), Worthy and Lee (2008, char. 23).

62. Mandible, deep groove in the ventral surface of the rostral portion of the mandibular rami: 0, absent; 1, present. Ericson (1997, char. set A: 20) and Ksepka (2009, char. 21).

63. Mandible, depth regio coronoidei: 0, shallower or slightly deeper than caudal end of dentary; 1, markedly deeper (>1.5x depth) than that of the caudal dentary; 2, markedly reduced, depth much less than depth at angulus mandibulae at caudal end of dentary, associated with rostral shift in ligamental insertions, e.g., *Dromornis*. Modified from Livezey (1996a: char. 5), Worthy and Lee (2008, char. 24), Ksepka (2009, char. 18).

64: Retroarticular process, shape: 0, narrow (low dorsal-ventral height); 1 blade-like (dorsoventrally tall) but with short caudal projection (subequal to height at rostral base); 2 blade-like and long, length (about twice height of blade at rostral base; 3, short and rounded in lateral view (e.g., *Struthio*). We reformulated the states for this character to better accommodate the range of morphologies observed in fossil taxa.

65. Mandible, impressio musculi depressor mandibulae, recessus conicalis: 0, absent; 1, present, shallow (e.g. *Anseranas*) or deep. Worthy and Lee (2008, char. 26). We re-coded *Anatalavis* (1) for this character based on direct examination.

66. Mandible, proc. medialis mandibulae, foramen pneumaticum articulare: 0, present (e.g. *Anseranas*); 1, absent. Worthy and Lee (2008, char 27).

67. Mandible, splenial fused to dentary in adults: 0, yes; 1, no; weakly fused, only in part usually dorsal margin.

68. Mandible, processus medialis mandibulae, long, narrow, and dorsally oriented: 0, no; 1, yes. A long, narrow, and dorsally oriented processus was listed as a synapomorphy of Galloanseres by Cracraft and Clarke (2001[102], char. 41), but Mayr and Clarke (2003, char. 45) found it more widely distributed, although it distinguishes palaeognaths from galloanserans.

69. Mandibular rami, lateral compression defining long, very narrow inter-ramal region: 0, absent; 1, present. See Livezey (1996b[103]: char. 72), Worthy and Lee (2008, char. 128).

Vertebrae

*70. Vertebrae – total number of cervical and thoracic vertebrae: 0, 20 or fewer; 1, 21-22; 2, 23-25; 3, 26-30. Modified from Mayr and Clarke (2003, char. 55) and see Worthy and Lee (2008, char. 124) for data sources.

71. Thoracic vertebrae, pleurocoelous (with deep lateral depressions in the corpus) with or without pneumatisation: 0, no, lacks deep lateral fossae and not pneumatic; 1, yes, deep lateral fossae but not pneumatic; 2, corpus with large pneumatic foramen, but walls not compressed into fossa. From Ericson (1997, char. set A: 23) and Ksepka (2009, char. 24). Pleurocoelous vertebrae occur in Presbyornithidae, see Mayr and Clarke (2003, char. 58), but in Anhimidae the walls are highly pneumatic rather than compressed into a fossa and thus more similar to lithornithids.

72. Atlas, foramina transversaria: 0, absent; 1, present. Mayr and Clarke (2003, char. 47), see also Worthy and Scofield (2012: char. 66).

73. Axis, foramina transversaria: 0, present; 1, absent. Mayr and Clarke (2003, char. 49, fig. 6A) and Ksepka (2009, char. 22).

74. Axis, processus costales: 0, present; 1, absent. Mayr and Clarke (2003, char. 50, fig. 6B).

75. Axis, processus ventralis, size and shape: 0, low, not deeper than facies articularis of centrum; 1, present, pronounced, >depth facies articularis of centrum.

76. Third cervical vertebra, osseous bridge from processus transversus to processus articularis caudalis enclosing a foramen: 0, absent; 1, present. From Mayr and Clarke (2003, char. 52) who code galloanserans as invariant, with Anhimidae, Anatidae, and Galliforms all 1 - but in *Anhima* MV B12574, the foramen is open; see Ksepka (2009, char. 23).

77. Posterior caudal vertebrae with well-developed processus haemales ventrally, projects cranially off pygostyle: 0, no; 1, yes. From Mayr and Clarke (2003, char. 59, fig. 6H).

*78. Thoracic vertebrae fused/co-ossified forming a notarium: 0, no; 1, yes two vertebrae fuse, e.g., *Anseranas*; 2, yes, three or four vertebrae fuse forming notarium. Modified from Worthy and Lee (2008, char. 127) and Ksepka (2009, char. 25).

Sternum

79. Sternum, corpus sterni, presence of pneumatic foramina on sulcus medianus sterni (midline): 0, yes, multiple, no single large one, and extending more caudally (e.g. *Anseranas*); 1, single well-defined foramen cranially; 2, no foramen; 3, large well-defined foramen on midline centred on costal processes, may have smaller foramina associated with it, e.g. *Gallus*. Modified from Livezey (1986, char. 78; 1996a, char. 24) and Worthy and Lee (2008, char. 29).

*80. Sternum, corpus sterni, pars cardiaca, pori pneumatici: 0, widely scattered on it (e.g. *Anseranas*); 1, limited to caudal margin of pila coracoidea (e.g. *Cereopsis*); 2, essentially absent. From Livezey (1986, char. 89; 1996a, char. 23); Worthy and Lee (2008, char. 30).

*81. Sternum, corpus sterni, margo costalis, number of proc. costalis: 0, seven or eight; 1, five or six, e.g. *Anseranas*, *Cereopsis*; 2, three or four, e.g. galliforms. See Livezey (1996a: char. 25), Mayr and Clarke (2003, char. 71), and Worthy and Lee (2008, char. 31).

82. Sternum, corpus sterni, margo caudalis with thickened ridge: 0, present; 1, absent (e.g. *Cereopsis*, coincident with carina sterni not extending to caudal margin). Modified from Livezey (1996a, char. 26) and Worthy and Lee (2008, char. 32).

83. Sternum, rostrum sterni, spina interna rostri (dorsal manubrial spine): 0, absent, or a broad shallow medial notch bound by prominences on the labrum internum, includes situation where a broad notch has a medial prominence (e.g. *Anas*); 1, present, either a rectanguloid flange (e.g. *Malacorhynchus*) or triangular protuberance, e.g. galliforms. Modified from Livezey (1986: char. 82; 1996a, char. 28), Worthy and Lee (2008, char. 33), Ksepka (2009, char. 33).

84. Sternum, rostrum sterni, pila coracoidea: 0, thickened, robust ridge; 1, thin, not at all thickened (e.g. *Oxyura*). Worthy and Lee (2008, char. 34).

85. Sternum, rostrum sterni, spina externa rostri (ventral manubrial spine): 0, lacking (e.g. *Dendrocygna*); 1, present, robust, short to long, bifid or pointed, but not connecting to spina interna; 2, present and bladelike, connecting to spina interna. Mayr and Clarke (2003, char. 70), Worthy and Lee (2008, char. 35), Ksepka (2009, char. 34).

86. Sternum, margo costalis, location of distal-most costal process: 0, in distal half of corpus sterni (basin) measured from dorsal lip coracoidal sulcus and costal length >1/2 basin length (e.g. *Anseranas*); 1, in distal half of basin but costal length <1/2 basin length (e.g. *Dendrocygna*); 2, at or cranial to midpoint of basin length, costal length <1/2 basin length. Modified from Livezey (1986, char. 86), Worthy and Lee (2008, char 37).

87. Sternum, caudal margin, number of notches or fenestrae: 0, four; 1, two; 2, none. Mayr and Clarke (2003, char. 73), Ksepka (2009, char. 40).

Scapula

88. Scapula, scapus scapulae (blade), dorsoventral height: 0, uniform or decreases over first 2/3 of length; 1, increases distally of collum scapulae to a maximum at about ½ to ¾ blade length. Modified from Livezey (1986, char. 108; 1996a, char. 40); Worthy and Lee (2008, char. 38). We re-coded *Chauna* (0) as the condition in this taxon is essentially indistinguishable from that in *Anhima*.

89. Scapula, acromion, cranial extent with collum scapulae horizontal: 0, equal to or caudal to tuberculum coracoideum (e.g. *Anseranas*); 1, extends distinctly craniad of tuberculum coracoideum. See Livezey (1986, char. 109; 1996a, char. 38); Ericson (1997, char. set A: 48); Worthy and Lee (2008, char. 39).

90. Scapula, cranial end, foramen pneumaticum: 0, present laterally, variable in shape; 1, absent. See Livezey (1986, char. 111; 1996a, char. 37), Worthy and Lee (2008, char. 40), Ksepka (2009, char. 46).

91. Scapula, ventral facies under facies articularis humeralis, pneumatic fossa present: 0, no; 1, yes.

92. Scapula, acromion, attachment for ligamentum acrocoraco-procoracoideum: 0, absent or poorly developed crista, e.g. *Anseranas*; 1, well-developed tuberculum projecting costally, e.g. *Megapodius*. The derived state (1) may relate to the much reduced processus procoracoideus in galliforms and transfer of the primary insertion of this ligament to the scapula from the coracoid. The derived state causes the 'hooked' state in Ksepka (2009, char. 43).

Coracoid

93. Coracoid, presence of foramen/incisura nervi supracoracoidei: 0, yes, foramen opens into corpus; 1, yes, but not opening into corpus; 2, no foramen. Modified from Livezey (1986, char. 92; 1996a, char. 43), Ericson (1997: char. set A: 37), Mayr and Clarke (2003, char. 65),

Livezey and Zusi (2006, char. 1286); Worthy and Lee (2008, char. 42), Ksepka (2009, char. 49). Galliforms are coded as lacking foramen even though they lack a procoracoid, because in tinamous and lithornithids the foramen enters the shaft and is not related to the procoracoid.

94. Coracoid, procoracoid, presence: 0, absent or present with minimal projection medially; 1, an obvious process extending medially of corpus. Ericson (1997, char. set A: 41) identified Tinamidae and Galliformes as lacking a processus, however tinamous exhibit a short and robust procoracoid process. Ksepka (2009, char. 48).

*95. Coracoid, omal end, facies articularis scapularis: 0, deep cotyla present, e.g. *Cereopsis*; 1, shallow cotyla, e.g. *Anseranas*; 2, forms a subplanar to convex subcondylar articulation. Ericson (1997, char. set A: 40); Livezey and Zusi (2006, char. 1281), Ksepka (2009, char. 47). This character complex is intrinsically linked to the presence or absence of a tuberculum coracoideum on the scapula, which therefore is not described as a separate character. We re-coded *Anhima* (0) for this character.

96. Coracoid, omal end, processus acrocoracoideus (acrocoracoid) with pneumatic foramina under facies artic. clavicularis (clavicle facet): 0, lacking; 1, present, in well-defined fossa below dorsal part of clavicle facet only; 2, present, in a broad area under clavicle facet (e.g., *Cereopsis*); 3, foramina present under ventral part of clavicle facet only. Modified from Livezey (1986, char. 95; 1996a, char. 42); Worthy and Lee (2008, char. 43).

97. Coracoid, omal end, ventral facies, processus acrocoracoideus, depth of sulcus medial to facies artic. humeralis and sternal to impressio ligamentum acrocoracohumeralis: 0, shallow groove, e.g. *Alectura*, *Anseranas*; 1, deep groove, e.g. *Gallus*, *Anhima*.

*98. Coracoid, omal end, processus acrocoracoideus, facies artic. clavicularis, dorsal and ventral lobes: 0, not projected over sulcus m. supracoracoidei; 1, not projected equally, only dorsal lobe overhangs sulcus; 2, both lobes slightly overhang supracoracoidal sulcus; 3, pronounced overhang of both lobes over supracoracoidal sulcus (e.g. *M. membranaceus*).

Modified from Livezey (1986, char. 97), Worthy and Lee (2008, char. 44). For flightless taxa with reduced coracoids this character is coded as inapplicable.

99. Coracoid, omal end, processus acrocoracoideus, orientation relative to facies articularis humeralis in dorsal view: 0, acrocoracoid directed primarily cranially forming wide angle with humeral facet; 1, directed primarily medially forming near right angle with medial margin of humeral facet, e.g. galliforms.

100. Coracoid, omal end, facies articularis humeralis: 0, concave articular surface in dorsoventral plane, e.g., *Cereopsis*; 1, flat or convex, e.g., *Gallus*. This does not relate to the omal-sternal plane.

101. Coracoid, omal end, processus acrocoracoideus, projection of cranial end over medial margin of sulcus m. supracoracoidei in dorsal aspect: 0, little or none (e.g. *Anseranas*, *Tadorna*); 1, significantly projected (e.g. *Gallus*). Modified from Worthy and Lee (2008, char. 45).

102. Coracoid, omal end, sulcus m. supracoracoidei, excavated under facies artic. humeralis: 0, absent; 1, present. Worthy and Lee (2008, char. 46). For flightless taxa with reduced coracoids this character is coded as inapplicable.

103. Coracoid, omal end, sulcus m. supracoracoidei, corpus at ventromedial margin: 0, rounded, relatively thick, e.g. megapodes; 1, compressed, keeled, e.g., *Gallus*.

104. Coracoid, corpus, facies dorsalis, foramen pneumaticum in impressio m. sternocoracoidei: 0, present; 1, absent. After Livezey (1986, char. 93; 1996a, char. 44); Mayr and Clarke (2003, char. 67), Worthy and Lee (2008, char. 47), Ksepka (2009, char. 51).

105. Coracoid, corpus, facies dorsalis, with several striae of muscle scars diagonally traversing it: 0, no; 1, yes. Ericson (1997, char. set A: 38) found such striae typify Anatidae, Anseranatidae, and Presbyornithidae, and are absent in galliforms.

*106. Coracoid, corpus, facies ventralis, a well-defined impressio m. supracoracoidei bound laterally by a linea muscularis and caudally by the facies artic. sternalis: 0, flat or convex ventrally, e.g., *Gallus*; 1, present, distinct but shallow (e.g. *Oxyura*, *Malacorhynchus*); 2, present deep, typified by *Stictonetta* and *Dendrocygna*. Modified from Livezey (1986, char. 96; 1996a, char. 45); Worthy and Lee (2008, char. 48).

107. Coracoid, ventral facies artic. sternalis: 0, ventral facet distinct with rounded cranial margin, may or may not be elevated with respect to adjacent facies, separated from dorsal facet by distinct crest (e.g. *Anseranas*); 1, ventral facet not prominent ventrally, directed sternally, continuous via rounded ridge to dorsal facet; 2, ventral facet absent or indistinct. Modified from Livezey (1986, char. 100), Worthy and Lee (2008, char. 49), Ksepka (2009, char. 52). We re-coded *Chauna* (1) for this character based on direct examination.

108. Coracoid, corpus, orientation, line linking proc. acrocoracoideus and angulus medialis forms angle with line linking lateral and medial extremes of sternal facet: 0, markedly greater than 90-100º; 1, approximates 90-100º. Worthy and Lee (2008, char. 50). For flightless taxa with reduced coracoids this character is coded as inapplicable.

109. Coracoid fused with scapula: 0, no; 1, yes. Mayr and Clarke (2003, char. 68).

Furcula

110. Furcula, processus acromialis: 0, broadly rounded; 1, pointed. Ericson (1997, char. set A: 45).

111. Furcula, claviculae, lateromedial curvature: 0, little; 1, significant curvature.

*112. Furcula, apophysis furculae (furcular process or hypocleideum) projecting dorsocaudally: 0, obsolete, no structure visible; 1, present as low ridge, either single (e.g. *Tadorna*) or paired (e.g. *Cereopsis*); 2, present as a prominent ridge or lobe, e.g., galliforms.

Modified from Livezey (1986, char. 102; 1996a, char. 33), Ericson (1997, char. set A: 46), Worthy and Lee (2008, char. 121), and Ksepka (2009, char. 32).

113. Furcula, scapus claviculae, facies lateralis: 0, lacking foramina pneumatica; 1, with foramina pneumatica, e.g., *Cereopsis*. See Livezey (1986, char. 105; 1996a, char. 35), Worthy and Lee (2008, char. 122).

114. Furcula, overall form apophysis furculae: 0, robust, tending towards V-shaped with furculae divergent dorsally; 1, robust, U-shaped; 2, slender, broadly U-shaped; 3, slender, V-shaped. Modified from Ericson (1997, char. set A: 44), Worthy and Lee (2008, char. 123), and Ksepka (2009, char. 29).

Humerus

115. Humerus, margo caudalis, capital shaft ridge present and extends alongside and proximal to fossa pneumotricipitalis: 0, yes; 1, no. Worthy and Lee (2008, char. 51).

*116. Humerus, capital shaft ridge, when present and prominent: 0, directed towards caput (head) (e.g. *Anseranas*); 1, directed towards the zone between the head and the tuber. dorsale (dorsal tuberosity); 2, directed/extends to dorsal tuberosity. Modified from Livezey (1986: char. 22; 1996a: char. 51) and Worthy and Lee (2008, char. 52).

117. Humerus, margo caudalis, area adjacent and distal to end of crista deltopectoralis compressed into a ridge that does not extend further proximally: 0, yes, e.g. megapodes; 1, no, e.g., *Gallus*. This ridge lies more distad than the capital shaft ridge of characters 115 and 116. Anseriforms in which the capital shaft ridge extends distad of the crista bicipitalis lack the angularity of the ridge as seen in e.g. *Leipoa* and are coded 1.

118. Humerus, proximal end, fossa pneumotricipitalis dorsalis (dorsal or secondary pneumotricipital fossa) between incisura capitis (capital groove) and tuberculum dorsale: 0, absent (e.g. *Anseranas*, *Cereopsis*); 1, dorsal head of M. humerotriceps inserts in a shallow

2132 flat fossa extending to base of head whose width < fossa pneumotricipitalis ventralis; 2, wide,
2133 shallow fossa ≥ width ventral pneumotricipital fossa; 3, Dorsal pneumotricipital fossa deep.
2134 Modified from Livezey (1986, char. 23 & 24), Worthy and Lee (2008, char. 53), Ksepka
2135 (2009, char. 55).
2136 119. Humerus, fossa pneumotricipitalis dorsalis (dorsal pneumotricipital fossa) excavated
2137 below caput humeri: 0, no; 1, yes. Worthy (2009[104], char. 134). Taxa lacking said fossa were
2138 coded non-comparable.
2139 120. Humerus, relationship of incisura capitis humeri to facies at its dorsal end: 0, opens
2140 dorsally at same level; 1, groove is elevated above (more caudal) the facies; 2, separated from
2141 the caudal facies by a distinct crista incisurae capitis distalis that closes the groove. Modified
2142 from Ksepka (2009, char. 58) and Worthy (2009, char. 135).
2143 121. Humerus, proximal end, crista deltopectoralis (deltoid crest): 0, caudally (anconally)
2144 concave, profile of crista rounded over length; 1, caudally flat or convex, profile angular.
2145 From Livezey (1986, char. 25), Ericson (1997, char. set A: 55) and Worthy and Lee (2008,
2146 char. 54). Note that anatids are polymorphic with more basal taxa having a caudally concave
2147 crista deltopectoralis (Worthy and Lee 2008).
2148 *122. Humerus, proximal end, crista deltopectoralis, in cranial/palmar view, length relative to
2149 junction of crista bicipitalis (bicipital crest) with shaft: 0, about 50% of length of deltoid crest
2150 extends distad of bicipital crest; 1, about 30-40% of length of deltoid crest extends distad of
2151 bicipital crest; 2, significantly less than 30% of deltoid crest extends distad of bicipital crest.
2152 Worthy and Lee (2008, char. 55).
2153 123. Humerus, proximal end, crista deltopectoralis, in cranial/palmar view, apex of crista
2154 markedly deflected ventrally to overhang cranial facies: 0, no; 1, yes.

124. Humerus, proximal end, tuberculum dorsale (dorsal tuberculum): 0, prominent, buttressed, elevated from surface of shaft; 1, essentially coplanar with shaft. Modified from Livezey (1986, char. 32) and Worthy and Lee (2008, char. 56).

125. Humerus, tuberculum dorsale shape: 0, width roughly equals length; 1, elongate ovate; 2, elongate, narrow lenticular scar merging with proximolateral facies of deltoid crest. Worthy (2009, char. 136). The scar in state 2 (galliforms) is proximal to the insertion of the principle part of the tendon of M. supracoracoideus, and the insertion area forms this elongate scar on a rounded elevated tuberosity.

126. Humerus, proximal end, insertion of the principle part of the tendon of M. supracoracoideus: 0, restricted to the tuberculum dorsale; 1, forms elongate scar extending distal to tuberculum dorsale, e.g., galliforms. Reinterprets Mayr and Clarke (2003, char. 76) and overlaps Ksepka (2009, char. 57).

127. Humerus, proximal end, attachment site of M. scapulohumeralis cranialis, see Matsuoka and Hasegawa (2007)[105], location relative to crus dorsal fossae: 0, partly on or dorsally to crus; 1, ventral to crus. In *Gallus* and *Leipoa*, the insertion lies distal to the fossa pneumotricipitalis and ventral to the crus, whereas in *Anseranas* and *Cereopsis*, it extends dorsal to the crus. Replaces Worthy (2009, char. 138).

128. Humerus, proximal end, tuber. ventrale, in caudal view: 0, directed proximally so does not overhang the fossa pneumotricipitalis ventralis; 1, directed caudo-cranially so its distal margin either is directed at right angles to the fossorial plane or overhangs the fossa pneumotricipitalis ventralis. Modified from Livezey (1986, char. 27) and Worthy and Lee (2008, char. 57).

129. Humerus, proximal end, fossa pneumotricipitalis ventralis: 0, open, highly pneumatic, cavity with bony struts extends under margo caudalis (shallow in *Anseranas*, deep in e.g. *Tadorna*); 1, closed by bony wall internally, forming a conical-shaped pocket or fossa with

the apex extending under the head and in caudal view the medial margin of this fossa forming a planar surface extending from the apex of the fossa to the junction of the bicipital crest and shaft. Modified from Livezey (1986, char. 28) and see Worthy and Lee (2008, char. 58) for notes on the distribution of states in this character related to diving.

*130. Humerus, proximal end, incisura capitis, either caudal or cranial view: 0, proximal profile not or barely interrupted by incisura; 1. proximal profile with very shallow notch, e.g., tadornines; 2, proximal profile with distinct notch created by incisura. Worthy and Lee (2008, char. 59).

*131. Humerus, proximal end, crista bicipitalis (bicipital crest), shape in caudal view: 0, width across the fossa pneumotricipitalis ventralis from crus dorsale fossae to crus ventrale fossae distinctly less than length from tuberculum ventralis to junction of crista bicipitalis and shaft (e.g. *Anseranas*); 1, width approximately equals length; 2, width distinctly greater than length e.g. *Anas*. Worthy and Lee (2008, char. 60). For *Cnemiornis* this character is coded as missing data as reduction of the humerus coincident with flightlessness precludes determining the homologous extent of the bicipital crest.

132. Humerus, insertion for M. coracobrachialis caudalis: 0, situated on tuberculum ventrale and separated from caput by incisura capitis; 1, forms distinct depressio insertii m. coracobrachialis caudalis (see Livezey and Zusi 2006, char. 1361) at dorsal side of incisura capitis indenting the crista incisurae capitis distalis. In most birds this insertion is on the tuberculum ventralis, but in galliforms it is situated at the dorsal side of the incisura capitis. See Ericson (1997, char. set A: 52, 53).

133. Humerus, insertion for M. coracobrachialis caudalis when at dorsal side of incisura capitis indenting the crista incisurae capitis distalis: 0, abuts a small distal projection (tuberculum intermedium) on the caput, e.g. megapodes; 1, is bound dorsally by marked

tuberculum intermedium projecting from caput, e.g. *Gallus*; 2, no project from caput bounding it dorsally. Anseriforms are inapplicable.

134. Humerus, attachment of m. latissimus dorsi pars cranialis (=latissimus dorsi anterioris) is: 0, located dorsad of the margo caudalis, e.g. megapodes and anseriforms; 1, ventral to the margo caudalis, e.g. all other galliforms (Mourer-Chauviré 1992[106]).

135. Humerus, shaft with essentially parallel sides in caudal or cranial views: 0, yes; 1, no, narrows distally (at least 10% reduction on mid-length width), narrowest point in distal third; 2, no, narrowest near midshaft point, e.g. galliforms. Modified from Worthy and Lee (2008, char. 61).

136. Humerus, proximal end, attachment scar of m. latissimus dorsi pars cranialis (=anterioris see Howard 1929: fig 20) (as distinct from attachment for m. latissimus dorsi posterioris), location, caudal view: 0, adjacent to and proximally overlaps with distal end of deltoid crest; 1, markedly caudad of and distal to crista deltopectoralis, e.g. galliforms; 2, markedly caudad of and broadly overlaps in proximodistal plane crista deltopectoralis. Modified from Worthy and Lee (2008, char. 62).

137. Humerus, distal end, relative distal extent of proc. flexorius (= entepicondyle) to line drawn across distal extreme of condyli ventralis et dorsalis, in cranial view: 0, short, ends markedly proximad to condyli, e.g. *Anseranas*; 1, long, distal extent roughly equal to that of the condyli, e.g. tadornines and anatines. Modified from Worthy (2009, char. 63). This is another way of assessing distal extent of condylus ventralis as in Ksepka (2009, char. 59).

138. Humerus, distal end, tuber. supracondylare dorsale (ectepicondylar prominence), in cranial view: 0, present, a distinct caudo-cranially thickened prominence on dorsal margin at proximal end of the dorsal condyle (e.g. *Anseranas*); 1, No prominence distinct from epicondylus dorsalis, which usually forms a low short proximally directed ridge. Note: In most birds, the tuber. supracondylare dorsale supports the origin of M. extensor carpi radialis

(see Baumel and Witmer 1993[107]), but in galloanserans, the two scars for the origin of M. extensor carpi radialis lie immediately proximal to the tuberculum and are less prominent dorsally. The scar for the insertion of M. ectepicondyloulnaris lies on the dorsal facies of the tuber. supracondylare dorsale, but the presence of this scar is not correlated with tuberculum size in anseriforms. All galloanserans have a tuberculum very much smaller than in taxa such as charadriiforms and procellariiforms.

139. Humerus, distal end, tuber. supracondylare ventrale (attachment of the anterior artic. ligament): 0, attachment facet parallel to shaft, not buttressed proximally (e.g. *Anseranas*); 1, facet buttressed proximally, tilted distally and/or medially (e.g. *Anas*). Modified from Livezey (1986, char. 26) and Worthy and Lee (2008, char. 65). Note, the facet is medially rotated in diving waterfowl (Worthy and Lee 2008), so rotation is not factored into this character. Presence/absence of a buttress is considered the primary feature here, so for *Anser* in which the tubercle has little distal tilt but is clearly buttressed, is assigned state '1'.

*140. Humerus, distal end, sulcus scapulotricipitalis (external tricipital groove): 0, absent or barely defined (e.g. *Anseranas*); 1, present on caudal face, but not extending around distal end of epicondylus dorsalis (e.g. *Dendrocygna*); 2, present, extends distally around epicondylus dorsalis, forms distal notch in caudal view. In part, Mayr and Clarke (2003, char. 81), Worthy and Lee (2008, char. 66).

141. Humerus, distal end, attachment of pronator brevis, *sensu* (Howard 1929[108]), origin of the proximal head of the M. pronator superficialis: 0, pit on ventral facies, separated from facet on tuber. supracondylare ventrale; 1, pit incorporated into ventral margin of facet on tuber. supracondylare ventrale. Worthy and Lee (2008, char. 67).

142. Humerus, proximal end, tuberculum ventrale, projection caudally, medial or proximal view: 0, projects more caudad than caput; 1, little projection about same as caput.

143. Humerus, distal end, ventral facies, scar for M. flexor carpi ulnaris on processus flexorius: 0, one large scar; 1, two scars of approximately equal depth; 2, two scars, caudal one shallow, cranial one deep. Ericson (1997, char. set A: 60) noted only a single scar in Tinamidae, Galliformes and a few other taxa; Anseriformes have a double scar.

144. Humerus, width of space between the facet on the tuber. supracondylare ventrale and the proximoventral apex of the dorsal condyle: 0, narrow, gap equal to or narrower than width facet; 1, wide, gap wider than facet. Derived from Woolfenden (1961[109]) and Worthy (2009, char. 137).

145. Humerus, fossa olecrani (olecranal fossa): 0, absent or shallow; 1, deep, well defined. Modified from Worthy (2009, char. 139) to incorporate galliforms.

Ulna

146. Ulna, proximal end, cranial (palmar) view, width: 0, dorsoventral width greater than breadth from olecranon to cranial margin of cotyla ventralis, e.g. *Cereopsis*; 1, dorsoventral width less than breadth from olecranon to cranial margin of cotyla ventralis, e.g. *Gallus*. This character captures the more significant of six features contributing to Bourdon's (2011, char. 64).

147. Ulna, proximal end, ventral facies, tuberculum lig. collateralis ventralis and insertion for trochlea humeroulnaris on side of olecranon: 0, tuberculum lig. collateralis ventralis large, ventrally convex, separated by a sulcus from insertion for trochlea humeroulnaris which is aligned craniocaudally across olecranon, e.g. *Tadorna*, *Anseranas*; 1, tuberculum lig. collateralis ventralis flat on ventral facies, with no sulcus between it and the insertion for trochlea humeroulnaris which is aligned proximodistally on the olecranon, e.g. *Leipoa*, *Gallus*; 2, tuberculum lig. collateralis ventralis flat on ventral facies, distinctly separated

distally from the insertion for trochlea humeroulnaris which is aligned craniocaudally across olecranon.

148. Ulna, proximal end, cranial (palmar) view, tuber. bicipitale ulnae (for insertion of *M. biceps brachii*): 0, forms single prominent elongate tuberculum extending from just distal to the cotyla ventralis diagonally and distally towards a point distad of the processus cotylaris dorsalis, although two insertions may form abutting scars (e.g. *Anseranas*); 1, two separated insertions, one starts adjacent to cotyla ventralis and extending disto-ventrally to a level distad of the cotyla dorsalis; the second lies further distally, distal to the dorsal cotylar process (e.g. *Malacorhynchus*, *Anhima*); 2, two separated insertions: one starts adjacent to cotyla ventralis and extends across incisura radialis ending proximal to distal end of cotyla dorsalis; the second lies distal to cotyla dorsalis, e.g. *Anser*; 3, forms single scar extending from distal to cotyla ventralis to a ridge extending distoventrally from cotyla dorsalis enclosing a marked incisura radialis. Modified from Worthy and Lee (2008, char. 69).

149. Ulna, proximal end, fossa or pneumatic foramen under processus cotylaris dorsalis: 0, absent; 1, present (e.g. *Malacorhynchus*). Worthy and Lee (2008, char. 70).

150. Ulna, length: 0, approximately equal to or greater than length humerus; 1, significantly (>5%) shorter than humerus. Modified from Mayr and Clarke (2003), Worthy and Lee (2008, char. 71) and Ksepka (2009, char. 60). Flightless taxa, or those with reduced flight ability, are scored as inapplicable. We coded *Vegavis* (1) as Clarke et al. (2016[110]) report an estimated length of 124mm for the humerus and a length of 86mm for the ulna.

151. Ulna, shaft compressed dorsoventrally with dorsoventral width markedly less than craniocaudal depth and ventral side flattened adjacent to the distal end of the brachial fossa: 0, yes; 1, no. From Ericson (1997, char. set A: 61) and Mayr and Clarke (2003, char. 83).

152. Ulna, distal end, condylus ventralis low, not prominent ventrally, with sulcus intercondylaris wide and shallow: 0, yes, e.g. megapodes; 1, no. Ericson (1997: char set A 62).

153. Ulna, distal end with marked depressio radialis: 0, no; 1, yes e.g., *Anseranas*. From Mayr and Clarke (2003, char. 84).

154. Ulna, distal end, tuberculum carpale, cranioventral projection: 0, tuberculum carpale large, projects more than half the craniocaudal width of the dorsal and ventral condyles, e.g. anseriforms; 1, tuberculum carpale small, projects less than half the craniocaudal width of the dorsal and ventral condyles, e.g. *Leipoa*, *Gallus*.

Carpometacarpus

155. Carpometacarpus, proximal end, dorsal and caudal aspects, external rim trochlea carpalis with marked notch caudally: 0, no, rim extensive with even convex profile caudally extending to fovea carpalis caudalis (e.g. *Anseranas*); 1, yes, rim extensive with marked notch caudally in rim that extends to fovea carpalis caudalis; 2, rim short, ends distally at position of notch in previous character state (e.g. galliforms). Modified from Livezey (1986, char. 37+38; 1996a, char. 55), Worthy and Lee (2008, char. 72), and from Ksepka (2009, char. 61).

*156. Carpometacarpus, proximal end, caudal view, distal extent of dorsal rim trochlea carpalis: 0, ending considerably short of ventral rim; 1, falling only slightly short of ventral rim; 2, equals or exceeds ventral rim. Ericson (1997, char. set A: 64).

157. Carpometacarpus, proximal end, fovea carpalis cranialis (anterior carpal fossa): 0, absent, cranial margin of trochlea carpalis flat or slightly convex (e.g. *Anseranas*); 1, present, cranial margin of trochlea carpalis distinctly concave, but lacking pneumatic foramen; 2, present and contains pneumatic foramen. Worthy and Lee (2008, char. 74).

158. Carpometacarpus, proximal end, fovea carpalis caudalis (cuniform fossa): 0, present, and pneumatic; 1, present and not pneumatic, deep, high dorsal margin bounding it, fossa extending markedly below plane of os metacarpale majus; 2, present and not pneumatic, shallow, not strongly emarginated dorsally. Modified from Livezey (1986, char. 46) and Worthy and Lee (2008, char. 75). A deep fossa appears to be correlated with diving, as it is uniformly present in diving taxa.

159. Carpometacarpus, proximal end, caudal view, position of ventral rim of trochlea carpalis relative to area of synostosis of os metacarpale minus on os metacarpale majus: 0, minor metacarpal extends dorsad of ventral rim; 1, os metacarpale minus entirely ventral to ventral rim of trochlea carpalis, e.g., galliforms.

*160. Carpometacarpus, proximal end, ventral facies, fossa infratrochlearis (internal ligamental fossa): 0, absent, region flat or convex, e.g. *Gallus*; 1, shallow, (e.g. *Anseranas*); 2, deep, extends to at or below level of ventral facies of processus extensorius (e.g. *Dendrocygna*). 3, deep, extends to at or below level of ventral facies of processus extensorius (e.g. *Dendrocygna*). Worthy and Lee (2008, char. 76). In taxa where the ventral surface of trochlea carpalis is roughly coplanar with the ventral surface of the processus extensorius, e.g. anserines, depth is coded as shallow if depth is c. < 25% width of fossa.

*161. Carpometacarpus, proximal end, ventral facies, ridge linking ventral rim of trochlea carpalis and processus pisiformis, relationship to ventral facies of processus extensorius: 0, rounded profile, little elevated (e.g. *Dendrocygna*); 1, sharp drop-off; 2, overhangs ventral facies of processus extensorius with resultant fovea under ledge (e.g. *Malacorhynchus*). Worthy and Lee (2008, char. 77). *Anhima* is not comparable so is coded inapplicable. In cracids the pisiform process markedly overhangs the extensor process but the character is restricted to the area on the proximal side of the pisiform process.

162. Carpometacarpus, proximal end, processus extensorius (process metacarpal I, extensor process), proximal margin: 0, perpendicular to, or proximally directed relative to shaft; 1, distinctly distally directed (e.g. *Cygnus*). Livezey (1986, char. 41) and Worthy and Lee (2008, char. 78).

163. Carpometacarpus, proximal end, craniocaudal length processus extensorius in ventral view: 0, short, less than width trochlea carpalis; 1, elongate, equal to or greater than width trochlea carpalis. Modified from Livezey (1986, char. 42; 1996a: char. 56), Worthy and Lee (2008, char. 79). The presence of a rugosity on the processus extensorius is related to fighting behaviour so is not characterised. The spur on carpometacarpi of *Anhima* is an autapomorphy not related to primary length of metacarpal 1 so *Anhima* is coded as non-comparable.

164. Carpometacarpus, proximal end, caudal facies, os metacarpale minus (metacarpal III): 0, rounded or flattened adjacent to fornix with metacarpal II; 1, distinctly grooved. Modified from Livezey (1986, char. 44; 1996a, char. 59) and Worthy and Lee (2008, char. 80).

165. Carpometacarpus, proximal end, length of metacarpal II from processus alularis (pollical facet) to start of spatium intermetacarpale relative to craniocaudal width (ventral view) of the fused metacarpals II and III: 0, long, ≥ width; 1, short, < width. Worthy and Lee (2008, char. 81).

166. Carpometacarpus, proximal end, facies dorsalis, ligament attachments on trochlea carpalis: 0, with a single distinct scar proximally for the insertion of lig. ulnocarpo-metacarpale dorsale (external ligamental) (e.g. *Anseranas*); 1, with a distinct scar for the external ligament and a second scar for the external scapholunar ligament (Woolfenden 1961: 25) located more distally. From Worthy and Lee (2008, char. 82). This character needs to be assessed with use of a microscope and is difficult or impossible to assess on greasy specimens.

167. Carpometacarpus, proximal end, facies dorsalis, ligament attachment on trochlea carpalis for the insertion of lig. ulnocarpo-metacarpale dorsale (external ligamental), location relative to proximal margin of processus extensorius: 0, primarily lies more proximal, e.g. *Anseranas*; 1, more distal, e.g. *Gallus*.

168. Carpometacarpus, proximal end, dorsal view, M. extensor metacarpi ulnaris or flexor attachment (*sensu* Howard 1929): 0, two distinct rugosities, one adjacent to fornix os metacarpale minus et majus (metacarpal II and III), the other more proximad (e.g. *Anseranas*, *Biziura*); 1, one rugosity, approximately adjacent to fornix metacarpals II and III; 2, one rugosity, distal to fornix. Modified from Livezey (1986, char. 43; 1996a, char. 57), Worthy and Lee (2008, char. 83). The processus intermetacarpalis of *Gallus* is treated as '2'.

169. Carpometacarpus, proximal end, dorsal view, distinct processus intermetacarpalis for M. extensor metacarpi ulnaris: 0, absent; 1, present, e.g. *Gallus*. Ksepka (2009, char. 63).

170. Carpometacarpus, proximal end, ventral view, insertion for lig. ulnocarpo-metacarpale ventralis: 0, not prominent; 1, a prominent tubercle.

171. Carpometacarpus, distal end, synostosis metacarpals II and III, maximum length, measured from distal end of spatium intermetacarpale to facies artic. digitalis minoris (facet for digit III): 0, short, length less than width measured just distal of spatium intermetacarpale (e.g. *Anseranas*, *Malacorhynchus*); 1, long, length ≥ width of synostosis, e.g. *Dendrocygna*. Worthy and Lee (2008, char. 84). In part Bourdon (2011, char. 68).

*172. Carpometacarpus, distal end, facies artic. digitalis minoris et major (facets for digits II and III): 0, facet for digit III extends farther distad than that for digit II, e.g. *Gallus*; 1, facets for digits III and II of equal distal extent; 2, facet for digit III ends proximad to facet for digit II, e.g. *Cereopsis*. See Livezey (1986, char. 45; 1996a, char. 61), Worthy and Lee (2008, char. 85). Contra Ericson (1997), but as per Livezey (1986, 1996a), *Anseranas* is state '0'.

Flightless taxa were coded noncomparable. We re-coded *Vegavis* (?) as the relative projection of the facets was unclear from available images.

Pelvis

173. Pelvis, relative length preacetabular region of synsacrum: 0, long, preacetabular length > 40% synsacral length; 1, short, preacetabular length < 40% synsacral length. Modified from Worthy (2009, char. 141).

174. Pelvis, corpus of the first synsacro-thoracic vertebra: 0, about equally compressed mediolaterally as corpi of the following vertebra; 1, considerably more compressed than following vertebra. Ericson (1997, char set A: 27). We re-coded *Chauna* (0) based on examination of multiple specimens.

175. Pelvis, ilia synostosed to synsacrum in adults: 0, not or only weakly fused, and then only cranially; 1, yes, extensively fused. From Ksepka (2009, char. 71).

*176. Pelvis, distinct fenestrae intertransversariae caudad of acetabulum: 0, absent; 1, fenestrae only in distal half of length, e.g. *Cereopsis*; 2, fenestrae present over whole length caudal to acetabulum. Worthy (2009, char. 142).

*177. Pelvis canalis iliosynsacralis: 0, absent, ilia entirely fused with processus spinosus of synsacral vertebrae and each other dorsally; 1, partial fusion of ilia leaving small, narrow paired openings directed caudally; 2, large paired openings caudally. See Ericson (1997, char. set A: 29), Ksepka (2009, char. 69) and Worthy (2009, char. 143). Large openings characterise Tinamidae, Cracidae, Megapodiidae, and Phasianidae. Note that Ericson (1997: Table 1) coded this character the inverse of the states described. *Burhinus* has unfused ilia but the articulated ilia and synsacrum lack the canalis.

178. Pelvis, lateral facies corpus ischia, with pneumatic foramen below the antitrochanter at junction of ischium and acetabulum: 0, no; 1, yes, e.g. *Cereopsis*. Worthy *et al.* (1997, char. 121) and Worthy (2009, char. 144).

179. Pelvis, antitrochanter: 0, with pneumatic openings medially to fossa renalis, or posteriorly into foramen ilioischiadicum; 1, none. Worthy (2009, char. 145). We re-coded *Anhima* (0) based on examination of multiple specimens.

*180. Pelvis, recessus caudalis fossae (=recessus iliacus): 0, deep, e.g. *Gallus*; 1, shallow and pneumatic; 2, absent. Livezey (1986, char. 120), Ericson (1997, char. set A: 31), Mayr and Clarke (2003, char. 95), Ksepka (2009, char. 75), Worthy (2009, char. 146). Ericson (1997) interpreting the fossa present in *Anseranas* and *Anhima* as a secondary effect of pneumatisation and so coded the recessus as lacking in these taxa, however, they are here treated as shallow and pneumatic.

181. Pelvis, spatium ischiopubicum: 0, dorsoventrally broad, pubis only approaching ischium immediately caudal of foramen obturatum and at processus terminalis ischii; 1, narrow, pubis often partly fused to ischium. From Ericson (1997, char. set A: 30), Ksepka (2009, char. 77).

*182. Pelvis, foramen ilioischiadicum: 0, very short, much <1/2 length ischium from foramen acetabulum; 1, approximately 1/2 length ischium from foramen acetabuli; 2, long, >1/2 length ischium from foramen acetabuli. Worthy (2009, char. 147).

183. Pelvis, foramen ilioischiadicum caudally closed: 0, no; 1, yes. From Mayr and Clarke (2003, char. 94), Ksepka (2009, char. 74).

184. Pelvis, tuberculum preacetabulare: 0, prominent, creates notch between it and ilium, e.g. *Gallus*; 1, absent or small, with no notch above it. Overlaps Mayr and Clarke (2003, char. 93), Ksepka (2009, char. 72), Worthy (2009, char. 148).

185. Pelvis, pubis: 0, dorsally concave over length; 1, straight or flat. Livezey (1986, char. 115), Worthy (2009, char. 149).

186. Pelvis, pubis, section distad of articulation with distal ischium with flattened caudal expansion, typically rounded in lateral view and with diameter significantly greater than area immediately craniad of it: 0, pubis lacks such caudal expansion; 1, expansion present, e.g. *Cygnus*. Livezey (1986, char. 117), Worthy (2009, char. 150).

Femur

187. Femur, constriction of collum femoris in caudal view: 0, not or slight; 1, constricted, neck narrower than ball. Modified from Bourdon et al. (2009[111], char. 81); Worthy and Scofield (2012, char. 115).

188. Femur, proximal end, facies articularis antitrochanterica, lateromedial plane: 0, surface concave (e.g. *Anseranas*); 1, surface convex. Worthy and Lee (2008, char. 87); Worthy and Scofield (2012, char. 114).

189. Femur, presence of a distinct fossa trochanteris: 0, yes; 1, no. In most galliforms, the trochanter femoris proximally overhangs the facies articularis antitrochanterica enclosing a distinct fossa.

190. Femur, proximal end, crista trochanteris and adjacent cranial facies: 0, cranial facies adjacent to crista flat or shallowly concave; 1, cranial facies deeply concave (e.g. *Anseranas*). Modified from Worthy and Lee (2008, char. 88).

191. Femur, proximal end, cranial facies, crista trochanteris, penetrated by pneumatic foramina: 0, no; 1, yes. Mayr and Clarke (2003, char. 98).

192. Femur, cranial facies, pneumatic foramina/fossa adjacent to facies articularis antitrochanterica at base of collum femoris in adults: 0, no; 1, yes. Note: often such fossa are evident in juveniles and disappear in adults – here the character codes its persistence in adults only. Modified Worthy and Holdaway (2002[112]: Appendix 3, char. 49). This feature is

distinguished from pneumatism under the crista trochanteris, as seen e.g. in *Leipoa*. Worthy and Scofield (2012, char. 129).

193. Femur, caudal facies, pneumatic openings adjacent to facies articularis antitrochanterica: 0, absent or small; 1, present and large. Modified Worthy and Holdaway (2002: Appendix 3, char. 50), Worthy and Scofield (2012, char. 128).

194. Femur, proximal end, caudolateral margin: 0, impressiones obturatoriae on a large bulbous area close to the facies articularis antitrochanterica extending from the lateral onto the caudal facies and the caudolateral margin further distally lacks further prominences; 1, an elevated impressiones obturatoriae close to the facies articularis antitrochanterica and a large prominence further distally on the caudolateral margin for m. ischiofemoralis that is separated from the former by a sulcus as broad as the impression.

195. Femur, proximomedial part caudal facies, scar for insertion of M. puboischiofemoralis pars medialis: 0, either absent or a weak crest; 1, a strongly developed, elevated, rugose crest, round or elongate. Note: *Anhima* has a round and prominent insertion of M. puboischiofemoralis pars medialis, here coded (1), because prominence is considered more significant than whether or not it is elongate. Worthy and Scofield (2012, char. 131).

196. Femur, proximal end, cranial view, linea intermuscularis cranialis (cranial intermuscular line) in proximal half: 0, line merges with distal end of crista trochanteris; 1, line passes distal end of crista trochanteris and is discrete and parallel to crista on pretrochanteric surface.

197. Femur, proximal end, cranial facies, trochanter: 0, elongate, extends distally past the level of the caput femoralis a distance exceeding the proximodistal width of the caput femoralis; 1, short, terminates distally at a point only slightly distad of the caput.

198. Femur, proximal end, cranial facies, impression of m. iliofemoralis internus: 0, not or weakly marked; 1, well-marked rugosity.

199. Femur, corpus femoris in caudal view, relative length, lateral and medial margins and least width: 0, shaft short, least width at or proximal of mid length, margins not parallel; 1, elongate, least width at mid length, margins parallel for about middle third of length. Modified from Bourdon et al. (2009, char. 84), Worthy and Scofield (2012, char. 118). We were able to assess this character in *Asteriornis* by manually re-articulating the two blocks of matrix containing parts of the femur.

*200. Femur, dorsoventral curvature of shaft, lateral view: 0, straight or slight; 1, moderate curvature of distal third; 2, strong curvature. From Livezey (1986, char. 55), Worthy and Lee (2008, char. 93), and Worthy and Scofield (2012, char. 130).

201. Femur, profile of medial facies in caudal aspect: 0, relatively straight or slight curvature; 1, markedly concave.

*202. Femur, proximal end, lateral facies, insertion area of m. iliotrochantericus caudalis: 0, located at mid depth; 1, in dorsal half of depth, but separated from dorsal margin; 2, on dorsal margin. See Zinoviev (2013[113]) for moas.

203. Femur, caudal facies, presence of tuberosity in area of convergence of crista supracondylaris medialis and linea intermuscularis caudalis, usually distal to mid-length, not insertion of M. caudofemoralis more proximally: 0, none or small, not distinguished from crista, included here taxa where lateral and medial crista do not converge; 1, yes, a distinct tuberosity, may be complex.

204. Femur, caudal facies, distal half, location of tuberosity or most prominent part crista medialis: 0, centred on shaft; 1, on medial margin of shaft; 2, on lateral margin of shaft.

205. Femur, distal end, cranial aspect, orientation of condylus lateralis: 0, not divergent, or only slightly divergent, from axis; 1, markedly divergent.

206. Femur, proximal end, lateral facies, area for the insertion of the m. obturatorius medialis (Zinoviev 2013) proximally and insertion area of the m. ischiofemoralis more distally: 0,

widely separated with gap wider than length of insertion of the m. obturatorius lateralis; 1, adjacent or narrowly separated with gap less than length of insertion of the m. obturatorius lateralis.

207. Femur, distal end, tuber. m. gastrocnemialis lateralis, form: 0, round scar, close to or abutting trochlea fibularis on caudal facies; 1, rounded scar, well separated from trochlea fibularis on caudal facies; 2, an elongate scar/ridge with distinct medial bend, or oriented medially, on caudal facies, may extend proximad of patella sulcus, e.g. most anatids; 3, elongate rugose scar in deep or shallow fossa, traversing caudal facies from lateral edge of trochlea fibularis to proximal end of crista tibiofibularis, may be merged with ansa m. iliofibularis caudalis; 4, a rugose scar or shallow fossa on the lateral facies proximocranial to the cond. fibularis.

Modified from Worthy and Lee (2008, char. 89) and Bourdon et al. (2009, char. 92) and Worthy and Scofield (2012, char. 127). We re-coded *Anhima* (0) based on examination of multiple specimens.

208. Femur, distal end, form impressio ansa m. iliofibularis caudalis, usually distal and lateral to tuberculum m. gastrocnemialis lateralis: 0, scar entirely on lateral facies dorsal to trochlea fibularis, e.g. megapodes; 1, scar on lateral facies but also wraps around the caudolateral margin at the proximal side of the trochlea fibularis; 2, scar on caudal facies above trochlea fibularis and merged with tuberculum m. gastrocnemialis.

209. Femur, caudal aspect, trochlea fibularis with distinct depression immediately proximal of the articular surface: 0, not so; 1, yes. Worthy and Lee (2008, char. 125).

210. Femur, distal extent in caudal view of condylus medialis: 0, approximately equal to that of condylus lateralis, e.g. *Anseranas*; 1, distinctly less than that of external condyle. From Livezey (1986, char. 53), Worthy and Lee (2008, char. 91), Worthy and Scofield (2012, char. 120). We re-coded *Chauna* (1) based on examination of multiple specimens.

211. Femur, cond. medialis, proportion of maximum distal width: 0, approximately half; 1, clearly greater than half. Overlaps Lee et al. (1997[114], char. 44), Worthy and Scofield (2012, char. 121). We re-coded *Chauna* (1) based on examination of multiple specimens.

212. Femur, cond. medialis, profile in medial aspect: 0, evenly rounded, e.g. *Alectura*; 1, subangular between articular surface of condyle and its cranial surface; 2, dorsoventrally much deeper than long, so proximodistally flattened. We coded *Presbyornis* (1) based on direct examination.

213. Femur, distal end, width sulcus patellaris in cranial view, taken at half the depth of the bounding condyles: 0, broad and flat, wider than condylus lateralis; 1, narrow and deep, less than width condylus lateralis plus trochlea fibularis.

214. Femur, the notch, or fovea tendineus m. tibialis, on the distal end of cond. lateralis, in distal view: 0, notch present; 1, notch absent. From Lee et al. (1997: char. 50) and modified form Worthy and Scofield (2012, char. 133).

215. Femur, distal end, fossa poplitea: 0, shallow, less than half depth medial condyle; 1, deep. See Livezey (1986, char. 56), in part Lee et al. (1997, char. 51), Worthy and Lee (2008, char. 94), Ksepka (2009, char. 79) and Worthy and Scofield (2012, char. 124).

216. Femur, distal end, fossa poplitea, pneumatic: 0, no; 1, yes, large pneumatic foramina are present. We re-coded *Conflicto* (0) basd on the original description which states this fossa lacks pneumatic foramina and re-coded *Anhima* (0/1) because we observed variation amongst studied specimens.

*217. Femur, crista supracondylaris medialis, distinct from its proximal continuation as linea intermuscularis ventralis along the shaft, length: 0, long, greater than width of condylus medialis; 1, short, less than width condylus medialis; 2, crista supracondylaris medialis lacking.

218. Femur, caudal facies, medial view, internal edge of distal end of shaft: 0, smoothly curving, continuous to condyle, e.g. *Leipoa*; 1, interrupted by caudally prominent crista supracondylaris medialis; 2, crista supracondylaris medialis short, and medial profile notched. Modified from Livezey (1986, char. 59), and Worthy and Lee (2008, char. 96).

219. Femur, distal end, caudal view, trochlea fibularis, distal extent: 0, equal with condylus lateralis; 1, shorter, merges distally with the lateral side of the condyle proximal to the distal end of the condyle forming a notch. We coded *Conflicto* (0) based on the CT renderings presented by Tambussi et al. (2019).

220. Femur, trochlea fibularis, form and orientation of articular surface: 0, directed caudally, roughly parallel to shaft, with lateral margin proximally merging with lateral facies of shaft smoothly cranial to the impressio ansa m. iliofibularis caudalis; 1, proximal part rotated cranially and facet directed proximally at low angle to shaft, and forms a prominence markedly offset from the lateral facies. Modified from Bourdon et al. (2009, char. 88), Worthy and Scofield (2012, char. 122).

221. Femur, extent impressio ligamenti cruciati cranialis: 0, well marked and excavated into caudodistal facies of cond. lateralis; 1, poorly defined and not extending onto cond. lateralis. Modified from Bourdon et al. (2009, char. 89) and Worthy and Scofield (2012, char. 123).

Tibiotarsus

222. Tibiotarsus, proximal end, proximal projection of crista cnemialis cranialis: 0, equal with or extending slightly proximal of crista patellaris; 1, extending well proximal of crista patellaris. In part Ericson (1997, char. set A: 66).

223. Tibiotarsus, proximal end, impressio lig. collateralis medialis: 0, low, not prominent (e.g. *Anseranas*); 1, prominent on facies (e.g. *Gallus*). From Worthy and Lee (2008, char. 97).

224. Tibiotarsus, proximal end, medial facies in medial view, linea extensoria (intermuscular line) extending from crista cnemialis cranialis, position relative to impressio lig. collateralis medialis: 0, intermuscular line straight from crista cnemialis cranialis to near mid length, separates lateral and cranial facies, is well separated from impressio (e.g. *Anseranas*, *Gallus*); 1, proximally the intermuscular line is shifted caudally to be narrowly separated from/abuts impressio, so that cranial facies is visible in medial view and cranial facies between ligament attachment and fibular crest is markedly convex. After Worthy and Lee (2008, char. 98).

225. Tibiotarsus, proximal end, alignment base of crista cnemialis cranialis: 0, aligned with axis of shaft; 1, deflected laterally from axis. See Livezey (1986, char. 63; 1996a, char. 70). After Worthy and Lee (2008, char. 102).

226. Tibiotarsus, crista cnemialis cranialis, proximal tip: 0, rolled or bent laterally relative to rest of crista; 1, straight. Note: *Apteryx* has a low crista cnemialis cranialis, but the lateral inflection of it is taken to be homologous to (0). *Rhea* and *Struthio* are non comparable. Modified from Worthy and Holdaway (2002, appendix 3, char. 56). Worthy and Scofield (2012, char 140.

*227. Tibiotarsus, proximal end, lateromedial constriction between cnemial crests and articular facets, breadth of crista patellaris: 0, not constricted, crista patellaris broad; 1, somewhat constricted, crista patellaris short; 2, markedly constricted, crista patellaris indistinct. These features are part of a single complex so are treated here as a single character. Modified from Bourdon et al. (2009, char. 93), Lee et al. (1997, char. 33), and Worthy and Scofield (2012, char. 137).

*228. Tibiotarsus, cranial aspect, angle formed by the lateral and ventral margins of the crista cnemialis lateralis: 0, angle >100° ie widely obtuse; 1, angle <100° and approximately right angle, e.g. Gallus; 2, angle < 60 degrees and clearly acute. See Worthy and Holdaway (2002:

588, char. 57). *Rhea* and *Struthio* are coded inapplicable because of constriction of the cnemial crests associated with character 227, state 2. Worthy and Scofield (2012, char. 139).

*229. Tibiotarsus, crista cnemialis cranialis (as distinct from the intermuscular line that may continue from its end), distal extent and location on shaft: 0, crista extends distal to the proximal end of the crista fibularis; 1, crista ends level with or just proximal to the proximal end of the crista fibularis, e.g. *Gallus, Anseranas*; 2, crista is well separated proximally from crista fibularis. Worthy and Scofield (2012, char. 141).

*230. Tibiotarsus, length of crista fibularis: 0, less than <20% of tibiotarsus length; 1, 20-25% of tibiotarsus length; 2, > 25% of tibiotarsus length. See Worthy and Holdaway (2002: 588, char. 59). Modified from Worthy and Scofield (2012, char. 142).

*231. Tibiotarsus, distal end, epicondylus medialis with internal ligamental prominence: 0, pronounced, visible in cranil view (e.g. *Cereopsis*); 1, present, not pronounced, occluded by rim of condylus medialis in cranial view (e.g. *Gallus*); 2, absent. Worthy and Lee (2008, char. 99).

232. Tibiotarsus, epicondylus medialis, form: 0, rounded prominence with no sharp margins; 1, enlarged and plate-like, bounded distally by deep depressio epicondylaris medialis (modified from Cracraft 1974[115]: 501, 506; Lee et al. 1997, char. 39). From Bourdon et al. (2009a, char. 105), Worthy and Scofield (2012, char. 155).

233. Tibiotarsus, cond. medialis, presence of ligamental pit cranially on the external facies: 0, none or shallow; 1, yes and deep, e.g. *Dromaius*. Modified from Bourdon et al. (2009a, char. 102), see Cracraft (1974, char. 7), Lee et al. (1997, char. 39) and Worthy and Scofield (2012, char. 152).

234. Tibiotarsus, lateral view, cranial side cond. lateralis: 0, merges with the shaft smoothly in a wide angle; 1, abruptly joins shaft, may form notch. Modified from Bourdon et al. (2009a, char. 100), Lee et al. (1997, char. 36), and Worthy and Scofield (2012, char. 150).

235. Tibiotarsus, distal view, cranial projection of condyles: 0, condylus medialis projects markedly relative to condylus lateralis; 1, medial condyle has roughly similar projection to lateral one, i.e. = or <10% taller. See Livezey (1986, char. 64), Lee et al. (1997, char. 38), Livezey & Zusi (2006, char. 2144), Worthy and Lee (2008, char. 103), Bourdon et al. (2009, char. 101), and Worthy and Scofield (2012, char. 151). We re-coded *Anhima* (0) based on multiple specimens.

*236. Tibiotarsus, conspicuous scar for lig. collaterale medialis proximocaudal to epicondylus medialis: 0, absent; 1, present short; 2, present and elongate. From Bourdon et al. (2009a, char. 103) and Worthy and Scofield (2012, char. 153).

237. Tibiotarsus, distal end, junction of crista trochlea cartilaginous tibialis and rim of condylus medialis marked by distinct shallow notch, usually at mid-depth: 0, no (e.g. *Anseranas*); 1, yes (e.g. *Gallus*, *Alectura*). See Livezey (1986, char. 62) and Worthy and Lee (2008, char. 100).

238. Tibiotarsus, cranial view, form junction of medial shaft facies and cond. medialis: 0, shaft with medial profile straight or concave immediately proximal to cond. medialis; 1, shaft medially convex just proximal to the condylus, due to a flange like projection. From Bourdon et al. (2009a, char. 104), see Worthy and Holdaway (2002, fig. A.3, appendix 3, char. 61), and Worthy and Scofield (2012, char. 154).

239. Tibiotarsus, distal end, area intercondylaris, presence of impressio ligamenti intercondylaris (= impressio for lig. anticum): 0, absent, as condyli merged; 1, present of variable size.

*240. Tibiotarsus, distal end, area intercondylaris, lateral to the pons supratendineus, impressio ligamentum meniscotibiale, = lig. meniscotibiale intertarsi of Zinoviev (2013), not impressio ligamenti intercondylaris, contra Worthy and Scofield (2012): 0, forms prominent facet proximal to fossa intercondylaris; 1, distinct low facet abutting fossa intercondylaris, e.g.

Dromaius, *Gallus*; 2, insertion does not form facet or is indistinct. From Bourdon et al. (2009, char. 97). Note: this is the tuberculum supratrochlearis of Mourer-Chauviré (2008[116]) and is the lig. meniscotibiale intertarsi of Zinoviev (2013), not impressio ligamenti intercondylaris, contra Worthy and Scofield (2012). From Worthy and Scofield (2012, char. 144).

241. Tibiotarsus, distal end, area intercondylaris, breadth impressio ligamenti intercondylaris (for lig. tibiometatarsale intercondylare): 0, confined between condyles, either essentially centrally located e.g. *Gallus* or slightly offset medially; 1, extends medially by excavation caudal to the cond. medialis e.g. *Cereopsis*. See Lee et al. (1997, char. 40), Livezey and Zusi (2006, char. 2168), Bourdon et al. (2009, char. 106) and Worthy and Scofield (2012, char. 145). Where the impressio ligamenti intercondylaris is absent, e.g. *Dromaius*, the state is coded as non-applicable (-).

242. Tibiotarsus, pons supratendineus: 0, present; 1, absent. After Lee et al. (1997, char. 35), Mayr and Clarke (2003, char. 73) and Worthy and Scofield (2012, char. 146).

*243. Tibiotarsus, distal end, distal opening of canalis extensorius opens towards impressio ligamenti intercondylaris between condylus lateralis and condylus medialis: 0, no, directed towards and broadly overlaps in lateromedial plane with condylus medialis (e.g. ratites); 1, no, partly overlaps in lateromedial plane with condylus medialis (e.g. galliforms); 2, yes, no overlap in lateromedial plane with condylus medialis. From Ericson (1997, char. set A: 69) and in part Worthy and Scofield (2012, char. 147). We re-coded *Conflicto* (2) based on figures in the original description.

244. Tibiotarsus, medial displacement of cond. medialis relative to facies medialis of shaft: 0, slight; 1, pronounced. Equals Livezey and Zusi (2006, char. 2150) and Worthy and Scofield (2012, char. 149).

245. Tibiotarsus, distal end, width incisura intercondylaris: 0, broad; 1, narrow, width subequal to canalis extensorius, e.g. *Gallus*; 2, incisura absent, e.g. *Dromaius*. Ericson (1997,

char. set A: 69). This is in part Bourdon's (2011, char. 69) identified as an apomorphy of Odontoanseres. Other components of Bourdon's (2011, char. 69) are addressed in char 241. We re-coded *Conflicto* (0) based on figures in the original description.

246. Tibiotarsus, distal end, sulcus m. fibularis (groove for peroneus profundus): 0, faces cranially; 1, faces laterally, e.g. galliforms.

247. Tibiotarsus, distal end, lateral insertion of the transverse ligament (= retinaculum extensorium tibiotarsi) adjacent to pons supratendineus/canalis extensorius: 0, yes, e.g. *Leipoa*; 1, no, located more laterad, and aligned more transversely e.g. *Dromaius*.

248. Tibiotarsus, distal end, distal opening of canalis extensorius, plane of long axis: 0, aligned across shaft, e.g. anseriforms; 1, aligned transversely, e.g. *Leiopoa*, *Gallus*.

Tarsometatarsus

*249. Tarsometatarsus, relative length: 0, less than 95% femur length; 1, approximately equal to femur (~ ±5%); 2, more than 105% femur length. From Worthy and Holdaway (2002); in part Bourdon et al. (2009, char. 121 & 123), Worthy and Lee (2008, char. 118), Worthy and Scofield (2012, char. 167).

250. Tarsometatarsus, cotyla medialis dorsoplantarly elongated, protruding dorsal to cotyla lateralis: 0, no; 1, yes. From Bourdon et al. (2009, char. 111). Worthy and Scofield (2012, char. 159).

251. Tarsometatarsus, facies dorsalis and cotyla medialis: 0, dorsal margin is a crest that separates the cotyla from the dorsal facies; 1, dorsally the cotyla laps onto the dorsal facies, forming a facet that articulates with an opposing facet on the tibiotarsus when the bird is sitting, with a distinct groove between this facet and the eminentia intercotylaris. In part Bourdon et al. (2009, char. 112), Worthy and Scofield (2012, char. 160).

252. Tarsometatarsus, distinct flange-like processus on plantarmedial edge of cotyla medialis: 0, no; 1, yes. From Bourdon et al. (2009, char. 113), Worthy and Scofield (2012, char. 161).

253. Tarsometatarsus, proximal end, plantarolateral side of cotyla medialis: 0, rim elevated proximally; 1, no proximal elevation of rim at this point. Note: the elevation of the rim appears to be the salient point of Bourdon's (2011, char. 70), which identified an elevated rim and the location of crista medialis hypotarsi in line with plantaromedial corner of cotyla medialis as an apomorphy of Odontoanseres, as the crista location mentioned also occurs in galliforms, which were coded as lacking this apomorphy.

254. Tarsometatarsus, eminentia intercotylaris, proximal view, relative to adjacent cotylae is prominent dorsally: 0, yes (*Anseranas*); 1, no (*Alectura*). Modified from Cracraft (1974, 503), Lee et al. (1997, char. 28), Bourdon et al. (2009, char. 114) and Worthy and Scofield (2012, char. 162).

255. Tarsometatarsus, eminentia intercotylaris, lateral view, relative to adjacent area intercotylaris is prominent proximally: 0, yes (*Anseranas*); 1, no (megapodes).

256. Tarsometatarsus, proximal end, crista medialis hypotarsi, or deepest one, caudal extent in proximal view: 0, depth of medial side of crista ≥ depth of cotyla medialis (e.g. *Anseranas*); 1, depth noticeably < depth of cotyla medialis. Modified from Livezey (1986, char. 70), Worthy and Lee (2008, char. 106).

*257. Tarsometatarsus, proximal end, hypotarsus, width adjacent to cotylae: 0, distinctly less than ½ proximal width; 1, approximately ½ of proximal width; 2, distinctly more than ½ proximal width. Worthy and Lee (2008, char. 107).

258. Tarsometatarsus, hypotarsus, major hypotarsal ridge, distal end: 0, markedly hooked caudodistally forming notch; 1, ridge terminates abruptly, drops steeply to shaft; 2, ridge terminates by gradually lowering to shaft. Worthy and Lee (2008, char. 117).

259. Tarsometatarsus, hypotarsus, number of hypotarsal ridges: 0, four (*Anseranas* and anhimids have two vestigial inner ridges); 1, three ridges (galliforms); 2, two ridges; 3, one centrally located ridge; 4, hypotarsus block-like, no ridges, plantarly flattened, very shallow sulcus slightly towards medial side, steep lateral and medial sides slightly narrowing distally (phorusrhacids). Modified from Cracraft (1974, 502), Lee et al. (1997, char. 27), Worthy and Scofield (2012, char. 163). This character is not necessarily a morphocline, as fusion of numerous close ridges could directly produce a single ridge.

260. Tarsometatarsus, hypotarsus, number of hypotarsal canals: 0, none; 1, one canal, for m. flexor digitorum longus (fdl); 2, two canals, i.e. for fdl and one for tendons for m. flexor perforatus digiti II and m. flexor perforans et perforatus digiti II (pII–ppII), located plantarlateral to fdl. Note: Overlaps Ksepka (2009, char. 81). In *Gallus*, near enclosure of canal for pII–ppII is intermediate between the broadly open state in megapodes and the closed condition in Odontophoridae and some Tetraonini (*Bonasa*, *Tympanuchus*), among phasianids (Holman 1964[117]).

*261. Tarsometatarsus, proximal end, fossa parahypotarsalis medialis: 0, very large deep and broad, >1/2 width at distal end of hypotarsus (e.g. *Leipoa*); 1, deep but narrow, <1/2 width at distal end of hypotarsus, (e.g. *Anseranas*); 2, shallow, surface from medial calcaneal ridge to cranial margin of medial shaft concave (e.g. *Cereopsis*); 3, absent, surface from medial calcaneal ridge to cranial margin of medial facies shaft flat or convex. From Worthy and Lee (2008, char. 108). State 0 correlates with a dorsoventrally thin shaft typical of megapodes.

*262. Tarsometatarsus, corpus tarsometatarsi, sulcus extensorius: 0, absent e.g. *Alectura*, *Leipoa*; 1, shallow and broad proximally, flattens out distally, e.g. *Gallus*, *Cereopsis*; 2, deep, well defined at mid-length, extending into distal half. See Lee et al. (1997, char. 30), Bourdon et al. (2009a, char. 122), Worthy and Lee (2008, char. 110), Worthy and Scofield (2012, char. 168). We re-coded *Anhima* (1) based on multiple specimens.

*263. Tarsometatarsus, tuberositas M. tibialis cranialis; 0, a single tuberosity distal to medial foramen which may have indications of the more lateral tendon as a very much smaller scar on its edge; 1, two distinct tuberosities; 2, two distinct tuberosities fused as one in the base of the extensor sulcus, with foramen passing through it, e.g. *Dromornis*. Worthy and Scofield (2012, char. 172).

264. Tarsometatarsus, tuberositas M. tibialis cranialis; 0, confined within extensor sulcus; 1, dorsally prominent.

265. Tarsometatarsus, foramina vascularis proximalis: 0, medial and lateral foramina of roughly equal size, e.g. *Anseranas*, *Anhima*; 1, medial foramen considerably larger than lateral one (e.g. *Alectura*, *Leipoa*); 2, a single fossa with foramina in it. 3, lateral foramen larger than medial.

266. Tarsometatarsus, impressiones retinaculi extensorii: 0, form two short crests proximal to the foramina vascularis proximalis; 1, two elongated crests with impressio retinaculum extensorii medialis extending distally on the shaft distad of the medial foramen vascularis proximalis.

267. Tarsometatarsus, corpus tarsometatarsi, dorsal view: 0, shaft long, sides essentially parallel over middle third of length; 1, shaft relatively shorter for bone width, narrowest in distal third of length and widen proximally. Not Character 165 of Worthy and Scofield (2012).

268. Tarsometatarsus, plantar facies, development of crista plantares medialis et lateralis: 0, little or no development; 1, well developed especially laterally. From Lee et al. (1997, char. 31) and Bourdon et al. (2009a, char. 118 & 121), Worthy and Scofield (2012, char. 166).

*269. Tarsometatarsus, shaft, width at mid-length: 0, wider than deep; 1, width approximately equals depth; 2, depth exceeds width. Worthy and Lee (2008, char. 116).

270. Tarsometatarsus, dorsal facies, distal shaft: 0, convex dorsally; 1, flat or concave, e.g. *Gallus*.

271. Tarsometatarsus, fossa metatarsi I: 0, present, well-marked; 1, absent or obsolete. See Livezey (1986, char. 71). Worthy and Lee (2008, char. 113).

*272. Tarsometatarsus, fossa metatarsi I, metatarsal articular facet: 0, absent; 1, present, does not protrude mesad of shaft; 2, present, large and protrudes mesad of shaft.

*273. Tarsometatarsus, dorsal view, trochlea metatarsi II, distal extent: 0, equal or greater than trochlea metatarsi IV (e.g. *Leipoa*); 1, proximal to trochlea metatarsi IV, but overlaps incisura intertrochlearis lateralis (e.g. *Anseranas*, *Cereopsis*); 2, proximal to incisura intertrochlearis lateralis (e.g. *Anser*, most anatids). Modified from Livezey (1986, char. 68; 1996a, char. 75); see also Worthy et al. (1997), Worthy and Lee (2008, char. 105), and Ksepka (2009, char. 84).

274. Tarsometatarsus, distal end, trochlea metatarsi II, central groove dorsally and distally: 0, groove absent (e.g. *Anseranas*); 1, groove present, so distal margin notched. See Livezey (1986, char. 74; 1996a, char. 76), Worthy and Lee (2008, char. 109), Worthy and Scofield (2012, char. 173). Note: In the megapodes and *Gallus*, development of a flange plantarly from the medial edge of the trochlea creates a notch in distal view, but the trochlea lacks a central groove so these taxa are coded (0).

275. Tarsometatarsus, cranial end of canalis interosseus distalis: 0, roofed over entirely in bone, not visible in dorsal view (e.g. *Anseranas*); 1, largely or completely exposed dorsally by reduction in bony covering. Livezey (1986, char. 69). Worthy and Lee (2008, char. 112).

276. Tarsometatarsus, distal end, trochlea metatarsi II outer rim: 0, expanded medially and/or caudally as a flange (e.g. *Anseranas*, *Leipoa*); 1, flattened medial facies, lacking flange. Modified from Livezey (1986, char. 73), Worthy and Lee (2008, char. 114).

277. Tarsometatarsus, distal end, plantar opening of foramen vasculare distale: 0, opens flush onto plantar surface; 1, directed distoplantarly, so partially recessed into incisura intertrochlearis lateralis. Livezey (1986, char. 77), Worthy and Lee (2008, char. 115).

*278. Tarsometatarsus, trochlea metatarsi II, dorsal view, point of maximum medial projection exclusive of plantar flange: 0, distal to maximum proximal extent of incisura intertrochlearis medialis; 1, level with maximum proximal extent of incisura; 2, proximal to incisura. See Worthy and Holdaway (2002, char. 67), after Worthy and Scofield (2012, char. 170).

*279. Tarsometatarsus, foramen vasculare distale: 0, large; 1, small and distinct; 2, tiny and indistinct; 3, absent. Worthy and Scofield (2012, char. 171).

*280. Pes, number of digits: 0, four digits; 1, three digits, II, III and IV; 2, two digits (III & IV). Derived from Bourdon et al. (2009, char. 125). Worthy and Scofield (2012, char. 174).

281. Ossa digiti IV, intermediate phalanges gradually shorten towards phalanx ungualis, so that phalanx just proximal to the latter is either wider than long or nearly square in shape: 0, no; 1, yes. From Bourdon et al. (2009a, char. 126). Worthy and Scofield (2012, char. 175).

282. Digitus IV pedis, number of phalanges: 0, five; 1, four. See Worthy and Holdaway (2002, Appendix 3, char. 72), and modified from Bourdon et al. (2009, char. 127), Worthy and Scofield (2012, char. 176).

*283. Ungual phalanges, digit 3, width and depth at midlength: 0, depth > width; 1, depth approximately = to depth (+-5%); 2, depth < width.

Other characters

284. Incubation type: 0, Endothermic, body heat used to incubate eggs; 1, ectothermic, environmental heat used to incubate eggs.

*285. Webbing between toes (tela interdigitalis), excluding hallux: 0, lacking; 1, rudimentary; 2, semipalmate; 3, palmate. From Livezey (1997).

286. Os sesamoideum intertarsale (within tibial cartilage) presence and form: 0, absent; 1, present and extends across width of the tarsometatarsus-tibiotarsus joint and is much wider than proximodistally long; 2, present and is restricted to medial side of the tarsometatarsus-tibiotarsus joint and usually proximodistally elongate.

287. Cranium, squamosal processus suprameaticus form: 0, robust, conical, cross-section circular and adpressed to cotyla quadratica oticum caudal to cotyla quadratica squamosum; 1, lateromedially flattened, sliver-like adpressed to cotyla quadratica oticum caudal to cotyla quadratica squamosum; 2, separated laterally from cotyla quadratica oticum and variably flattened. In palaeognaths the suprameatic area is fused with the processus zygomaticus rather than being a distinct process but here its separation from the cotyla is given priority and so they are coded 2.

288. Syrinx – presence of ossified pessulus (Clarke et al 2016): 0, absent; 1, present.

289. Syrinx – asymmetry at the tracheobronchial juncture (Clarke et al. 2016): 0, absent; 1, present.

290. Humerus, proximal caudal surface with fossa at the dorsal side of the incisura capitis that is bound distally by a transverse crus dorsale fossae and dorsally by the capital shaft ridge: 0, absent; 1, present (Anhimidae, Presbyornithidae, *Vegavis*). Following De Pietri et al. (2016), this structure is treated separately to the fossa pneumotricipitalis dorsalis that aligns parallel to the capital shaft ridge (when it is present), is separated from the fossa pneumotricipitalis ventralis by a proximodistally aligned crus dorsale fossa, and is open distally.

Newly added characters

291. Retroarticular process: 0, absent; 1, present.

292: Retroarticular process, shape: 0, unhooked, projects caudally; 1, unhooked, tip directed dorsally (e.g., *Vegavis*); 2, hooked, tip directed dorsally (e.g., *Anas*, *Anatalavis*). We added this character and modified character 64 to more fully represent the variation in the morphology of the retroarticular process.

293: Mandible, processus medialis, orientation in dorsal in view: 0, medially directed; 1, caudally deflected.

294: Interorbital region of frontals in dorsal view: 0, constricted at midpoint of orbit forming hourglass-like shape; 1, unconstricted at midpoint, lateral margins flat or convex in dorsal view.

295: Nasal-premaxilla contact at tomial margin, degree of fusion: 0, unfused, suture visible; 1, sutures obliterated; 2, no contact.

296: Mesethmoid, rostral extent: 0, restricted to region caudal of antorbital fenestra; 1, extends rostral to caudal margin of antorbital fenestra; 2 extends almost to rostral tip of beak.

297: Shape of occipital condyle: 0, not as follows; 1, heart-shaped, with pronounced incisure in dorsal margin of condyle.

IX: Supplementary References

1 Mayr, G. & Smith, T. Bony-toothed birds (Aves: Pelagornithidae) from the middle Eocene of Belgium. *Palaeontology* **53**, 365-376, doi:10.1111/j.1475-4983.2009.00930.x (2010).

2 Worthy, T. H., Degrange, F. J., Handley, W. D. & Lee, M. S. Y. The evolution of giant flightless birds and novel phylogenetic relationships for extinct fowl (Aves, Galloanseres). *Royal Society Open Science* **4**, doi:10.1098/rsos.170975 (2017).

3 Gonzalez, J., Düttmann, H. & Wink, M. Phylogenetic relationships based on two mitochondrial genes and hybridization patterns in Anatidae. *Journal of Zoology* **279**, 310-318 (2009).

4 Harris, R. B., Birks, S. M. & Leaché, A. D. Incubator birds: biogeographical origins and evolution of underground nesting in megapodes (Galliformes: Megapodiidae). *Journal of Biogeography* **41**, 2045-2056 (2014).

5 Jarvis, E. D. *et al.* Whole-genome analyses resolve early branches in the tree of life of modern birds. *Science* **346**, 1320-1331, doi:10.1126/science.1253451 (2014).

6 Prum, R. O. *et al.* A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA sequencing. *Nature* **526**, 569-573, doi:10.1038/nature15697 (2015).

7 Cloutier, A. *et al.* Whole-genome analyses resolve the phylogeny of flightless birds (Palaeognathae) in the presence of an empirical anomaly zone. *Systematic biology* **68**, 937-955 (2019).

8 Kimball, R. T. *et al.* A Phylogenomic Supertree of Birds. *Diversity* **11**, 109 (2019).

9 Hosner, P. A., Faircloth, B. C., Glenn, T. C., Braun, E. L. & Kimball, R. T. Avoiding missing data biases in phylogenomic inference: an empirical study in the landfowl (Aves: Galliformes). *Molecular Biology and Evolution* **33**, 1110-1125 (2015).

10 Reddy, S. *et al.* Why do phylogenomic data sets yield conflicting trees? Data type influences the avian tree of life more than taxon sampling. *Systematic biology* **66**, 857-879 (2017).

11 Tambussi, C. P., Degrange, F. J., De Mendoza, R. S., Sferco, E. & Santillana, S. A stem anseriform from the early Palaeocene of Antarctica provides new key evidence in the early evolution of waterfowl. *Zoological Journal of the Linnean Society* **186**, 673-700, doi:10.1093/zoolinnean/zly085 (2019).

12 Xie, W., Lewis, P. O., Fan, Y., Kuo, L. & Chen, M. H. Improving marginal likelihood estimation for Bayesian phylogenetic model selection. *Syst Biol* **60**, 150 - 160 (2011).

13 Kass, R. E. & Raftery, A. E. Bayes Factors. *J Am Statist Ass* **90**, 773 - 795 (1995).

14 Bergsten, J., Nilsson, A. N. & Ronquist, F. Bayesian tests of topology hypotheses with an example from diving beetles. *Systematic biology* **62**, 660-673 (2013).

15 Goloboff, P. A., Pittman, M., Pol, D. & Xu, X. Morphological data sets fit a common mechanism much more poorly than DNA sequences and call into question the Mkv model. *Systematic biology* **68**, 494-504 (2018).

16 Budd, G. E. & Mann, R. P. The dynamics of stem and crown groups. *bioRxiv*, 633008, doi:10.1101/633008 (2019).

17 Wright, A. M. & Hillis, D. M. Bayesian Analysis Using a Simple Likelihood Model Outperforms Parsimony for Estimation of Phylogeny from Discrete Morphological Data. *PLOS ONE* **9**, e109210, doi:10.1371/journal.pone.0109210 (2014).

18 O'Reilly, J. E. *et al.* Bayesian methods outperform parsimony but at the expense of precision in the estimation of phylogeny from discrete morphological data. *Biology Letters* **12** (2016).

19 Hartman, S. *et al.* A new paravian dinosaur from the Late Jurassic of North America supports a late acquisition of avian flight. *PeerJ* **So 7**, e7247, doi:10.7717/peerj.7247 (2019).

20 Matschiner, M. Selective Sampling of Species and Fossils Influences Age Estimates Under the Fossilized Birth-Death Model. *Frontiers in Genetics* **10**, 1064 (2019).

21 Berv, J. S. & Field, D. J. Genomic Signature of an Avian Lilliput Effect across the K-Pg Extinction. *Systematic Biology* **67**, 1-13, doi:10.1093/sysbio/syx064 (2018).

22 Field, D. J. *et al.* Timing the extant avian radiation: The rise of modern birds, and the importance of modeling molecular rate variation. *PeerJ Preprints* **7**, e27521v27521, doi:10.7287/peerj.preprints.27521v1 (2019).

23 Clarke, J. A., Tambussi, C. P., Noriega, J. I., Erickson, G. M. & Ketcham, R. A. Definitive fossil evidence for the extant avian radiation in the Cretaceous. *Nature* **433**, 305-308 (2005).

24 Ksepka, D. T. & Clarke, J. Phylogenetically vetted and stratigraphically constrained fossil calibrations within Aves. *Palaeontologia Electronica* **18.1.3FC**, 1-25, doi:palaeo-electronica.org/content/fc-3 (2015).

25 Mayr, G., De Pietri, V. L., Scofield, R. P. & Worthy, T. H. J. C. R. On the taxonomic composition and phylogenetic affinities of the recently proposed clade Vegaviidae Agnolín et al., 2017–neornithine birds from the Upper Cretaceous of the Southern Hemisphere. **86**, 178-185 (2018).

26 O'Connor, J. K., Chiappe, L. M. & Bell, A. in *Living Dinosaurs: The evolution of modern birds* (eds G. Dyke & G. Kaiser) 39-114 (Wiley-Blackwell, 2011).

27 McLachlan, S. M., Kaiser, G. W. & Longrich, N. R. Maaqwi cascadensis: A large, marine diving bird (Avialae: Ornithurae) from the Upper Cretaceous of British Columbia, Canada. *PloS one* **12**, e0189473 (2017).

28 Ericson, P. G. P. Systematic relationships of the palaeogene family Presbyornithidae (Aves: Anseriformes). *Zoological Journal of the Linnean Society* **121**, 429-483 (1997).

29 Livezey, B. C. A phylogenetic analysis of basal Anseriformes the fossil Presbyornis, and the interordinal relationships of waterfowl. *Zoological Journal of the Linnean Society* **121**, 361-428 (1997).

30 Olson, S. L. & Feduccia, A. Presbyornis and the origin of the Anseriformes (Aves: Charadriomorphae). *Smithsonian Contributions to Zoology* **323**, 1-24 (1980).

31 de Pietri, V. L., Scofield, R. P., Zelenkov, N., Boles, W. E. & Worthy, T. H. The unexpected survival of an ancient lineage of anseriform birds into the Neogene of Australia: The youngest record of Presbyornithidae. *Royal Society Open Science* **3**, doi:10.1098/rsos.150635 (2016).

32 Olson, S. L. The anseriform relationships of Anatalavis Olson and Parris (Anseranatidae), with a new species from the Lower Eocene London Clay. *Smithsonian Contributions to Paleobiology* **89**, 231-243 (1999).

33 Mayr, G. Cenozoic mystery birds - on the phylogenetic affinities of bony-toothed birds (Pelagornithidae). *Zoologica Scripta* **40**, 448-467, doi:10.1111/j.1463-6409.2011.00484.x (2011).

34 Bourdon, E. Osteological evidence for sister group relationship between pseudo-toothed birds (Aves: Odontopterygiformes) and waterfowls (Anseriformes). *Naturwissenschaften* **92**, 586-591, doi:10.1007/s00114-005-0047-0 (2005).

35 Felder, W. Lithostratigraphische Gliederung der Oberen Kreide in Süd-Limburg (Niederlande) und den Nachbargebieten. 1. Teil: Der Raum westlich der Maas, Typusgebiet des' Maastricht'. *Publ. Nat. Hist. Gen. Limburg* **24**, 43 (1975).

36 Felder, W. Lithostratigrafie van het Boven-Krijt en het Dano-Montien in Zuid-Limburg en het aangrenzende gebied. *Toelichting bij geologische overzichtskaarten van Nederland. Rijks Geologische Dienst (Haarlem)*, 63-72 (1975).

37 Jagt, J. & Jagt-Yazykova, E. Stratigraphy of the type Maastrichtian-a synthesis. *Scripta Geologica* (2012).

38 Christensen, W., Schmid, F. & Schulz, M. Belemnitella from the Upper Maastrichtian of Hemmoor, Northwest Germany. *Geologisches Jahrbuch A* **157**, 23-67 (2004).

39 Jagt, J. W. & Jagt-Yazykova, E. A. Stratigraphical ranges of tegulated inoceramid bivalves in the type area of the Maastrichtian Stage (Belgium, the Netherlands). *Cretaceous Research* **87**, 385-394 (2018).

40 Keutgen, N. A bioclast-based astronomical timescale for the Maastrichtian in the type area (southeast Netherlands, northeast Belgium) and stratigraphic implications: the legacy of PJ Felder. *Netherlands Journal of Geosciences* **97**, 229-260 (2018).

41 Dyke, G. J. *et al.* Europe's last Mesozoic bird. *Naturwissenschaften* **89**, 408-411, doi:10.1007/s00114-002-0352-9 (2002).

42 Dyke, G. J., Schulp, A. & Jagt, J. Bird remains from the Maastrichtian type area (Late Cretaceous). *Netherlands Journal of Geosciences* **87**, 353-358 (2008).

43 Schiøler, P., Brinkhuis, H., Roncaglia, L. & Wilson, G. J. Dinoflagellate biostratigraphy and sequence stratigraphy of the type Maastrichtian (Upper Cretaceous), ENCI Quarry, The Netherlands. *Marine Micropaleontology* **31**, 65-95 (1997).

44 Villain, J.-M. Le Maastrichtien dans sa région type (Limbourg, Pays-Bas). Étude stratigraphique et micropaléontologique. *Palaeontographica Abteilung A*, 1-87 (1977).

45 Liebau, A. Paläobathymetrische und paläoklimatische veränderungen im mikrofaunenbild der maastrichter tuffkreide. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **157**, 233-237 (1978).

46 Gauthier, J. Saurischian monophyly and the origin of birds. *Memoirs of the California Academy of Sciences* **8** (1986).

47 Maryanska, T., Osmólska, H. & Wolsan, M. Avialian status for Oviraptorosauria. *Acta Palaeontologica Polonica* **42**, 361-371 (2002).

48 Godefroit, P. *et al.* A Jurassic avialan dinosaur from China resolves the early phylogenetic history of birds. *Nature* **498**, 359-362, doi:10.1038/nature12168 (2013).

49 Hendrickx, C., Hartman, S. A. & Mateus, O. An overview of non-avian theropod discoveries and classification. *PalArch's Journal of Vertebrate Palaeontology* **12**, 1-73 (2015).

50 Gadow, H. On the classification of birds. *Proceedings of the Zoological Society of London* **1892**, 229-256 (1892).

51 Sereno, P. C. A rationale for phylogenetic definitions, with application to the higher-level taxonomy of Dinosauria. *Neues Jahrbuch fur Geologie und Palaontologie - Abhandlungen* **210**, 41-83 (1998).

52 Gauthier, J. A. & de Queiroz, K. in *New Perspectives on the Origin and Early Evolution of Birds: Proceedings of the International Symposium in Honor of John H. Ostrom* (eds Jacques A. Gauthier & Larry F. Gall) (Peabody Museum of Natural History, Yale University, 2001).

53 Pycraft, W. P. *Transactions of the Zoological Society of London* **15**, 149 (1900).

54 Harshman, J. *et al.* Phylogenomic evidence for multiple losses of flight in ratite birds. *Proceedings of the National Academy of Sciences* **105**, 13462 (2008).

55 Phillips, M. J., Gibb, G. C., Crimp, E. A. & Penny, D. Tinamous and Moa Flock Together: Mitochondrial Genome Sequence Analysis Reveals Independent Losses of Flight among Ratites. *Systematic Biology* **59**, 90-107, doi:10.1093/sysbio/syp079 (2010).

56 Smith, J. V., Braun, E. L. & Kimball, R. T. Ratite Nonmonophyly: Independent Evidence from 40 Novel Loci. *Systematic Biology* **62**, 35-49, doi:10.1093/sysbio/sys067 (2013).

57 Baker, A. J., Haddrath, O., McPherson, J. D. & Cloutier, A. Genomic support for a moa-tinamou clade and adaptive morphological convergence in flightless ratites. *Molecular Biology and Evolution* **31**, 1686-1696, doi:10.1093/molbev/msu153 (2014).

58 Mitchell, K. J. *et al.* Ancient DNA reveals elephant birds and kiwi are sister taxa and clarifies ratite bird evolution. *Science* **344**, 898-900, doi:10.1126/science.1251981 (2014).

59 Faux, C. & Field, D. J. Distinct developmental pathways underlie independent losses of flight in ratites. *Biology Letters* **13**, doi:10.1098/rsbl.2017.0234 (2017).

60 Yonezawa, T. *et al.* Phylogenomics and Morphology of Extinct Paleognaths Reveal the Origin and Evolution of the Ratites. *Current Biology* **27**, 68-77, doi:https://doi.org/10.1016/j.cub.2016.10.029 (2017).

61 Yuri, T. *et al.* Parsimony and model-based analyses of indels in avian nuclear genes reveal congruent and incongruent phylogenetic signals. *Biology* **2**, 419-444, doi:10.3390/biology2010419 (2013).

62 Sibley, C. G., Ahlquist, J. E. & Monroe B.L, Jr. A classification of the living birds of the world based on DNA-DNA hybridization studies. *Auk* **105**, 409-423 (1988).

63 Mayr, G. Metaves, Mirandornithes, Strisores and other novelties - a critical review of the higher-level phylogeny of neornithine birds. *Journal of Zoological Systematics and Evolutionary Research* **49**, 58-76, doi:10.1111/j.1439-0469.2010.00586.x (2011).

64 Weber, E. Zur Evolution basicranialer Gelenke bei Vögeln, insbesondere bei Hühner- und Entenvögeln (Galloanseres). *Zeitschrift für Zoologische Systematik und Evolutionsforschung* **31**, 300-317 (1993).

65 Andors, A. V. Reappraisal of the Eocene groundbird Diatryma (Aves: Anserimorphae). *Papers in Avian Paleontology Honoring Pierce Brodkorb* **36**, 109-125 (1992).

66 Nesbitt, S. J. The Early Evolution of Archosaurs: Relationships and the Origin of Major Clades. *Bulletin of the American Museum of Natural History* **2011**, 1-292, 292 (2011).

67 Cau, A. The assembly of the avian body plan: a 160-million-year long process. *Bollettino della Società Paleontologica Italiana* **57**, 1-25, doi:10.4435/BSPI.2018.01 (2018).

68 Chen, A., White, N. D., Benson, R. B. J., Braun, M. J. & Field, D. J. Total-Evidence Framework Reveals Complex Morphological Evolution in Nightbirds (Strisores). **11**, 143 (2019).

69 Wagler, J. G. Einige mittheilungen über thiere Mexicos. *Isis von Oken* **5**, 510-535 (1831).

70 Martyniuk, M. P. *A Field Guide to Mesozoic Birds and Other Winged Dinosaurs.*, 195pp (Pan Aves, 2012).

71 Linnaeus, C. *Systema naturae*. Vol. Vol. 1 (1758).

72 Leach, W. E. Eleventh room. *Synopsis of the Contents of the British Museum*, 65-70 (1820).

73 Clarke, J. A. Morphology, phylogenetic taxonomy, and systematics of *Ichthyornis* and *Apatornis* (Avialae: Ornithurae). *Bulletin of the American Museum of Natural History* **286**, 1-179 (2004).

74 Temminck, C. J. *Manuel d'ornithologie*. 439 pp. (Chez H. Cousin, 1820).

75 Vigors, N. A. XXII. Observations on the Natural Affinities that connect the Orders and Families of Birds. *Transactions of the Linnean Society of London* **14**, 395-517 (1825).

76 Crowe, T. M. *et al.* Supra-generic cladistics of landfowl (Order Galliformes). *Acta Zool. Sinica* **52**, 358-361 (2006).

77 Hosner, P. A., Tobias, J. A., Braun, E. L. & Kimball, R. T. How do seemingly non-vagile clades accomplish trans-marine dispersal? Trait and dispersal evolution in the

landfowl (Aves: Galliformes). *Proceedings of the Royal Society B: Biological Sciences* **284**, doi:10.1098/rspb.2017.0210 (2017).

78 Tumarkin-Deratzian, A. R., Vann, D. R. & Dodson, P. Bone surface texture as an ontogenetic indicator in long bones of the Canada goose Branta canadensis (Anseriformes: Anatidae). *Zoological Journal of the Linnean Society* **148**, 133-168, doi:10.1111/j.1096-3642.2006.00232.x (2006).

79 Mayr, G. Comparative morphology of the avian maxillary bone (os maxillare) based on an examination of macerated juvenile skeletons. *Acta Zoologica* (2018).

80 Livezey, B. C. & Zusi, R. L. Higher-order phylogeny of modern birds (Theropoda, Aves: Neornithes) based on comparative anatomy. I. Methods and characters. *Bulletin of the Carnegie Museum of Natural History* **37**, 1-544 (2006).

81 Wang, M. & Hu, H. A comparative morphological study of the jugal and quadratojugal in early birds and their dinosaurian relatives. *The Anatomical Record* **300**, 62-75 (2017).

82 Field, D. J. *et al.* Complete Ichthyornis skull illuminates mosaic assembly of the avian head. *Nature* **557**, 96-100, doi:10.1038/s41586-018-0053-y (2018).

83 Cracraft, J. The lacrimal-ectethmoid bone complex in birds: A single character analysis. *American Midland Naturalist* **80**, 316-359 (1968).

84 Wang, X. *et al.* The earliest evidence for a supraorbital salt gland in dinosaurs in new Early Cretaceous ornithurines. *Scientific Reports* **8**, 3969, doi:10.1038/s41598-018-22412-8 (2018).

85 Elzanowski, A. & Stidham, T. A. A Galloanserine Quadrate from the Late Cretaceous Lance Formation of Wyoming. *The Auk* **128**, 138-145, doi:10.1525/auk.2011.10113 (2011).

86 Elzanowski, A. & Stidham, T. A. Morphology of the quadrate in the Eocene anseriform Presbyornis and extant galloanserine birds. *Journal of Morphology* **271**, 305-323, doi:10.1002/jmor.10799 (2010).

87 Zelenkov, N. & Stidham, T. Possible filter-feeding in the extinct Presbyornis and the evolution of Anseriformes (Aves). *Zoologischesky Zhurnal* **97**, 943-956 (2018).

88 Weber, E. & Hesse, A. The systematic position of Aptornis, a flightless bird from New Zealand. *Courier Forschungsinstitut Senckenberg* **181**, 293-301 (1995).

89 Field, D. J. & Hsiang, A. Y. A North American stem turaco, and the complex biogeographic history of modern birds. *BMC Evolutionary Biology* **18**, 102, doi:10.1186/s12862-018-1212-3 (2018).

90 Worthy, T. H. & Lee, M. S. Y. Affinities of miocene waterfowl (anatidae: Manuherikia, dunstanetta and miotadorna) from the St Bathans Fauna, New Zealand. *Palaeontology* **51**, 677-708, doi:10.1111/j.1475-4983.2008.00778.x (2008).

91 Livezey, B. C. A phylogenetic analysis of geese and swans (Anseriformes: Anserinae), including selected fossil species. *Systematic Biology* **45**, 415-450 (1996).

92 Livezey, B. C. A phylogenetic analysis of Recent anseriform genera using morphological characters. *Auk* **105**, 681-698 (1986).

93 Parkes, K. C. & Clark, G. A. An additional character linking ratites and tinamous, and an interpretation of their monophyly. *The Condor* **68**, 459-471 (1966).

94 Worthy, T. H. & Scofield, R. P. Twenty-first century advances in knowledge of the biology of moa (Aves: Dinornithiformes): a new morphological analysis and moa diagnoses revised. *New Zealand Journal of Zoology* **39**, 87-153 (2012).

95 Mayr, G. & Clarke, J. The deep divergences of neornithine birds: a phylogenetic analysis of morphological characters. *Cladistics* **19**, 527-553 (2003).

96 Ksepka, D. T. Broken gears in the avian molecular clock: new phylogenetic analyses support stem galliform status for *Gallinuloides wyomingensis* and rallid affinities for *Amitabha urbsinterdictensis*. *Cladistics* **25**, 173-197 (2009).

97 Bourdon, E., Dyke, G. & Kaiser, G. The pseudo-toothed birds (Aves, Odontopterygiformes) and their bearing on the early evolution of modern birds. *Living Dinosaurs, The Evolutionary History of Modern Birds, London, John Wiley and Sons Ltd*, 209-234 (2011).

98 Worthy, T., Holdaway, R., Sorenson, M. & Cooper, A. Description of the first complete skeleton of the extinct New Zealand goose Cnemiornis calcitrans (Aves: Anatidae), and a reassessment of the relationships of Cnemiornis. *Journal of Zoology* **243**, 695-718 (1997).

99 Zusi, R. L. & Livezey, B. C. Homology and phylogenetic implications of some enigmatic cranial features in Galliform and anseriform birds. *Annals of Carnegie Museum* **69**, 157-193 (2000).

100 Parker, T. J. *Transactions of the Zoological Society of London* **13**, 373 (1895).

101 Raikow, R. J. The osteology and taxonomic position of the White-backed Duck, Thalassornis leuconotus. *The Wilson Bulletin*, 270-277 (1971).

102 Cracraft, J. & Clarke, J. The basal clades of modern birds. *New Perspectives on the Origin and Early Evolution of Birds: Proceedings of the International Symposium in Honor of John H. Ostrom (J. Gauthier and LF Gall, Eds.). Peabody Museum of Natural History, Yale University, New Haven, Connecticut*, 143–156 (2001).

103 Livezey, B. C. A phylogenetic reassessment of the tadornine-anatine divergence (aves: anseriformes: Anatidae). *Annals of Carnegie Museum* **65**, 27-88 (1996).

104 Worthy, T. H. Descriptions and phylogenetic relationships of two new genera and four new species of Oligo-Miocene waterfowl (Aves: Anatidae) from Australia.

Zoological Journal of the Linnean Society **156**, 411-454, doi:10.1111/j.1096-3642.2008.00483.x (2009).

105 Matsuoka, H. & Hasegawa, Y. Myology and osteology of the Whooper Swan Cygnus cygnus (Aves: Anatidae) part 1. Muscles attached to the sternum, coracoid, clavicle, scapula and humerus. *Bulletin of the Gunma Museum of Natural History* **11**, 7-14 (2007).

106 Mourer-Chauviré, C. The Galliformes (Aves) from the Phosphorites du Quercy (France): Systematics and biostratigraphy. *Papers in Avian Paleontology Honoring Pierce Brodkorb* **36**, 67-95 (1992).

107 Baumel, J. J. & Witmer, L. M. in *Handbook of Avian Anatomy: Nomina Anatomica Avium* Vol. 23 (eds Julian J. Baumel *et al.*) 45-132 (Publications of the Nuttall Ornithological Club, 1993).

108 Howard, H. The avifauna of Emeryville Shellmound. *University of California Publications in Zoology* **32**, 301-394 (1929).

109 Woolfenden, G. E. Postcranial osteology of the waterfowl. Bulletin of the Florida state museum. *Biological Sciences* **6** (1961).

110 Clarke, J. A. *et al.* Fossil evidence of the avian vocal organ from the Mesozoic. *Nature* **538**, 502, doi:10.1038/nature19852 (2016).

111 Bourdon, E., De Ricqles, A. & Cubo, J. A new Transantarctic relationship: Morphological evidence for a rheidae?dromaiidae?casuariidae clade (Aves, Palaeognathaes, Ratitae). *Zoological Journal of the Linnean Society* **156**, 641-663, doi:10.1111/j.1096-3642.2008.00509.x (2009).

112 Worthy, T. H. & Holdaway, R. N. The lost world of the moa: Prehistoric life of New Zealand. *The Lost World of the Moa* (2002).

113 Zinoviev, A. in *Paleornithological Research 2013: Proceedings of the 8th International Meeting of the Society of Avian Paleontology and Evolution, Vienna.* 253-278.

114 Lee, K., Feinstein, J. & Cracraft, J. The phylogeny of ratite birds: Resolving conflicts between molecular and morphological data sets. *Avian Molecular Evolution and Systematics,* 173-211 (1997).

115 Cracraft, J. Phylogeny and evolution of the ratite birds. *Ibis* **116**, 494-521 (1974).

116 Mourer-Chauviré, C. Birds (Aves) from the Early Miocene of the Northern Sperrgebiet, Namibia. *Memoir of the Geological Survey of Namibia,* 147-167 (2008).

117 Holman, J. A. Osteology of gallinaceous birds. *Quarterly Journal of the Florida Academy of Sciences* **27**, 230-252 (1964).