# Osteology and neuroanatomy of a Miocene phasianid (Aves: Galliformes) from the Miocene of Nebraska

Daniel T. Ksepka[1*], Catherine M. Early[2], Kate Dzikiewicz[1], and Amy M. Balanoff[3]

[1]Bruce Museum, Greenwich, Connecticut 06830, USA <dksepka@brucemuseum.org>

[2]Biology Department, Science Museum of Minnesota, Saint Paul, Minnesota 55102, USA <cearly@smm.org>

[3]Department of Psychological and Brain Sciences, Johns Hopkins University, Baltimore, MD, 21218, USA <abalano2@jhu.edu>

**Running Header: Miocene fossil phasianid**

**Abstract.**— Tetraoninae (grouse) and Meleagridinae (turkeys) are conspicuous representatives of the modern North American avifauna. The pre-Pleistocene fossil record of these clades has historically been limited to fragmentary remains, in some cases contributing to confusion rather than improving our understanding of how these charismatic landfowl evolved. We report an exquisitely preserved partial skeleton representing a new species of Late Miocene phasianid from the Ash Hollow Formation of Nebraska. *Centuriavis lioae* is a phasianid species close in size to modern sage-grouse that diverged prior to the grouse-turkey split and thus offers insight into the early history of this radiation. The cranial endocast resembles other North American phasianids and differs from odontophorids in exhibiting a strongly projected Wulst bordered by a well-defined vallecula. Phylogenetic analyses indicate that *Centuriavis lioae* gen. et sp. nov. forms a clade with Tetraoninae, Meleagridinae, and *Pucrasia macrolopha* (Koklass pheasant). The new fossil species provides a late Miocene minimum calibration for the divergence of these extant taxa from other Galliformes and supports the hypothesis of a single dispersal from Asia to North America by a lineage that later gave rise to grouse and turkeys.

UUID: https://zoobank.org:34ecda2f-f2f2-4c92-a82f-292e23cf2da1

# Introduction

Phasianidae represent the most species-rich and morphologically diverse radiation of Galliformes (landfowl or gamebirds) (del Hoyo et al., 1994). This family includes pheasants, Old World quails, partridges, peafowl, grouse, and turkeys. North America is today inhabited by two native phasianid clades, the Meleagridinae (turkeys) and the Tetraoninae (grouse). Several other phasianid species, including *Phasianus colchicus* (Common Pheasant) and *Alectoris chuckar* (Chukar) have been introduced by humans in historical times and established breeding populations. Aside from Phasianidae, two other families of Galliformes also occur in North America today: the Odontophoridae (New World quail) and Cracidae (chachalacas, guans, and curassows).

Meleagridinae are distinctive birds that are easily identified by their large size, bare heads, and iridescent plumage. Today the clade is represented by just two species, *Meleagris gallopavo* (Wild Turkey) and the *Meleagris ocellata* (Ocellated Turkey) (placed in the separate genus *Agriocharis* in some earlier taxonomies). Tetraoninae are widespread throughout the Holarctic and represented by 19 extant species, 12 of which occur in North America (Gill et al., 2021). These species range in size from the small ptarmigans to the impressive capercaillies, and share various adaptations to cold winter conditions including feathered nostrils and feathered and/or pectinate toes that aid in traveling atop snow.

The phylogenetic relationships of Meleagridinae and Tetraoninae have been the subject of substantial debate. Some early taxonomies depicted turkeys and grouse as successive branches on the galliform tree (e.g., Johngard, 1986), whereas others placed them in their own families separate from Phasianidae (Meleagrididae and Tetraonidae; e.g.

Porter, 1994; de Juana, 1994). Somewhat surprisingly, previous phylogenetic analyses based on morphological data failed to support a sister-group relationship between these two rather similar groups of birds (Dyke et al., 2003; Ksepka, 2009). Early molecular analyses based on DNA hybridization (Sibley and Alhquist, 1990) and mitochondrial DNA supported a sister-group relationship between grouse and turkeys (Kimball et al., 1999; Dimcheff et al., 2002), but subsequent studies based on larger sequence samples recovered alternate topologies (Crowe et al., 2006; Kan et al., 2010). Most recently, molecular phylogenetic analyses have converged on a topology supporting a sister-group relationship between Meleagridinae and Tetraoninae, suggesting they shared a relatively recent common ancestor, and possibly split from one another following a dispersal event into North America (Kriegs et al., 2007; Kaiser et al., 2007; Kimball and Braun, 2008; Kimball et al., 2011; Wang et al., 2013; Hosner et al., 2017). Most recent work suggests that the closest living relative of the turkey + grouse clade is the Koklass pheasant *Pucrasia macrolopha*, a modest-sized bird that ranges throughout high-altitude forests in the Himalayas and China (Wang et al., 2013; Hosner et al., 2017).

*Fossil record of North American Galliformes.*—Until now, the fossil record has offered little insight into the early evolution of the turkey + grouse clade. Interestingly, the earliest records of North American landfowl appear to belong to stem taxa, revealing that at least one colonization of the continent ultimately ended in extinction, followed by later more successful arrivals of Cracidae, Odontophoridae, and Phasianidae. The oldest putative record of Pan-Galliformes is the Late Cretaceous *Austinornis lentus* (Marsh, 1877; Shufeldt, 1915; Clarke, 2004). However, this taxon is known only from a partial

77 tarsometatarsus and its phylogenetic position is best considered uncertain pending better
78 material (Mayr, 2016a). Complete skeletons of the stem landfowl species *Gallinuloides*
79 *wyomingensis* from the Early Eocene Green River Formation of Wyoming provide more
80 definitive records. *Gallinuloides* appears to have lacked skeletal accommodations for a
81 large crop and shows no evidence of consuming gastroliths, suggesting it was not adapted
82 to consuming the tough foodstuffs such as seeds favored by many modern landfowl (Mayr
83 and Weidig, 2004).

84 Several Eocene and Oligocene fossils were formerly assigned to crown Galliformes
85 but now appear to represent stem taxa. *Procrax brevipes* from the Late Eocene of South
86 Dakota is known from a single nearly complete skeleton. Tordoff and Macdonald (1957)
87 considered this taxon to be closely related to Cracidae, but its phylogenetic affinities are in
88 need of re-appraisal and it likely represents another stem member of Pan-Galliformes
89 (Mayr, 2009). *Archaealectrornis sibleyi* is known only from a humerus from the early
90 Oligocene of South Dakota, which lacks the distal projection of the caput humeri that
91 separates the incisura capitis and fossa tricipitalis dorsalis in all extant Galliformes (Crowe
92 and Short, 1992). This species thus likely also belongs outside crown Galliformes (Mayr,
93 2009). *Palaeonossax senectus* was based on the distal end of a humerus from the Upper
94 Oligocene Brule Formation of South Dakota. Wetmore (1956) considered the fossil to
95 closely resemble the extant cracid *Ortalis vetula*, but at least as illustrated the specimen
96 shows no obvious derived features of Cracidae and the orientation of the distal condyles
97 raises doubts over whether it even belongs to a galliform bird. The fossil record of stem
98 landfowl from North America otherwise consists of taxa based on very limited material
99 (reviewed in Stidham et al., 2020).

Discounting dubious records discussed above, Cracidae have their earliest record in the Miocene of Florida (Olson and Farrand, 1974). Multiple cracid species have been described from sparse material from the Miocene and Pliocene of California, Kansas, Florida, South Dakota, and Nebraska. All were assigned to the genus *Boreortalis* by Brodkorb (1964), though this taxonomic decision was considered arbitrary by Olson (1985).

A partial skull from the latest Eocene or earliest Oligocene of Washington state appears to belong to an archaic member of Phasianoidea (Odontophoridae + Numididae + Phasianidae) (Mayr et al., 2021). If this phylogenetic placement is substantiated, the skull would be a contender for the oldest record of crown Galliformes in North America.

The fossil record of Odontophoridae is in need of major revision. The oldest alleged record of Odontophoridae, *Nanortyx inexpectus* from the Eocene of Canada (Weigel, 1963), most likely represents the stem landfowl clade Quercymegapodiidae (see Mourer-Chauviré 1992). The distal end of a putative odontophorid tarsometatarsus from the Oligocene of Colorado was described but not figured by Tordoff (1951). Re-examination of this specimen is necessary to establish the affinities of this fossil, which may prove simply too incomplete to assign to any family. Fragmentary material from the Miocene of California and South Dakota assigned to Odontophoridae is likewise best treated with skepticism (see Olson, 1985). *Miortyx terres* from the early Miocene of South Dakota was assigned to Odontophoridae based primarily on the deep fossa tricipitalis dorsalis by Miller (1944). Howard (1966) later described a fragmentary humerus from the early Miocene of South Dakota as *Miortyx aldeni*, also based on the deep fossa tricipitalis dorsalis. This humerus, however, is 50% larger than the holotype humerus of *Miortyx terres*, and falls well outside

123 the size range of extant Odontophoridae. Given the large size of *Miortyx terres*, the fact that
124 a deep fossa tricipitalis dorsalis is present in many fossil taxa such as *Palaeortyx*, and the
125 distinct shape of the incisura capitis of *Miortyx* (which is unlike that in any extant New
126 World quail), it is possible that this genus is non-monophyletic and that one or both species
127 fall outside Odontophoridae. Abundant skeletal material from the Pliocene of Florida,
128 including skulls, has been assigned to the extant *Colinus virginianus* (Northern Bobwhite)
129 (Emslie, 1998), marking the earliest confirmed record of Odontophoridae in North America
130 pending re-examination of older fragmentary fossils.
131 The North American record of Phasianidae comprises a number of taxa assigned to
132 Tetraoninae and Meleagridinae, along with some putative records that are best considered
133 Galliformes *incertae sedis*. One often-overlooked taxon is *Archaeophasianus*, a former
134 contender for the oldest record North American of Phasianidae. Shufeldt (1915) described
135 two fossil species, which he assigned to the extant genus *Phasianus*: *Phasianus*
136 *americanus,* based on a partial tarsometatarsus and pedal phalanx collected from the
137 Middle John Day of Paulina Creek, Oregon (misspelled as "Parilina Creek" in the original
138 description, see Brodkorb, 1964) and *Phasianus mioceanus,* based on a partial humerus
139 from Scott's Bluff, Nebraska and a partial femur from Chimney Rock, Nebraska. Stone
140 (1915) noted this name was preoccupied by *Phasianus americanus* Audubon 1839 and
141 proposed the new species name *Phasianus roberti*. Subsequently, Lambrecht (1933) erected
142 the genus *Archaeophasianus* to accommodate these two species, in recognition of their
143 distinctness from *Phasianus*. Brodkorb (1964) considered the genus to belong to
144 Tetraoninae.

The precise stratigraphic horizon from which the *Archaeophasianus roberti* holotype was collected is uncertain. Shufeldt (1915) considered it Oligocene in age. Brodkorb later (1964) attributed it without explanation to the Upper Miocene Mascall Formation, whereas Fremd (2010) attributed it to beds A-D of the Turtle Cove assemblage of the John Day, indicating a latest Oligocene age. *Archaeophasianus mioceanus* is considered to be Miocene in age, but the precise stratigraphic horizon is again uncertain. Brodkorb (1964) attributed the co-types to the Sheep Creek or Marsland Formation, without comment. Whether *Archaeophasianus roberti* and *Archaeophasianus mioceanus* should be assigned to a single species cannot be adequately evaluated, as no overlapping elements are preserved for both species. Like *Archaealectrornis sibleyi*, the humerus of *Archaeophasianus mioceanus* lacks the distal projection of the caput humeri that characterizes extant Galliformes, and the incisura capitis and fossa tricipitalis dorsalis are instead separated only by a weak ridge. This suggests *Archaeophasianus mioceanus* may fall not only outside Phasianidae, but also outside of crown Galliformes.

The oldest reported fossil record of the turkey lineage is *Rhegminornis calobates*, based on a partial tarsometatarsus from the Miocene Thomas Farm locality of Florida. Originally considered a shorebird (Wetmore, 1943), this species was re-identified as a turkey by Olson and Farrand (1974). Steadman (1980:140), in a major review of the turkey fossil record, considered the material "insufficient to place it unequivocally within Meleagridinae, although such a placement may very well be correct". Assignment of *Rhegminornis* to Meleagridinae relied in part on the presence of an "inner intertrochlear foramen" which opens between the bases of trochlea metatarsi II and III. This foramen is typically present in *Meleagris gallopavo*, but it is absent in several specimens of *Meleagris*

*ocellata* examined during the present study. Further, this foramen occurs in at least some individuals of *Pucrasia macrolopha*, *Perdix perdix*, and *Polyplectron inoptinatum*. Upon re-examination of the material, we failed to find a strong resemblance to modern turkeys, and consider assignment to Meleagridinae poorly founded.

*Proagriocharis kimballensis* is another small fossil species identified as a turkey. Martin and Tate (1970) named the species based on two coracoids and three tarsometatarsi in varying states of completeness. Originally considered Late Pliocene in age, the holotype and referred specimens were since re-dated to the Miocene (Olson, 1985). *Proagriocharis* can confidently be assigned to at least Phasianidae, though the paucity of material raises uncertainty about its placement in Meleagridinae and it is worth considering the possibility that this taxon may instead represent a stem member of the turkey + grouse clade. This issue will likely remain unresolved until better material surfaces.

All remaining turkey fossils are presently assigned, at least tentatively, to the extant genus *Meleagris*. The oldest of these is a large tibiotarsus from the Late Miocene of Virginia considered cf. *Meleagris* by Steadman (1980). Valid extinct species include the Late Pliocene *Meleagris leopoldi* from Texas (with possible additional records from Florida), the Early Pleistocene *Meleagris anza* from California, and the Late Pleistocene *Meleagris crassipes* from New Mexico. It is debatable whether *Meleagris progenes,* known from the Pliocene of Kansas and possibly also Arizona, represents an additional distinct species or a synonym of *Meleagris leopoldi* (see Stidham, 2011). By far the most well-known fossil turkey, however, is *Meleagris californicus,* which is abundant at the renowned Late Pleistocene Rancho La Brea site in California. This species appears to have ranged

throughout the western United States before being wiped out by a combination of regional aridification and hunting by humans (Bocheński and Campbell, 2006).

The North American fossil record of grouse remains scrappy, and no pre-Pleistocene specimens can be confidently identified to an extant genus (Drovetski, 2003). Wetmore (1932) described a partial humerus from the Miocene of Nebraska as *Palaealectoris incertus*, assigning the species to Tetraonidae (equivalent to Tetraoninae). This assignment is doubtful however, as the fossa pneumotricipitalis dorsalis in this fossil is deeply excavated, unlike extant grouse. This, together with the very small size of the humerus (maximum head width 11.1mm), suggests *Palaealectoris* may instead be a close relative of *Palaeortyx*. Another poorly established taxon, "*Tympanuchus*" *stirtoni*, was based on a proximal portion of a tarsometatarsus from the Miocene of South Dakota (Miller, 1941). The material is insufficient to support this assignment and this fragmentary fossil is best considered Galliformes indet.. The only convincing fossil records of grouse thus come from the extant genus *Dendragapus*: *Dendragapus lucasi* and *Dendragapus gilli* from the Pleistocene of Oregon, along with some additional Pleistocene remains from California referred to the subspecies *Dendragapus gilli milleri* (see Jehl, 1969).

In this contribution, we describe a new species of phasianid from the Miocene of Nebraska. The holotype specimen was collected in articulation and preserves the skull, presacral vertebral series, partial synsacrum, and partial pectoral girdle and wings. We present a revised phylogeny of Galliformes along with comments on the neuroanatomy of Phasianidae based on virtual endocasts from the new fossil and several extant phasianid taxa.

*Geological setting.*— AMNH FARB 8629 was collected by the Skinner Expedition of 1932 at the *Machaerodus* Quarry, a locality in Cherry County, Nebraska. The mammalian fauna from this quarry indicates a Clarendonian North American Land Mammal Age (NALMA) (Tedford, et al., 2004). The Machaerodus Quarry is located within the Merritt Dam Member of the Ash Hollow Formation (Ogallala Group), and represents a channel fill cut into the underlying Cap Rock Member. An ash layer overlies the fossiliferous layer from which the specimen was collected. This layer has traditionally been referred to as the Machaerodus Ash. However, Lander (2008) argued that the Machaerodus Ash is equivalent to the Davis Ash, observing that these two ash layers, previously considered separate, never occur in superposition even at sections within <1km proximity of one another. Provided the Machaerodus Ash and Davis Ash are indeed one and the same, an $Ar^{40}/Ar^{39}$ age of 11.5 +/- 0.1Ma obtained from the Davis Ash (Swisher, 1992) provides a hard minimum age of 11.4Ma for the *Centuriavis lioae* holotype, which is also likely a close approximation for the actual age of the fossil.

## Materials and methods

*Anatomical nomenclature.*— Osteological terminology follows Baumel & Witmer (1993) with additional terminology for the quadrate following Elzanowski et al., (2000).

*Computed tomography scanning and visualization.*— AMNH FARB 8629 was microCT scanned at the AMNH Microscopy and Imaging Facility at a resolution of 74.2 microns.

Virtual models of the brain endocast and quadrate of this specimen were generated by segmenting these structures in Avizo (Thermo Fisher Scientific, Waltham, MA, USA). Portions of the braincase were broken and slightly offset, as can be seen on the right cerebral hemisphere, or missing, as is the case with the rostral portion of the braincase ventral to the olfactory bulbs and dorsal to the hypophysis. In those areas, we created smooth connections between the preserved bones that approximated the shape of a galliform endocast without fabricating anatomy, following best-practices approaches outlined by Balanoff et al. (2016). For comparative purposes, we rendered endocasts from the skulls of three North American galliform species: the turkey *Meleagris gallopavo* (OUVC 10599, scanned at OUmicroCT at 47.2 micron resolution), the grouse *Bonasa umbellus* (AMNH SKEL 21616, scanned at AMNH Microscopy and Imaging Facility at 34.9 micron resolution), and the odontophorid *Colinus virginianus* (AMNH SKEL 2310, scanned at AMNH Microscopy and Imaging Facility at 27.4 micron resolution). Endocasts for each of these specimens were generated using the same methods as for the fossil.

*Body mass estimation.*— Field et al. (2013) reported that maximum coracoid length showed the strongest correlation to body mass in Galliformes. In order to estimate the body mass of the *Centuriavis lioae* holotype individual we utilized Field et al's (2013) regression:

$$\ln(\text{mass}) = 3.06\,(\ln \text{coracoid length}) - 5.11$$

This yielded a mass estimate of 1.718kg.

*Phylogenetic analyses.*— In order to resolve the phylogenetic placement of *Centuriavis lioae*, we scored the new taxon into the morphological data matrix of Ksepka (2009). We added 16 new characters and two additional fossil taxa, the possible stem phasianid *Palaeortyx gallica* and the recently described crown phasianid *Panraogallus hezhengensis*. The expanded matrix contains 136 characters based on osteology, soft tissue anatomy, and reproductive biology and samples seven outgroup species (Lithornithiformes, Tinamiformes and Anseriformes), 55 extant species of Galliformes, and five fossil species of Galliformes. A list of extant specimens examined for scoring the matrix is provided in Ksepka (2009). *Palaeortyx gallica* and *Panraogallus hezhengensis* were scored from the literature.

In order to constrain the relationships of extant taxa, we applied a backbone constraint topology based on the results of a recent ML analysis of 2,208,355 bp of molecular sequence data from 4,817 concatenated UCE loci by Hosner et al. (2017). The backbone constraint contains the 38 extant species that overlap between the Ksepka et al. (2009) matrix and the Hosner et al. (2017) tree. The positions of the remaining 25 extant species (and all fossil species) were unconstrained. Parsimony analyses were conducted in PAUP*4.a168 (Swofford, 2002), using the heuristic search option and 10,000 replicates of random taxon addition with TBR branch swapping, with all characters equally weighted, multi-state codings treated as polymorphism, and branches of minimum length 0 collapsed. Instability in the position of *Panraogallus* resulted in poor resolution in the strict consensus tree, so we conducted an additional analysis with this taxon excluded.

*Repositories and institutional abbreviations.*— American Museum of Natural History (AMNH), New York, USA; Ohio University Vertebrate Collection (OUVC), Ohio, USA; Yale Peabody Museum of Natural History, New Haven, Connecticut, USA (YPM).

## Systematic Paleontology

Aves Linnaeus, 1758

Galliformes Temminck, 1820

Phasianidae Horsfield, 1821

*Centuriavis* new genus

Figures 1, 2, 3

*Type species.—Centuriavis lioae*

*Diagnosis.— Centuriavis lioae* can be differentiated from other fossil and extant North American Galliformes by the following combination of features: absence of fenestra mandibularis caudalis (versus presence in Tetraoninae), presence of a large pneumatic fossa in the area of the impressio m. sternocoracoidei of the coracoid (absent in Gallinuloididae and Odontophoridae), shallow cotylaris scapularis (deep in Gallinuloididae, Paraortygidae, and *Procrax*), medially deflected acromion (straight in Meleagridinae and Tetraoninae), absence of pneumatic foramina on the scapula (a foramen is always present on the dorsal surface of the facies articularis humeralis in *Meleagris ocellata* and variably present in *Meleagris gallopavo*, whereas a foramen is present between the acromion and facies articularis humeralis in Tetraoninae), presence of a distal projection of the articular surface

of the caput humeri which forms a ridge separating the fossa pneumotricipitalis dorsalis from the incisura capitis (absent in Gallinuloididae, Paraortygidae, and Quercymegapodiidae, separated by a faint ridge rather than a projection of the caput humeri in *Archaealectrornis* and *Archaeophasianus*), and moderately deep fossa pneumotricipitalis dorsalis (shallow in *Archaeophasianus*, Cracidae, and Meleagridinae; extremely deep in *Miortyx* and Odontophoridae). Only the coracoid can be directly compared with *Proagriocharis.* This bone differs in having a proximo-distally elongate scapular cotyle (circular in *Proagriocharis*) and smaller size: coracoid length equals 60.6mm in *Centuriavis* versus 66mm to 67.2mm in *Proagriocharis* (range due to different estimates for the same slightly damaged specimen reported by Martin and Tate [1970] and Steadman [1980]). Although no elements overlap directly, *Centuriavis* can be differentiated by larger size from *Rhegminornis* (inferred to be ~70-85% the size of *Centuriavis* based on the coracoid: tarsometatarsus proportions of *Proagriocharis*).

*Occurrence.*— Miocene of Nebraska.

*Etymology.*—From the Latin centuria (one hundred) referencing the history of the fossil, which despite exceptional preservation remained undescribed for nearly a century.

*Remarks.*—Although only a single species of *Centuriavis* is yet known, we divide the diagnosis into a genus level diagnosis comparing the new taxon to other North American Galliformes and a species diagnosis including finer level traits.

## *Centuriavis lioae* new species

Figures 1, 2, 3

*Holotype.*—AMNH FARB 8629, articulated partial skeleton preserving the skull, presacral vertebral series, synsacrum, furcula, complete left and partial right coracoid, scapulae, right and left humerus, right radius, right ulna, right radiale, damaged right ulnare, and isolated sesamoid.

*Diagnosis.*— Two potential autapomorphies diagnose *Centuriavis lioae*: Sharp ventral deflection of the crista deltopectoralis and presence of a foramen in the depressio ligamentosa on the caudal face of the radius. We note that a similar foramen was present in a single specimen of *Meleagris gallopavo* (AMNH 18704), but absent in all other observed specimens of that species as well as all other galliform taxa surveyed for this study.

*Occurrence.*— Machaerodus Quarry, Cherry County, Nebraska. This quarry exposes the Late Miocene Merritt Dam Member of the Ash Hollow Formation (Ogallala Group).

*Description.*—The remarkably well-preserved skull is exposed in right lateral view (Fig. 1). The beak is shorter proportional to overall skull length than in *Meleagris* (beak length varies greatly among Tetraoninae). The tip of the beak is downturned, but not hooked. The nares are sub-ovoid with a taller caudal border, which is a result of the descending process of the nasal extending almost directly ventrally rather than slanting in a more rostroventral

direction. The nares are relatively small as in the grouse *Tympanuchus* and *Lagopus*, whereas the nares are more elongated in *Meleagris* and most other grouse (e.g. *Dendragapus*, *Tetrao* and *Bonasa*). A thin internarial bar is formed by the nasal processes of the premaxillae, which maintain a clear sutural contact throughout their length. Caudally, the premaxillae intervene between the frontals for a short distance. The frontals are wide between the orbits, and are deeply depressed at midline. The skull roof is generally smooth, lacking the rugosities developed along the margin of the orbit in some individuals of *Meleagris* and in Tetraoninae. As in most Galliformes, the cranial tip of the jugal is slightly dorsally deflected and abuts the caudal margin of the nasal, which creates a "notch" between the jugal and the freely projecting caudal end of the maxilla. Although the lacrimal head has been displaced, it is clear that the caudal border projected into the orbit forming a gently rounded supraorbital spine as in *Pucrasia* and Tetraoninae (sharper in Meleagridinae). In most members of Phasianidae, the processus postorbitalis is elongated and fuses with the ossified aponeurosis zygomaticus in adults (see Zusi and Livesey, 2000). Broken edges indicate that both of these delicate structures are missing their distal ends, so it is not possible to discern whether they were fused in *Centuriavis*. A contact between these structures cannot be identified on the left side of the skull in the CT data, but the processus zygomaticus shows an open break at the distal preserved margin, and so we consider the presence or absence of a contact to be uncertain.

The right quadrate is partially obscured because it remains in articulation, but it can be observed that the orbital process of the quadrate is elongate as in most Phasianidae, as opposed to the greatly shortened process in Odontophoridae. A well-developed tuberculum subcapitulare is present as in other Galloanserae. As in other representatives of Phasianidae,

373 the cotyla quadratojugalis has a strongly projected caudal margin, creating a deep socket for
374 the quadratojugal (shallower in Odontophoridae). The left quadrate was digitally segmented
375 from the CT scan data (Fig. 2), revealing that the capitulum oticum and captitulum
376 squamosum are merged, a derived feature shared by Numididae, Odontophoridae, and
377 Phasianidae. The scans also confirm the presence of a foramen pneumaticum rostromediale
378 and absence of a pneumaticum caudomediale, as well as a bicondylar articulation for the
379 mandible.

380 The mandible is more strongly downcurved than in *Meleagris.* As in other
381 Phasianidae the symphysis is short. A fenestra mandibularis caudalis is absent as in
382 *Meleagris*, whereas a very large fenestra mandibularis caudalis is present in Tetraoninae.
383 As in most other Galloanserae, the processus retroarticularis is elongate and blade-like
384 (mediolaterally compressed).

385 Fifteen free vertebrae are present cranial to the notarium, which agrees with the
386 number observed in other crown Galliformes. The atlas and axis are obscured by the skull.
387 An osseous bridge connects the processus transversus to the processus articularis caudalis
388 in cervical vertebrae three and four. A strong midline ridge also projects from the ventral
389 surfaces of these vertebrae. This ridge is very weak in cervical vertebra five and absent in
390 cervical vertebrae six through nine (the ventral surfaces of more caudal vertebrae are
391 hidden). The thoracic vertebrae are mediolaterally thin, lack pneumatic foramina, and bear
392 cuplike cotylae for the thoracic ribs. At least the last two free thoracic vertebrae have a
393 strongly projected processus ventralis. A notarium is present and is formed by four fused
394 thoracic vertebrae. Each of these vertebrae bears a strongly projected ventral spine, and
395 those of the second and third vertebrae of the notarium fuse to enclose a round fenestra.

Ribs from the free thoracic vertebrae bear unfused uncinate processes. The ribs of the caudalmost two vertebrae of the notarium are intact, and both lack a pneumatic opening on the cranial face between the rami. The spike-like distal end of an additional rib, probably that of the 15th presacral vertebra, is partially visible. The synsacrum is rather poorly preserved. As in other galliforms the body of the synsacrum is rounded and expanded near the midpoint. The crista spinosa synsacri is quite thin.

A portion of the furcula is preserved, including both omal ends but lacking the apophysis. The omal portion of the scapus claviculae is subcylindrical as in Tetraoninae, unlike the condition in *Meleagris* where it is mediolaterally flattened and further bears a pneumatized excavation on the medial face. Likewise, at least along the intact portion, the scapus maintains uniform thickness as in Tetraoninae, rather than expanding as in *Meleagris* (Fig. 3.1).

Both scapulae are preserved in articulation and are subequal in length to the humerus. The acromion is medially deflected, in contrast to the straight condition in *Meleagris* and Tetraoninae (Fig. 5). The facies articularis humeralis is large and subcircular. No pneumatic foramina are present on the scapula. A pneumatic opening is present between the acromion and facies articularis humeralis in Tetraoninae (Fig 5.7) and present on the dorsal surface of the facies articularis humeralis in *Meleagris* (Fig 5.12). The scapular blade is curved with a thick ventral margin and a sharp dorsal margin. A small tubercle is located on the ventral margin of the scapula, as in most crown Galliformes. This differs from the condition in some Cracidae as well as in the stem galliform *Paraortygoides messelensis* in which this tubercle is placed on the lateral face of the scapula (see Mayr, 2000).

The complete left coracoid was freed from the matrix (Fig. 3.2 + 3.3). As in other crown Galliformes, the bone is slender, bears a flat facies articularis scapularis and lacks a processus procoracoideus and foramen nervi supracoracoidei. The processus acrocoracoideus is not hooked. On the dorsal surface of the coracoid, a large ovoid pneumatic fossa opens in the area of the impressio m. sternocoracoidei as in most phasianids (absent in quails, some partridges, and junglefowl). A pronounced lip bounds the facies articularis sternalis distally. The angulus medialis terminates in a rounded knob, which is present but shows substantial variation in development within extant Numididae and Phasianidae. The processus lateralis is short and triangular, more closely resembling the condition in *Meleagris* than the well-projected process in Tetraoninae or the rounded process in *Pucrasia*.

A well-developed fossa tricipitalis dorsalis excavates the humerus, steeply undercutting the head (Fig. 3.5). The depth of the fossa is similar to that in *Pucrasia* and most Tetraoninae (Fig. 5.1-5.3). *Meleagris* and some grouse taxa (*Tympanuchus* and *Centrocercus*) show a shallower fossa (Fig. 5.4), whereas Odontophoridae and many of the polyphyletic "partridges" (e.g., *Rollulus*, *Alectoris*, *Ammoperdix*) show a much deeper excavation. A deep incisura capitalis partially undercuts the head of the humerus. A strong ridge formed by the distal projection of the caput humeri separates the fossa pneumotricipitalis dorsalis from the incisura capitis as in other crown Galliformes. The fossa pneumotricipitalis is large, deep and subdivided by trabeculae. The sulcus ligamentous transversus is unusually deep and well defined. A distinct, slightly raised supracoracoideus scar marks the caudal face of the humerus. The crista deltopectoralis is strongly ventrally inturned and comes to a thick triangular point. The distal margin of the

crista deltopectoralis merges abruptly with the shaft so as to create a squared outline, contrasting with the typical condition in Phasianidae in which the crest merges more smoothly into the shaft. Along the caudal face of the shaft a thin, raised line marks the insertion of m. latissimus dorsi. As in most Phasianidae, the fossa m. brachialis is shallow. The tuberculum supracondylaris ventralis is a small, low triangular projection. The processus supracondylaris dorsalis takes the form of a low, compact process (more projected than in *Meleagris* and Tetraoninae). The epicondylaris ventralis bears a deep circular depression on its distal face. The processus flexorius is weakly projected.

The ulna is quite straight as preserved (Fig. 3.6+3.7), as opposed to the more bowed shape in Tetraoninae and *Pucrasia macrolopha* (*Meleagris gallopavo* shows significant variation). However, this may be at least in part an artifact of crushing. Though somewhat obscured by deformation, an ovoid impressio brachialis can be identified on the ventral face of the ulna. The impressio scapulotricipitalis is ovoid and slightly depressed. Feather papillae are weakly raised. The incisura tendinosa is essentially absent.

The radius is similar in general morphology to that of other Phasianidae (Fig. 3.8+3.9). The tuberculum bicipitale radii is strongly developed. A foramen opens within the depressio ligamentosa on the caudal face of the radius, which may represent an apomorphy of *Centuriavis lioae* provided it does not represent individual variation. Although this foramen is absent in almost all extant phasianid specimens we examined for this study, a similar foramen was noted in a single specimen of *Meleagris gallopavo* and two much smaller foramina were observed in this region in one specimen of *Centrocercus urophasianus*.

The radiale (Fig. 3.10+3.11) is slightly proportionally shorter in the proximo-distal dimension than in turkey or grouse. As in other crown galliforms, the dorsal end of the bone is unusually wide (Mayr, 2014). Only the crus breve of the ulnare is preserved, but it is too incomplete to provide informative observations.

A small element preserved in isolation appears to be a sesamoid ossification (Fig. 3.12). We observed a nearly identical element near the plantar surface of the tarsometatarsus, adjacent to the joint between the tibiotarsus and tarsometatarsus, in an articulated skeleton of *Lyrurus tetrix* (AMNH 12813). The distribution of this sesamoid across Phasianidae is difficult to establish as it is presumably easily lost during skeletonization of museum specimens, but we confirmed that it is present and similar in shape in disarticulated skeletons of *Meleagris gallopavo*.

*Etymology.*—In honor of Suzanne Lio, in recognition of her support for science and tireless efforts to advance the mission of the Bruce Museum.

*Remarks.*—We note that the specimen is embedded in a beige matrix. The red color was added at some stage between discovery of the fossil and the present study in an attempt to increase contrast between the bone and matrix.

cf. *Centuriavis lioae*

Figure 4

*Occurrence.— Machaerodus* Quarry, Cherry County, Nebraska.

*Description*.—An isolated humerus (Fig. 4.1-4.2) from the *Machaerodus* quarry closely resembles that of the *Centuriavis lioae* holotype, agreeing in general proportions, the well-developed fossa tricipitalis dorsalis, the characteristic shape of the crista deltopectoralis, and the weak processus supracondylaris dorsalis. The only notable difference is the slightly greater degree of curvature of the shaft. However, there is a prominent break line just proximal to midshaft, so it is possible the shape is exaggerated by postmortem deformation.

An isolated tarsometatarsus (Fig. 4.3-4.7) from the *Machaerodus* quarry represents another possible specimen of *Centuriavis lioae*. The bone is slender and elongated, resembling *Pucrasia* and modern turkeys in general proportions, as opposed to the stouter tarsometatarsus of grouse. It is substantially larger than that of *Rhegminornis calobates* holotype (distal width 13.5 mm versus 9.5 mm). The eminentia intercotylaris is strongly projected and the sulcus extensorius is deep and sharply bounded on its lateral and medial margins. The hypotarsus is monocanaliculate (*sensu* Mayr, 2016b) with a single canal for the tendon of m. flexor digitorum longus. This tendon is fully enclosed in a bony canal in almost all Phasianidae, but instead runs through a deep sulcus in a few grouse (e.g., *Tetrastes*). The crista medialis flexoris digitorum longus is the most strongly projected of the hypotarsal crests and is continuous with a sharply hooked distal projection. A low, sharp crest is present along the plantar-medial margin of the tarsometatarsus. There is no evidence of a spur, which is present in males in *Pucrasia* and Meleagridinae, but absent in both sexes in Tetraoninae.

In extant phasianids, an intratendinous ossification of m. gastrocnemius typically fuses to the distal margin of the crista medialis flexoris digitorum longus and the plantar face of the tarsometatarsus over the course of ontogeny (Hudson et al.,1965). We observed that in some immature birds, this ossification is completely separated from the tarsometatarsus, and in others it is fused to the crista medialis flexoris digitorum longus, but remains unfused to the plantar surface of the tarsometatarsus (Fig. 4.8). Thus we interpret the projection in the fossil as the partially ossified portion of m. gastrocnemius, and consider this indicative of immature status.

*Materials.*— AMNH FARB 8627, right humerus; AMNH FARB 8628, left tarsometatarsus. Measurements in Table 1.

*Remarks.*—These specimens were recovered in the same quarry and potentially represent additional individuals of *Centuriavis lioae*, to which we tentatively refer them. The humerus is approximately 88% the length of the holotype humerus. This difference is well within the range of sexual dimorphism observed in extant *Pucrasia*, Meleagridinae, and Tetraonidae (in which some species show almost no size dimorphism and others show substantial levels). It is plausible that the holotype individual of *Centuriavis lioae* was male and the smaller humerus belonged to a female individual. However, the possibility that AMNH FARB 8627 belongs to a second smaller phasianid species cannot be conclusively ruled out. The relative proportions of the humerus and tarsometatarsus vary dramatically in extant Phasianidae, with the tarsometatarsus being much shorter than the humerus in many extant grouse, nearly as long as the humerus in *Pucrasia*, and slightly longer than the

humerus in extant turkeys. We consider it more likely than not that the tarsometatarsus also belongs to *Centuriavis lioae*. However, because no major leg bones are preserved in the holotype, conclusive referral of AMNH FARB 8628 to this species or a separate taxon will have to await discovery of more complete associated specimens.

## Phasianid Neuroanatomy

Avian endocasts have been shown to be faithful proxies for the volume and surface morphology of the brain (Iwaniuk and Nelson, 2002; Watanabe et al., 2019; Early et al., 2020a). However, fossil endocasts remain relatively rare, as few avian fossils preserve the skull and in those that do, the braincase is often flattened so that no details of the endocast can be recovered. Thus, the well-preserved skull of *Centuriavis lioae* provides potentially valuable insight into galliform paleoneuroanatomy (Fig. 6).

Volumetric data for the *Centuriavis lioae* endocast were reported by Early et al. (2020b), who referred to the specimen as an unnamed Miocene galliform. The endocast is complete except for damage to the right optic lobe. In dorsal view, the cerebral hemispheres differ from those in all three sampled extant species in having a more circular shape, with less pronounced rostral tapering. As is typical of Galliformes (Bang and Cobb, 1968), the olfactory bulbs are small. The Wulst is strongly projected and most closely resembles that of *Meleagris*. In contrast, the Wulst is not as wide in *Bonasa* and only weakly projected in *Colinus* and in the Eocene-Oligocene phasianoid skull described by Mayr et al. (2021). Both extant phasianids and *Centuriavis* exhibit a pronounced vallecula running along the

lateral border of the Wulst, which furthermore shows caudal branching in *Meleagris* and *Bonasa*. In *Colinus*, the vallecula is not as well developed, which may be related at least in part to the smaller size of the endocast. The optic lobes in the *Centuriavis* endocast are well-developed and positioned almost entirely caudal to the widest point of the cerebral hemispheres. The degree of lateral projection (in ventral view) is similar to that in *Meleagris*, whereas the optic lobes project farther laterally in *Bonasa* and *Colinus*.

The cerebellum of *Centuriavis* is complete except for the caudal margin. The cerebellar folia are strongly defined, most similar to the condition in *Colinus.* The folia are slightly less well-defined in *Bonasa* and relatively poorly defined in *Meleagris*. A pronounced sinus occipitalis runs along the midline of the cerebellum in all four taxa sampled here, but is weaker in *Colinus* than in the phasianids. The floccular lobes are large and project from body of the cerebellum at an approximately 45-degree angle, and are intermediate in relative width to those of *Meleagris* and *Bonasa*.

## Phylogenetic Relationships

When the morphological dataset is analyzed without the backbone constraint, Gallinuloididae, Megapodidae, Cracidae, and Numididae are recovered on successive branches within Pan-Galliformes. A monophyletic Odontophoridae is nested within a large polytomy of phasianid taxa, rendering Phasianidae polyphyletic.

The primary phylogenetic analysis using the molecular backbone constraint from the Hosner et al. (2017) study resulted in 3,642 most parsimonious trees (MPTs) of 478

577 steps. Throughout the strict consensus tree (Fig. 7), placement of taxa via morphological
578 data appears to be largely consistent with molecular phylogenies of Galliformes.
579 Specifically, all sampled but unconstrained species of Megapodidae, Cracidae, Numididae,
580 Odontophoridae, and Phasianidae were recovered in their "correct" family (i.e. matching
581 their placement in molecular phylogenies with larger taxonomic samples). *Gallinuloides*
582 and *Paraortygoides* were recovered as stem landfowl and *Palaeortyx* was recovered as the
583 sister taxon to Odontophoridae + Phasianidae. *Centuriavis* and *Panraogallus* were
584 recovered within Phasianidae, as part of a large polytomy including turkeys, grouse,
585 *Pucrasia*, *Perdix*, and several other phasianids. This polytomy is primarily due to the
586 instability of *Panraogallus*, which is equally parsimonious to place as a stem turkey, a stem
587 grouse, or elsewhere in Phasianidae (e.g. as a close relative of *Chrysolophus*).
588 Following exclusion of *Panraogallus*, the second analysis resulted in 1,816 MPTs of
589 474 steps. In the strict consensus tree (Fig. 8), relationships are better resolved in
590 Phasianidae. *Centuriavis* is recovered as part of a polytomy with *Pucrasia* and a clade
591 uniting Tetraoninae + Meleagridinae. Due to incomplete preservation in *Centuriavis*,
592 substantial differences in skeletal anatomy of grouse and turkeys, and lack of resolution of
593 the position of *Centuriavis* relative to *Pucrasia*, only a single unambiguous character can be
594 resolved as a synapomorphy of the clade uniting *Pucrasia*, *Centuriavis*, Meleagridinae and
595 Tetraoninae. This character (60:1, furcula facet of coracoid with strong concavity in caudal
596 margin) is further secondarily reversed in Tetraoninae. The most convincing character
597 uniting turkeys and grouse to the exclusion of *Centuriavis* and *Pucrasia* is the shape of the
598 acromion (character 55), which is strongly medially deflected in *Centuriavis* and *Pucrasia*
599 as in most Phasianidae, but straight in grouse and turkeys (Fig. 4). Grouse and turkeys also

600 share complete fusion of the uncinate processes to the ribs (character 40: unfused in
601 *Centuriavis* and *Pucrasia*), though this feature is also convergently present in many other
602 phasianids. Because the femur is not preserved in *Centuriavis*, it is uncertain if limb bone
603 proportions (91:0, humerus exceeds femur in length) represent a synapomorphy of the
604 grouse + turkey clade or instead support a sister group relationship between *Centuriavis*
605 and the grouse + turkey clade to the exclusion of *Pucrasia*.
606 Monophyly of crown Meleagridinae is supported by nine unambiguous
607 synapomorphies in our results, most of which show some degree of homoplasy: (7:1)
608 lacrimal forming sharply projecting supraorbital spine (convergently evolved in several
609 other phasianid lineages), (43:1) scapus claviculae of furcula maintains uniform width near
610 omal end (convergently evolved in Pavoninae), (53:1) incisurae medialis et lateralis of
611 sternum shallow, (65:1) facies articularis sternalis of coracoid bounded by strong ridge
612 (convergently evolved in several other phasianid lineages), (68:0) weakly developed fossa
613 pneumotricipitalis dorsalis (convergently evolved in the grouse *Tympanuchus* and
614 *Centrocercus*, as well as *Polyplectron*), (93:1) crista cnemialis cranialis forming strong
615 triangular point in cranial view (convergently evolved in several other phasianid lineages),
616 (107:1) head largely featherless (also present in *Argusianus*), (126:1) presence of frontal
617 caruncle (snood), and (127:1) presence of a single neck wattle.
618 Monophyly of crown Tetraoninae is supported by nine unambiguous characters:
619 (29:1) presence of fenestra mandibularis caudalis (convergently evolved in *Perdix*,
620 *Ithaginus* and some Coturnicinae), (58:1) presence of a pneumatic foramen between the
621 acromion and facies articularis humeralis of the scapula (convergently evolved in
622 Pavoninae), (72:1) strong projection of the condylus ventralis of the humerus, (85:1)

623 reduction of the tuberculum preacetabulare (convergently evolved in *Arborophila*,
624 *Polyplectron, Ammoperdix*), (88:0) shallow recessus caudalis fossa of pelvis (convergently
625 evolved in *Rollulus* and some Coturnicinae), (89:1) wide and shallow ischium, (98:0) loss
626 of tarsometatarsal spur (convergently lost in Arborophilinae, *Perdix* and some
627 Coturnicinae), (120:1) feathered tarsus, and (123:1) presence of a fleshy comb above the
628 eye.

629 We were unable to fully resolve the phylogenetic position of *Panraogallus*. This
630 Miocene species is represented by an exceptional skeleton with intact tracheal rings
631 indicating the trachea was longer than the bird's entire body (Li et al.,2018). Elongated
632 trachea occur today in the extant grouse *Tetrao urogallus* and *Lagopus mutus*, many
633 Cracidae, and the numidid *Guttera plumifera*. It is tempting to speculate that *Panraogallus*
634 falls close to the grouse + turkey clade, as it shares an unhooked acromion with these taxa.
635 Unfortunately, key features of the humerus and pelvis are obscured by preservation in
636 *Panraogallus*, precluding better resolution of its phylogenetic affinities. Interestingly, the
637 alular digit bears a distal phalanx in most Phasianidae, with development varying from a
638 claw-like element (e.g., in Pavoninae) to a rudimentary button-like ossicle (e.g., in *Perdix*
639 and *Pucrasia*). We found this claw to be absent in grouse and in all *Meleagris gallopavo*
640 specimens we examined. However, we observed a rudimentary claw in some specimens of
641 *Meleagris ocellata*. There is no distal phalanx preserved in *Panraogallus*, which would be
642 consistent with a placement as a stem member of either the grouse or grouse + turkey
643 lineage. However, because this small element is easily lost in macerated skeletons, the
644 possibility it was not preserved (or even destroyed during preparation) in the fossil cannot
645 be ignored.

Resolving the relationships of the small fossil galliform *Palaeortyx gallica* provides additional information on the timing of the galliform radiation. Oligocene specimens of *Palaeortyx* potentially represent the oldest record of crown Galliformes, pending better material of some poorly known taxa. Similarities in the humerus morphology of *Palaeortyx* and modern New World quail led Milne-Edwards (1867–1871) to assign the fossil taxon to Odontophoridae. As understanding of galliform phylogeny has improved, it has become clear that these similarities are likely either primitive or convergent features. Mayr et al. (2006) hypothesized that *Palaeortyx* instead represents the sister taxon to Odontophoridae and Phasianidae. Zelenkov (2019) argued for a more nested position, depicting *Palaeortyx* as the sister taxon to crown Phasianidae. Our results support the more stemward placement, resolving *Palaeortyx* as sister taxon to Odontophoridae + Phasianidae. Characters supporting the sister group relationship between *Palaeortyx* and Odontophoridae + Phasianidae include (53:1) deep incisurae in caudal margin of sternum and (76:1) presence of a large processus intermetacarpalis. However, *Palaeortyx* retains primitive limb bone proportions that support its exclusion from total-group Phasianidae. As in Anseriformes, stem Galliformes, most Megapodidae, Cracidae, and most Numididae, the humerus of *Palaeortyx* is longer than the femur (90:0), albeit only slightly so. In contrast, the femur is longer than the humerus in Odontophoridae and almost all Phasianidae, the exceptions being very large species such as turkeys, grouse, and some peafowl. In addition, the sulcus for the tendon of m. flexor hallucis longus faces plantarly in *Palaeortyx*, as in Megapodidae, Cracidae, and Numididae (character state 95:0), whereas this sulcus is oriented laterally and bounded by a well-developed crest in Odontophoridae and most Phasianidae (Mayr, 2015). In favor of the more nested placement, Zelenkov (2019) noted

669 that the proximal margin of the rim of the trochlea carpalis is only weakly notched in
670 Odontophoridae, whereas it is more strongly notched in *Palaeortyx* and Phasianidae. In our
671 matrix, character 74 only considers the presence or absence of this notch, which we scored
672 as "present" in Odontophoridae, *Palaeortyx*, and Phasianidae. However, we note that
673 editing our scoring for Odontophoridae to "absent" to reflect this alternate interpretation
674 does not alter the result of the phylogenetic analysis.
675

676 ## Discussion

677

678 Through a combination of territoriality and inattention to basic taxonomic research,
679 a large number of important avian fossils linger unstudied in museum collections. Despite
680 its exquisite preservation, the holotype of *Centuriavis lioae* remained undescribed for
681 nearly a century. Formal description of the species opens a window into the assembly of the
682 modern North American landfowl fauna. As with many avian clades, there is growing
683 evidence for the replacement of stem taxa by crown taxa close to the Paleogene-Neogene
684 boundary. The Paleogene stem fauna included large gallinuloidids and smaller, enigmatic
685 taxa. It is tempting to equate these groups to the large grouse and turkeys and to the small
686 New World Quail, respectively, of the modern North American avifauna. However, this
687 would be premature since gallinuloidids likely had different dietary preferences than
688 modern landfowl (Mayr and Weidig, 2004) and the smaller taxa are known only from
689 fragmentary remains that obscure their paleocology. Whatever their ecological roles, these
690 stem taxa were replaced by a modern fauna composed of Cracidae, Odontophoridae,
691 Meleagridinae, and Tetraoninae. A more complete understanding of the evolution of the

692 North American galliform fauna will require a combination of new collecting efforts to fill
693 in the substantial gaps in the stratigraphic record and resolve the affinities of poorly known
694 taxa like *Nanortyx* and *Rhegminornis*, and re-examination of material already in collections
695 such as *Procrax*.

696 Although the precise position of *Centuriavis* relative to *Pucrasia* remains uncertain,
697 the occurrence of *Centuriavis* in North American leads us to prefer a placement as sister
698 taxon to Tetraoninae + Meleagridinae. This hypothesis is consistent with a dispersal event
699 from Asia into North America prior to the divergence between grouse and turkeys. Previous
700 results have suggested such a dispersal event may have occurred in the Early Miocene
701 based on molecular divergence dates, with some grouse lineages later dispersing back and
702 forth between North America and Europe (Persons et al.,2016; Wang et al.,2017). These
703 analyses, however, included only extant taxa. Pliocene-Pleistocene fossils, albeit often
704 highly incomplete, have been assigned to *Tetrao*, *Lagopus*, and *Bonasa* (e.g. Jánossy, 1974;
705 Tyrberg, 1998; Boev, 2002; Marco, 2009). In particular, if putative European fossil records
706 of the basally diverging *Bonasa* are correctly identified to that genus (rather than perhaps
707 representing the similar *Tetrastes*), the possibility of a Eurasian origin of both Tetraoninae
708 and the Tetraoninae + Meleagridinae clade would bear consideration. Under either
709 biogeographic scenario, *Centuriavis lioae* would be too young to be a plausible ancestor of
710 turkey and grouse, suggesting it may represent a more basally diverging taxon that
711 coexisted with early grouse and turkeys.

712 Turkeys and large grouse such as capercaillies and Black Grouse (*Tetrao*) are among
713 the heaviest of all volant birds. The estimated body mass of *Centuriavis lioae* is ~1.7kg,
714 which falls close to the average size for females of the Greater Sage-Grouse based on

values reported by Dunning at al. (2008). It thus exceeds most extant grouse but falls short of the sizes observed in the largest grouse species and extant turkeys. Turkeys and most grouse exhibit polygynous breeding, whereas the small *Tetrastes* (hazel grouse) and *Lagopus* (ptarmigans), as well as *Pucrasia*, are monogamous breeders (De Juana, 1994; Porter, 1994). Any reconstruction of the breeding system of *Centuriavis lioae* would be speculative at this stage, though if the additional specimens confirm that the smaller referred humerus belongs to the species, it would be consistent with significant sexual dimorphism.

## Acknowledgements

We thank Mark Norell for permitting access and permission to scan the specimen, Carl Mehling and Ruth O'Leary for facilitating loan of the holotype, and Mick Ellison for photography at the AMNH. We also thank Dan Brinkman, Rick Prum, Vanessa Rhue, and Kristof Zyskowski (YPM), Helen James and Chris Milensky (USNM), Zhiheng Li (IVPP) for providing images of *Panraogallus,* and David Steadman (FLMNH) for access to comparative material, and Ruger Porter and Larry Witmer (OU) for access to *Meleagris* scans. We thank the AMNH Microscopic and Imaging Facility for providing support for microCT scanning. This work was funded in part by NSF award DEB 1655736 (to D.T.K.), NSF GRFP DGE1060934 and DGE 1645419 (to C.M.E.), and NSF DEB 1801224 (to A.M.B.).

## Accessibility of supplemental data

The morphological matrix utilized in this study is available as a supplemental data file.

738

739

740 ## References


741 Balanoff, A.M., Bever, G.S., Colbert, M.W., Clarke, J.A., Field, D.J., Gignac, P.M., Ksepka, D.T.,
742 Ridgely, R.C., Smith, N.A., Torres, C.R., Walsh, S., and Witmer, L.M., 2016, Best
743 practices for digitally constructing endocranial casts: examples from birds and their
744 dinosaurian relatives: J Anat, v. 229, p. 173-190.

745 Bang, B., and Cobb, S., 1968, The size of the olfactory bulb in l08 species of birds: Auk, v. 85, p.
746 55-61.

747 Boev, Z. N., 2002, Tetraonidae Vigors, 1825 (Galliformes - Aves) in the Neogene-Quaternary
748 record of Bulgaria and the origin and evolution of the family: Acta Zoologica Cracoviensia,
749 v. 45, p. 263-282.

750 Boon, W.-M., Robinet, O., Rawlence, N., Bretagnolle, V., Norman, J. A., Christidis, L., and
751 Chambers, G. K., 2008, Morphological, behavioural and genetic differentiation within the
752 Horned Parakeet (*Eunymphicus cornutus*) and its affinities to *Cyanoramphus* and
753 *Prosopeia*: Emu, v. 108, p. 251-260.

754 Bocheński, Z. M., and Campbell, K. E., 2006, The extinct California turkey, *Meleagris californica*,
755 from Rancho La Brea: comparative osteology and systematics: Contributions in Science of
756 the Natural History Museum of Los Angeles County v. 509, p 1-92.

757 Brodkorb, P., 1964, Catalog of Fossil Birds. Part 2 (Anseriformes through Galliformes): Bulletin of
758 the Florida State Museum Bcciological Sciences, v. 8, p. 195-335.

759 Clarke, J. A., 2004, Morphology, phylogenetic taxonomy, and systematics of *Ichthyornis* and
760 *Apatornis* (Avialae: Ornithurae): Bulletin of the American Museum of Natural History, v.
761 2004, p. 1-179.
762 Crowe, T. M., Bowie, R. C. K., Bloomer, P., Mandiwana, T. G., Hedderson, T. A. J., Randi, E.,
763 Pereira, S. L., and Wakeling, J., 2006, Phylogenetics, biogeography and classification of,
764 and character evolution in, gamebirds (Aves: Galliformes): effects of character exclusion,
765 data partitioning and missing data: Cladistics, v. 22, p. 495-532.
766 Crowe, T. M., and Short, L. L., 1992, A new gallinaceous bird from the Oligocene of Nebraska,
767 with comments on the phylogenetic position of Gallinuloididae: Natural History Museum
768 of Los Angeles County, Science Series v. 36, p. 179-185.
769 De Juana, E., 1994, Family Tetraonidae (grouse), pp In: , *in* del Hoyo, J., Elliot, A., and Sargatal,
770 J., eds., Handbook of the Birds of the World Volume 2: New World Vultures to
771 Guineafowl : Barcelona, Lynx Edicions, p. 376-411.
772 Del Hoyo, J., Elliot, A., and Sargatal, J., 1994, Handbook of the Birds of the World Volume 2:
773 New World Vultures to Guineafowl, Barcelona, Lynx Edicions, 638p.
774 Dimcheff, D. E., Drovetski, S. V., and Mindell, D. P., 2002, Phylogeny of Tetraoninae and other
775 galliform birds using mitochondrial 12S and ND2 genes: Molecular phylogenetics and
776 evolution, v. 24, p. 203-215.
777 Drovetski, S. V., 2003, Plio-Pleistocene climatic oscilations, Holarctic biogeography and
778 speciation in an avian subfamily: Journal of Biogeography, v. 30, p. 1173-1181.
779 Dunning Jr., J. B., 2008, CRC Handbook of Avian Body Masses, 2nd Edition, Boca Raton, CRC
780 Press, 666p.

781 Dyke, G. J., Gulas, B. E., and Crowe, T. M., 2003, Suprageneric relationships of galliform birds
782 (Aves, Galliformes): a cladistic analysis of morphological characters: Zoological Journal of
783 the Linnean Society, v. 137, p. 227-244.
784 Early, C. M., Iwaniuk, A. N., Ridgely, R. C., and Witmer, L. M., 2020a, Endocast structures are
785 reliable proxies for the sizes of corresponding regions of the brain in extant birds: Journal
786 of Anatomy, v. 237, p. 1162-1176.
787 Early, C. M., Ridgely, R. C., and Witmer, L. M., 2020b, Beyond endocasts: using predicted brain-
788 structure volumes of extinct birds to assess neuroanatomical and behavioral inferences:
789 Diversity, v. 12, p. 34.
790 Emslie, S. D., 1998, Avian community, climate, and sea-level changes in the Plio-Pleistocene of
791 the Florida peninsula: Ornithological Monographs, v. 50, p. 1-113.
792 Elzanowski, A., Paul, G. S., and Stidham, T. A., 2001, An avian quadrate from the Late Cretaceous
793 Lance formation of Wyoming: Journal of Vertebrate Paleontology, v. 20, p. 712-719.
794 Fremd, T. J., 2010, Guidebook: SVP Field Symposium 2010 John Day Basin Field Conference.
795 Gill, F., Donsker, D., Rasmussen, P., and . 2021, IOC World Bird List. 202:
796 https://www.worldbirdnames.org/new/.
797 Horsfield, T., 1821, XIV. Systematic arrangement and description of birds from the island of Java:
798 Transactions of the Linnean Society of London, v. 1, p. 133-200.
799 Hosner, P. A., Tobias, J. A., Braun, E. L., and Kimball, R. T., 2017, How do seemingly non-vagile
800 clades accomplish trans-marine dispersal? Trait and dispersal evolution in the landfowl
801 (Aves: Galliformes): Proceedings of the Royal Society B: Biological Sciences, v. 284, p.
802 20170210.

803 Hudson, G. E., Wang, S. Y. C., and Provost, E. E., 1965, Ontogeny of the supernumerary
804 sesamoids in the leg muscles of the ring-necked pheasant: The Auk, v. 82, p. 427-437.
805 Iwaniuk, A., and Nelson, J., 2002, Can Endocranial volume be used as an estimate of brain size in
806 birds?: Canadian Journal of Zoology, v. 80, p. 16-23.
807 Iwaniuk, A. N., and Wylie, D. R. W., 2006, The evolution of steropsis and the Wulst in
808 caprimulgiform birds: a comparative analysis: Journal of Comparative Physiology A, v.
809 192, p. 1313-1326.
810 Jánossy, D., 1974, Die mittelpleistozäne Vogelfauna von Hundsheim (Niederösterreich):
811 Sitzungsberichte der Österreichischen Akademie der Wissenschaften, Mathematisch-
812 Naturwissenschftliche Klasse, Abteilung I, v. 182, p. 211-257.
813 Johnsgard, P. A., 1986, The Pheasants of the World, Oxford, Oxford University Press.
814 Kaiser, V. B., van Tuinen, M., and Ellegren, H., 2007, Insertion events of CR1 retrotransposable
815 elements elucidate the phylogenetic branching order in galliform birds: Molecular biology
816 and evolution, v. 24, p. 338-347.
817 Kan, X., Yang, J., Li, X., Chen, L., Lei, Z., Wang, M., Qian, C., Gao, H., and Yang, Z., 2010,
818 Phylogeny of major lineages of galliform birds (Aves: Galliformes) based on complete
819 mitochondrial genomes.
820 Kimball, R. T., and Braun, E. L., 2008, A multigene phylogeny of Galliformes supports a single
821 origin of erectile ability in non-feathered facial traits: Journal of Avian Biology, v. 39, p.
822 438-445.
823 Kimball, R., Braun, E., Zwartjes, P., Crowe, T., and Ligon, J., 1999, A molecular phylogeny of the
824 pheasants and partridges suggests that these lineages are not monophyletic: Molecular
825 phylogenetics and evolution, v. 11, p. 38-54.

826 Kimball, R. T., Mary, C. M. S., and Braun, E. L., 2011, A macroevolutionary perspective on
827 multiple sexual traits in the Phasianidae (Galliformes): International Journal of
828 Evolutionary Biology, v. 2011.
829 Kriegs, J. O., Matzke, A., Churakov, G., Kuritzin, A., Mayr, G., Brosius, J., and Schmitz, J., 2007,
830 Waves of genomic hitchhikers shed light on the evolution of gamebirds (Aves:
831 Galliformes): BMC Evolutionary Biology, v. 7, p. 1-11.
832 Ksepka, D. T., 2009, Broken gears in the avian molecular clock: new phylogenetic analyses
833 support stem galliform status for *Gallinuloides wyomingensis* and rallid affinities for
834 *Amitabha urbsinterdictensis*: Cladistics, v. 25, p. 173-197.
835 Lander, E. B., 2008, Early Clarendonian (late middle Miocene) fossil land mammal assemblages
836 from the Lake Mathews Formation, Riverside County, southern California, and a
837 preliminary review of Merychyus (Mammalia, Artiodactyla, Oreodontidae): Geology and
838 Vertebrate Paleontology of Western and Southern North America: Contributions in Honor
839 of David P. Whistler. Natural History Museum of Los Angeles County Science Series, v.
840 41, p. 181-212.
841 Li, Z., Clarke, J. A., Eliason, C. M., Stidham, T. A., Deng, T., and Zhou, Z., 2018, Vocal
842 specialization through tracheal elongation in an extinct Miocene pheasant from China:
843 Scientific Reports, v. 8, p. 8099.
844 Linnaeus, C., 1758, Systema naturæ per regna tria naturæ, secundum classes, ordines, genera,
845 species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima,
846 reformata, Holmiæ, Salvius, 824 p.
847 Marco, A. S., 2009, New Iberian galliforms and reappraisal of some Pliocene and Pleistocene
848 Eurasian taxa: Journal of Vertebrate Paleontology, v. 29, p. 1148-1161.

849 Marsh, O. C., 1877, New fossil vertebrates.: American Journal of Science, v. 14, p. 249-256.
850 Martin, L. D., and Tate, J., 1970, A new turkey from the Pliocene of Nebraska: The Wilson
851 Bulletin, v. 82, p. 214-218.
852 Mayr, G., 2000, A new basal galliform bird from the Middle Eocene of Messel (Hessen,
853 Germany): Senckenbergiana Lethaea, v. 80, p. 45-57.
854 Mayr, G., 2009, Paleogene Fossil Birds, Heidelberg, Springer, 262 p.
855 Mayr, G., 2014, Comparative morphology of the radial carpal bone of neornithine birds and the
856 phylogenetic significance of character variation: Zoomorphology, v. 133, p. 425-434.
857 Mayr, G., 2016q, Avian evolution: the fossil record of birds and its paleobiological significance,
858 John Wiley & Sons.
859 Mayr, G., 2016b, Variations in the hypotarsus morphology of birds and their evolutionary
860 significance: Acta Zoologica, v. 97, p. 196-210.
861 Mayr, G., Goedert, J. L., and Rabenstein, R., 2022, Cranium of an Eocene/Oligocene
862 pheasant-sized galliform bird from western North America, with the description of a
863 vascular autapomorphy of the Galliformes: Journal of Ornithology, v. 163, p 315-326.
864 Mayr, G., Poschmann, M., and Wuttke, M., 2006, A nearly complete skeleton of the fossil
865 galliform bird Palaeortyx from the late Oligocene of Germany: Acta Ornithologica, v. 41,
866 p. 129-135.
867 Mayr, G., and Weidig, I., 2004, The Early Eocene bird *Gallinuloides wyomingensis*—a stem group
868 representative of Galliformes: Acta Palaeontologica Polonica, v. 49, p. 211-217.
869 Milne-Edwards, A., 1867-1871, Recherches anatomiques et paléontologiques pour servir à
870 l'histoire des oiseaux fossiles de la France, Paris, Masson, 627 p.

871 Mourer-Chauviré, C., 1992, Les Galliformes (Aves) of Phosphorites du Quercy (France)
872 Systematics and Biostratigraphy: Natural History Museum of Los Angeles County Science
873 Series, v. 36, p. 37-95.
874 Olson, S. L., 1985, The fossil record of birds, *in* Farner, D. S., King, J. R., and Parkes, K. C., eds.,
875 Avian Biology, Volume 8: New York, Academic Press, p. 79-238.
876 Olson, S. L., and Farrand Jr, J., 1974, *Rhegminornis* restudied: a tiny Miocene turkey: The Wilson
877 Bulletin, p. 114-120.
878 Persons, N. W., Hosner, P. A., Meiklejohn, K. A., Braun, E. L., and Kimball, R. T., 2016, Sorting
879 out relationships among the grouse and ptarmigan using intron, mitochondrial, and ultra-
880 conserved element sequences: Molecular Phylogenetics and Evolution, v. 98, p. 123-132.
881 Porter, W. F., 1994, Family Meleagrididae (turkeys), *in* del Hoyo, J., Elliot, A., and Sargatal, J.,
882 eds., Handbook of the Birds of the World Volume 2: New World Vultures to Guineafowl:
883 Barcelona, Lynx Edicions, p. 364-375.
884 Shufeldt, R. W., 1915, Fossil birds in the Marsh Collections of Yale University: Transactions of
885 the Connecticut Academy of Arts and Sciences, v. 19, p. 1-110.
886 Sibley, C. G., and Ahlquist, J. E., 1990, Phylogeny and Classification of Birds: A Study in
887 Molecular Evolution, New Haven, Yale University Press, 976 p.
888 Steadman, D. W., 1980, A review of the osteology and paleontology of turkeys (Aves:
889 Meleagridinae): Contributions in Science, Natural History Museum of Los Angeles County,
890 v. 330, p. 131-207.
891 Stidham, T. A., 2011, The carpometacarpus of the Pliocene turkey Meleagris leopoldi
892 (Galliformes: Phasianidae) and the problem of morphological variability in turkeys:
893 PaleoBios, v. 30, p. 13-17.

894 Stidham, T. A., Townsend, K., and Holroyd, P. A., 2020, Evidence for wide dispersal in a stem
895 galliform clade from a new small-sized Middle Eocene Pangalliform (Aves: Paraortygidae)
896 from the Uinta Basin of Utah (USA): Diversity, v. 12, no. 3, p. 90.
897 Swofford, D. L., 2003, PAUP*. Phylogenetic Analysis Using Parsimony (* and Other Methods):
898 Sunderland, Sinauer Associates.
899 Tedford, R. H., Albright III, L. B., Barnosky, A. D., Ferrusquia-Villafranca, I., Hunt Jr, R. M.,
900 Storer, J. E., Swisher III, C. C., Voorhies, M. R., Webb, S. D., and Whistler, D. P., 2004,
901 Mammalian biochronology of the Arikareean through Hemphillian interval (late Oligocene
902 through early Pliocene epochs): Late Cretaceous and Cenozoic Mammals of North
903 America: Biostratigraphy and Geochronology. Columbia University Press, New York, p.
904 169-231.
905 Temminck, C. J., . M, 1820, anuel d'ornithologie, ou tableau systématique des oiseaux qui se
906 trouvent en Europe: precédé d'une analyse du système général d'ornithologie, et suivi d'une
907 table alphabétique des espèces, Dufour.
908 Tordoff, H. B., 1951, A quail from the Oligocene of Colorado: The Condor, v. 53, p. 203-204.
909 Tordoff, H. B., and MacDonald, J., 1957, A new bird (family Cracidae) from the early Oligocene
910 of South Dakota: The Auk, v. 74, p. 174-184.
911 Tyrberg, T., 1998, Pleistocene birds of the palearctic: a catalogue, Cambridge, Publications of the
912 Nuttall Ornithological Club.
913 Wang, N., Kimball, R. T., Braun, E. L., Liang, B., and Zhang, Z., 2013, Assessing phylogenetic
914 relationships among Galliformes: a multigene phylogeny with expanded taxon sampling in
915 Phasianidae: PloS one, v. 8, p. e64312.

916 Watanabe, A., Gignac, P. M., Balanoff, A. M., Green, T. L., Kley, N. J., and Norell, M. A., 2019,
917 Are endocasts good proxies for brain size and shape in archosaurs throughout ontogeny?:
918 Journal of anatomy, v. 234, p. 291-305.
919 Weigel, R. D., 1963, Oligocene birds from Saskatchewan: Quarterly Journal of the Florida
920 Academy of Sciences, v. 26, p. 257-262.
921 Wetmore, A., 1943, Fossil birds from the Tertiary deposits of Florida: Proceedings of the New
922 England Zoological Club, v. 22, p. 59-68.
923 Wetmore, A., 1956, A fossil guan from the Oligocene of South Dakota: Condor, v. 58, p. 234-235.
924 Zelenkov, N. V., and Panteleyev, A. V., 2019, A small stem-galliform bird (Aves: Paraortygidae)
925 from the Eocene of Uzbekistan: Comptes Rendus Palevol, v. 18, p. 517-523.
926 Zusi, R. L., and Livezey, B. C., 2000, Homology and phylogenetic implications of some enigmatic
927 cranial features in galliform and anseriform birds: Annals of Carnegie Museum, v. 69, p.
928 157-193.

## Appendix: Phylogenetic character list (newly added characters marked with asterisk)

*Osteology*

1. Rostrum: (0) dorsoventrally shallow; (1) dorsoventrally deep.

2. Beak, spatulate shape in dorsal view: (0) absent; (1) present.

3. Width of pila supranasalis between external nares: (0) wide; (1) narrow.

4*. Premaxilla, processus nasalis: (0) divides rostral portion of frontal; (1) does not divide rostral portion of frontal.

5*. Premaxilla, processus nasalis: (0) left and right premaxilla remain separate along midline of internarial bar; (1) left and right premaxilla fused along internarial bar.

6. Nasal septum: (0) absent; (1) present.

7. Lacrimal, processus supraorbitalis: (0) no caudal projection into orbit, or weak and blunt projection; (1) forms a sharp spine projecting into orbit.

8. Lacrimal, facies articularis frontonasalis in dorsal view: (0) contact with frontal forms a straight suture; (1) lacrimal occupies a notch in lateral margin of frontal.

9. Ectethmoid: (0) present; (1) highly reduced or lost.

10. Maxillopalatine shelf: (0) absent; (1) present.

11. Palatine and pterygoid: (0) fused; (1) separate.

12. Processus postorbitalis: (0) short; (1) greatly elongated.

13. Processus zygomaticus: (0) well-developed; (1) absent or poorly-developed; (2) processus zygomaticus short, but continuous with well-ossified aponeurosis zygomatica which extends rostral to near or beyond the level of the postorbital process.

14. Processus postorbitalis and processus zygomaticus (including aponeuroses if present): (0) unfused; (1) fused distally.

15. Rounded flange projecting ventrally from dorsal margin of tympanic region: (0) absent or weak; (1) strongly developed. See Figure 7 of Ksepka (2009).

16. Processus basipterygoideus: (0) long and arising caudally; (1) short and arising rostrally on parasphenoid rostrum.

17. Quadratojugal-quadrate articulation: (0) quadratojugal articulates at the level of the ventral extent of the condylus caudalis; (1) quadratojugal articulates well dorsal to the level of the condylus caudalis.

18*. Quadrate, cotylaris quadratojugalis: (0) complete; (1) with notch in caudal rim.

19*. Quadrate, capitulum oticum and captitulum squamosum: (0) widely separated; (1) nearly in contact, (2) merged.

20. Quadrate, processus orbitalis: (0) short; (1) long.

21*. Quadrate, strongly projected tubercle on caudal surface of processus oticus, just dorsal of processus mandibularis: (0) absent; (1) present.

22*.Quadrate, tubercle on ventral margin of processus opticus: absent (0); present (1).

23*. Quadrate, foramen pneumaticum caudomediale: (0) absent; (1) present.

24*. Quadrate, foramen pneumaticum rostromediale: (0) absent; (1) present.

25*. Quadrate, foramen pneumaticum basiorbitale: (0) absent; (1) present.

26*. Quadrate, articulation for mandible: (0) three condyles; (1) bicondylar.

27. Mandible, processus coronoideus: (0) absent or poorly developed; (1) strongly projected.

28. Mandible, deep groove on ventral surface of symphysis: (0) absent; (1) present .

29. Mandible, fenestra mandibularis caudalis: (0) absent; (1) present.

30. Mandible, two strong grooves on ventral surface of symphysis: (0) absent; (1) present.

31*. Mandible, processus retroarticularis: (0) absent; (1) present.

32*. Mandible, processus retroarticularis: (0) unhooked; (1) hooked.

33*. Mandible, processus retroarticularis: (0) narrow; (1) blade-like (dorsoventally tall), but short; (2) blade-like and elongated.

34. Axis, foramina transversaria: (0) absent; (1) present.

35. Cervical vertebrae 3 and 4, bony bridge from processus transversus to processus articularis caudalis: (0) absent; (1) present.

36. Thoracic vertebrae, lateral pneumatic fossa: (0) absent; (1) present.

37. Notarium, degree of fusion of thoracic vertebrae: (0) partial; (1) complete.

38. Notarium, number of incorporated vertebrae: (0) four or less; (1) five.

39. Synsacrum, processes transversus of sacral vertebrae at level of acetabulum forming dorsoventrally tall lamina that contacts the medial margin of acetabulum: (0) absent; (1) present.

40. Processus uncinatus: (0) fused to ribs; (1) not fused to ribs; (2) absent.

41. Furcula: (0) U-shaped; (1) V-shaped.

42. Furcula, scapus claviculae: (0) stout; (1) slender.

43. Furcula, scapus claviculae: (0) widening towards extremitas omalis; (1) of uniform thickness (1).

44. Furcula, apophysis furculae: (0) small or obsolete; (1) pronounced projection.

45. Sternum, spina interna: (0) absent; (1) present.

46. Sternum, spina externa: (0) absent; (1) present.

47. Sternum, processus craniolateralis: (0) perpendicular to carina; (1) oriented at angle of 45 degrees with respect to carina; (2) parallel to carina. Ordered.

48. Sternum, processus craniolateralis: (0) short; (1) moderate length; (2) long. Ordered.

49. Sternum, processus craniolateralis: (0) wide; (1) moderate width; (2) narrow.

50. Sternum, apex carinae: (0) extends far cranially; (1) shifted caudally.

51. Sternum, marked sulcus along cranial face of carina: (0) absent; (1) present.

52. Sternum, caudal incisurae: (0) single; (1) double.

53. Sternum, incisurae medialis et lateralis: (0) shallow; (1) deep.

54. Sternum, caudal margin: (0) wide; (1) tapering.

55. Scapula, acromion: (0) medially deflected; (1) straight.

56. Scapula, facies articularis humeralis: (0) parallel to corpus scapulae; (1) acute with respect to corpus.

57. Scapula, pneumatic foramen piercing dorsal surface of facies articularis humeralis: (0) absent; (1) present.

58. Scapula, pneumatic foramen between acromion and facies articularis humeralis: (0) absent; (1) present.

59. Coracoid, cotyla scapularis: (0) cup-like, deeply excavated; (1) shallow.

60*. Coracoid, facies articularis furcularis: (0) round; (1) notched, with concavity in caudal margin.

61. Coracoid, distinctly projected processus procoracoideus: (0) absent; (1) present.

62. Coracoid, foramen nervi supracoracoidei: (0) present; (1) absent.

63. Coracoid, blunt ventral projection at omal end, adjacent to facies articularis clavicularis: (0) absent; (1) present.

64. Coracoid, distinct fossa pneumaticum on dorsal surface: (0) absent; (1) present.

65. Coracoid, facies articularis sternalis: (0) grades smoothly into dorsal surface of shaft; (1) bordered dorsally by a strong raised lip.

66. Coracoid, processus lateralis: (0) rounded, with weak projection; (1) pointed, with strong projection.

67. Humerus, crista bicipitalis in cranial view: (0) rounded; (1) squared.

68. Humerus, fossa pneumotricipitalis dorsalis (0) rudimentary or absent; (1) moderately developed; (2) strongly developed, forming deep excavation. Ordered. *Panraogallus* was coded 0/1 as the state is uncertain due to preservation (see Li et al.,2018).

69. Humerus, caudal surface, foramen pneumaticum: (0) small; (1) large; (2) absent. State (2) was added to represent the apomorphic condition in *Palaeortyx*.

70. Humerus, elongate raised crest on shaft, distal to tuberculum dorsale (this crest represents an accessory insertion of the tendon of m. supracoracoideus): (0) absent; (1) present.

71 Humerus, incisura capitis: (0) continuous with fossa tricipitalis dorsalis; (1) separated from fossa tricipitalis dorsalis by a ridge.

72. Humerus, distal extent of condylus ventralis in cranial view: (0) not markedly extended distally; (1) markedly protrudes distally.

73. Ulna: (0) shorter or equal to humerus in length; (1) longer than humerus.

74. Carpometacarpus, ventral face, proximal margin of rim of trochlea carpalis: (0) smoothly rounded; (1) with small notch.

75. Carpometacarpus, spatium intermetacarpale: (0) narrow; (1) wide.

76. Carpometacarpus, processus intermetacarpalis: (0) absent; (1) present and overlapping metacarpal III.

77. Carpometacarpus, large bony spur projecting from cranial face of carpometacarpus: (0) absent; (1) present.

78. Carpometacarpus, cranial face: (0) flat or rounded; (1) sharp ridge present.

79. Carpometacarpus, metacarpal III: (0) shaft untwisted; (1) strongly twisted.

80. Alular digit, rudimentary claw: absent (0); very small and button-shaped (1); claw-like (2). Ordered. This small claw is often lost during maceration of specimens, and so taxa that lacked a claw were coded "?" unless true absence could be confirmed from the literature.

81. Pelvis, cranial margin: (0) flared laterally; (1) not flared laterally.

82. Pelvis, canalis iliosynsacralis opens caudally at two large, depressed foramina located between the iliac crests and the crista spinosa synsacra: (0) absent; (1) present.

83. Pelvis, cranially directed tab-like process placed dorsal to the antitrochanter: absent (0); present (1).

84. Pelvis, ilia and crista spinosa synsacri: (0) remain separate; (1) fused at dorsal margin.

85. Pelvis, tuberculum preacetabulare (pectineal process): (0) long and projected; (1) small point.

86. Pelvis, spina dorsolateralis ilii projects as sharp mediolaterally narrow process, adjacent to lateral margin of synsacrum and proximal caudal vertebrae: (0) absent; (1) present.

87. Foramen ilioischiadicum: (0) open caudally; (1) closed.

88. Pelvis, recessus caudalis fossa: (0) shallow; (1) deep; (2) absent.

89. Depth of ischium relative to the width of the synsacrum: (0) deep; (1) shallow and wide (1).

90. Spatium ischiopubicum: (0) dorsoventrally wide; (1) dorsoventrally narrow and slit-like (1).

91. Femur, length: (0) shorter or equal to humerus; (1) longer than humerus.

92. Femur, fossa poplitea: (0) deeply recessed with pneumatic foramen/fossa; (1) not deeply recessed, foramen variably present.

93. Tibiotarsus, crista cnemialis cranialis, proximal apex: (0) flat or rounded in cranial view; (1) pointed.

94. Tarsometatarsus, passage of tendon of m. flexor digitorum longus: (0) sulcus, (1) bony canal.

*95. Tarsometatarsus, sulcus for tendon of m. flexor hallucis longus: (0) open edge plantarly directed, (1) open edge laterally directed. Discussed by Mayr (2016b).

*96. Tarsometatarsus, shared canal for tendons of m. flexor perforans digiti 2 and m. flexor perforans et perforatus digiti II: absent (0); present (1). Discussed by Mayr (2016b).

*97: Tarsometatarsus, well developed crest along plantar surface (formed by fusion of intratendinous ossification): (0) absent; (1) present.

98. Tarsometatarsus, spurs in males: absent (0); present (1). This character cannot be scored absent with certainty in fossil taxa known from small numbers of specimens, as the possibility that males have not been sampled cannot be ruled out.

99. Tarsometatarsus, foramen at distal end of shaft between trochlea metatarsi II and III: (0) absent; (1) present.

100. Tarsometatarsus, relative length of trochleae: (0) trochlea metatarsi II and IV of similar length; (1) trochlea metatarsi II distinctly shorter than trochlea metatarsi IV.

101. Tarsometatarsus, plantar side of articular surface of trochlea metatarsi III: (0) symmetrical; (1) distinctly asymmetrical with lateral ridge protruding farther proximally than medial ridge.

102. Tarsometatarsus, trochleae: (0) splayed; (1) close together.

103. Length of toes relative to tarsometatarsus: (0) short; (1) long, digit III subequal or longer than tarsometatarsus.

104. Hallux: (0) significantly shorter than remaining pedal digits; (1) greatly elongated, approaches or exceeds other digits in length.

105. Hallux: (0) incumbent (at same level as remaining pedal digits); (1) elevated, more proximally located than remaining digits.

*Arthrology*

106. Ligamentum postorbito-mandibulare: (0) absent; (1) present.

*Plumage*

107. Integument of head: (0) largely feathered; (1) largely naked. *Lophura bulweri* is coded variable, as males have a largely naked head while females have a largely feathered head.

108. Single elongate ornamental plume on head: (0) absent; (1) present.

109. Tuft of ornamental plumes with expanded distal ends on head: (0) absent; (1) present.

110. Orbital region: (0) feathered; (1) patch of bare skin surrounds orbit.

111. Body plumage black, spotted with white vermiculations: (0) absent; (1) present.

112. Body plumage, black and white vertical barred plumage on flank: (0) absent; (1) present.

113. Contour feathers, downy barbules at base: (0) lack detachable nodes; (1) possess detachable nodes.

114. Wing: (0) longer than tail; (1) shorter than tail (1). *Gallus gallus* is coded 0/1 to reflect the variation in tail length between males and females.

115. Wing feathers: (0) diastataxic; (1) eutaxic (1)

116. Outermost primaries: (0) unmodified; (1) tip bowed and stiffened for acoustic use (1).

117. Number of tail feathers: (0) less than 16; (1) equal to or greater than 16.

118. Tail shape: (0) round; (1) wedged or graduated; (2) vaulted.

119. Tail feather moult: (0) irregular or bi-directional; (1) centrifugal; (2) centripetal.

120. Tarsus: (0) unfeathered; (1) at least partially feathered.

121. Sexual dimorphism in plumage: (0) absent; (1) slight, (2) marked.

122. Integument of hatchling: (0) downy; (1) true feathers.

*Miscellaneous soft tissue*

123. Fleshy, brightly colored comb dorsal to eye: (0) absent; (1) present.

124. Lower beak, serrations on cutting edge of rhamphotheca: (0) absent; (1) present.

125. Filtering lamellae: (0) absent; (1) rudimentary; (2) well-developed.

126. Frontal caruncle (snood): (0) absent; (1) present.

127. Single wattle formed by skin of neck: (0) absent; (1) present.

128. Paired wattles formed by skin on side of face (at least in male): (0) absent; (1) present.

129. Inflatable cervical air sacs: (0) absent; (1) present.

130. Tracheal elongation in males: (0) absent; (1) present.

131. Intromittant organ: absent (0) absent; (1) present.

132. Uropygial gland: (0) naked; (1) tufted.

*Eggs and reproductive behavior*

133. Eggshell, pinkish brown powdery covering: (0) absent; (1) present.

134. Average clutch size: (0) four or more eggs; (1) two or three eggs.

135. Mating system: (0) monogamous; (1) polygynous.

136. Incubation system: (0) egg incubated by parents; (1) egg incubated by external means, e.g. geothermal heat or decaying vegetation.

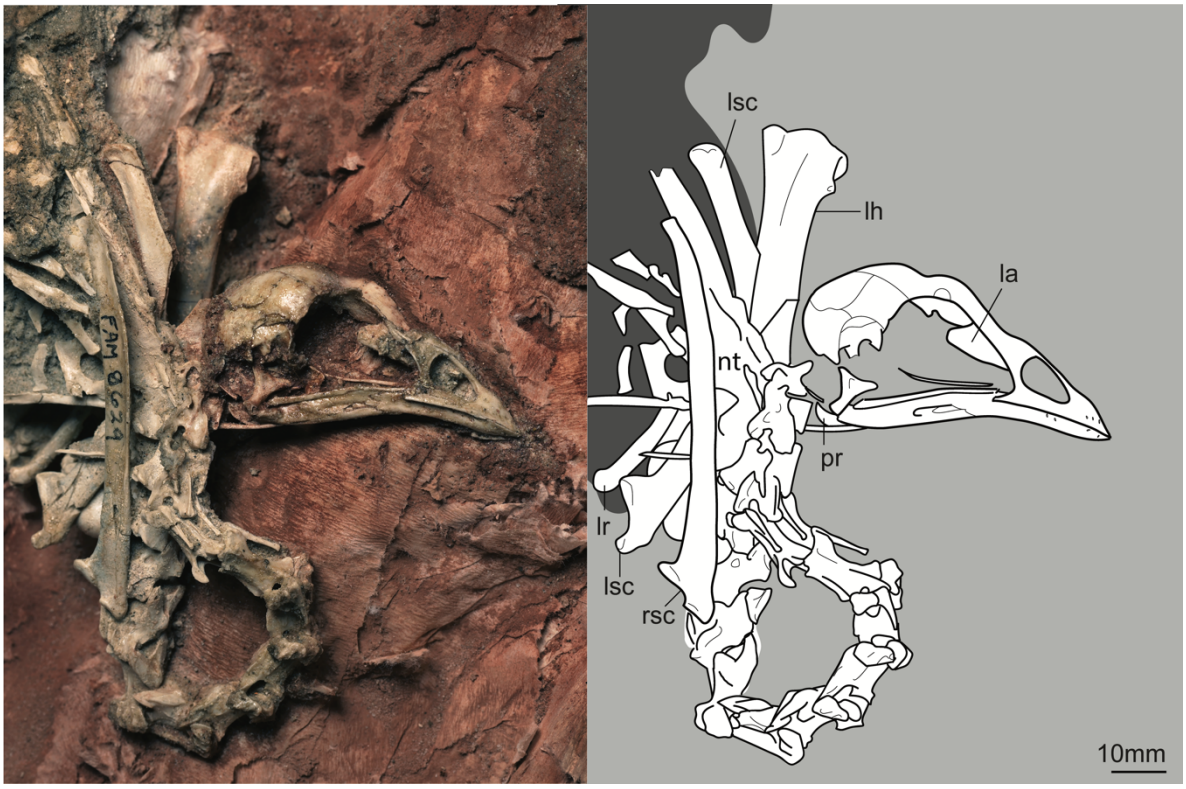
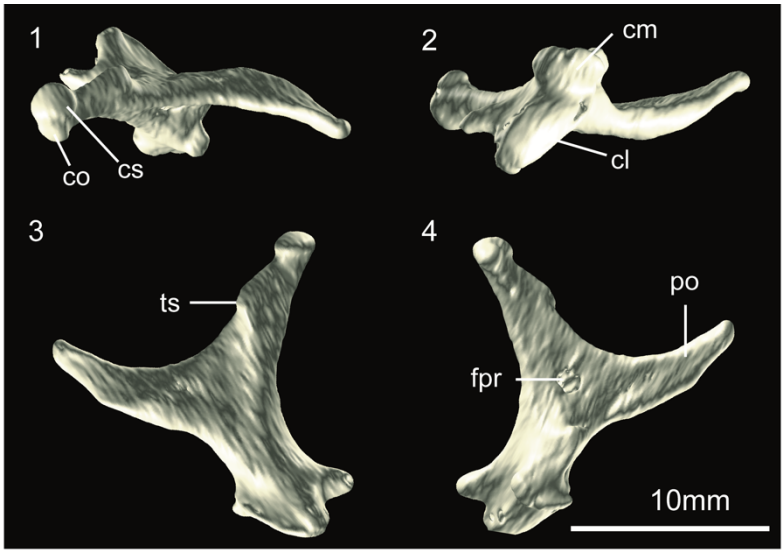



**Figure 1**. Holotype *Centuriavis lioae* (AMNH FARB 8629). The right humerus, left coracoid, and left radius and ulna were removed during preparation of the block. Abbreviations: la=lacrimal, lh=left humerus, lr=left radius, lsc=left scapula, pr=processus retroarticularis, nt=notarium, rsc=right scapula.




1151

1152 **Figure 2**. CT rendering of the left quadrate of the *Centuriavis lioae* holotype (AMNH

1153 FARB 8629) in (**1**) dorsal, (**2**) ventral, (**3**) lateral, (**4**) medial views. Abbreviations:

1154 cl=condylus lateralis, cm=condylus medialis, co=capitulum oticum, cs=captitulum

1155 squamosum, fpr=foramen pneumaticum rostromediale, po=processus orbitalis,

1156 ts=tuberculum subcapitulare.


**Figure 3**. Postcranial elements of the *Centuriavis lioae* holotype (AMNH FARB 8629): (**1**) omal fragment of furcula, right coracoid in (**2**) ventral and (**3**) dorsal views, right humerus in (**4**) cranial and (**5**) caudal views, right ulna in (**6**) dorsal (due to crushing, the distal end is partly rotated) and (**7**) ventral views, right radius in (**8**) dorsal and (**9**) ventral views, right radiale in (**10**) cranial and (**11**) caudal views, and (**12**) sesamoid. Abbreviations: cd=crista deltopectoralis, d=damaged area, ev=epicondylaris ventralis, f=foramen, fas=faces articularis scapularis, fl=processus flexorius, fos=fossa in impressio m. sternocoracoidei,

1165 fr=facet for radius, lip=lip bounding facies articularis sternalis, ftd=fossa tricipitalis

1166 dorsalis, kn= knob at angulis medialis; om=omal end of furcula, psd=processus

1167 supracondylaris dorsalis, r= ridge formed by distal projection of caput humeri; sc=scar for

1168 insertion of m. supracoracoideus, uv=notch for tendon of musculus ulnometacarpalis

1169 ventralis.

1170


1171

1172 **Figure 4**. Specimens of cf. *Centuriavis lioae*: (**1**) Cranial and (**2**) caudal views of small

1173 humerus (AMNH FARB 8627). (**3**) Proximal, (**4**) distal, (**5**) dorsal, (**6**) plantar, and (**7**)

1174 medial views of referred tarsometatarsus (AMNH FARB 8628) with (**8**) medial view of an

1175 immature individual of the extant grouse *Bonasa umbelllus* (Bruce Museum uncatalogued)

1176 for comparison. Abbreviations: io=intratendinous ossification of m. gastrocnemius. Images

1177 (**3**) and (**4**) are not to scale.

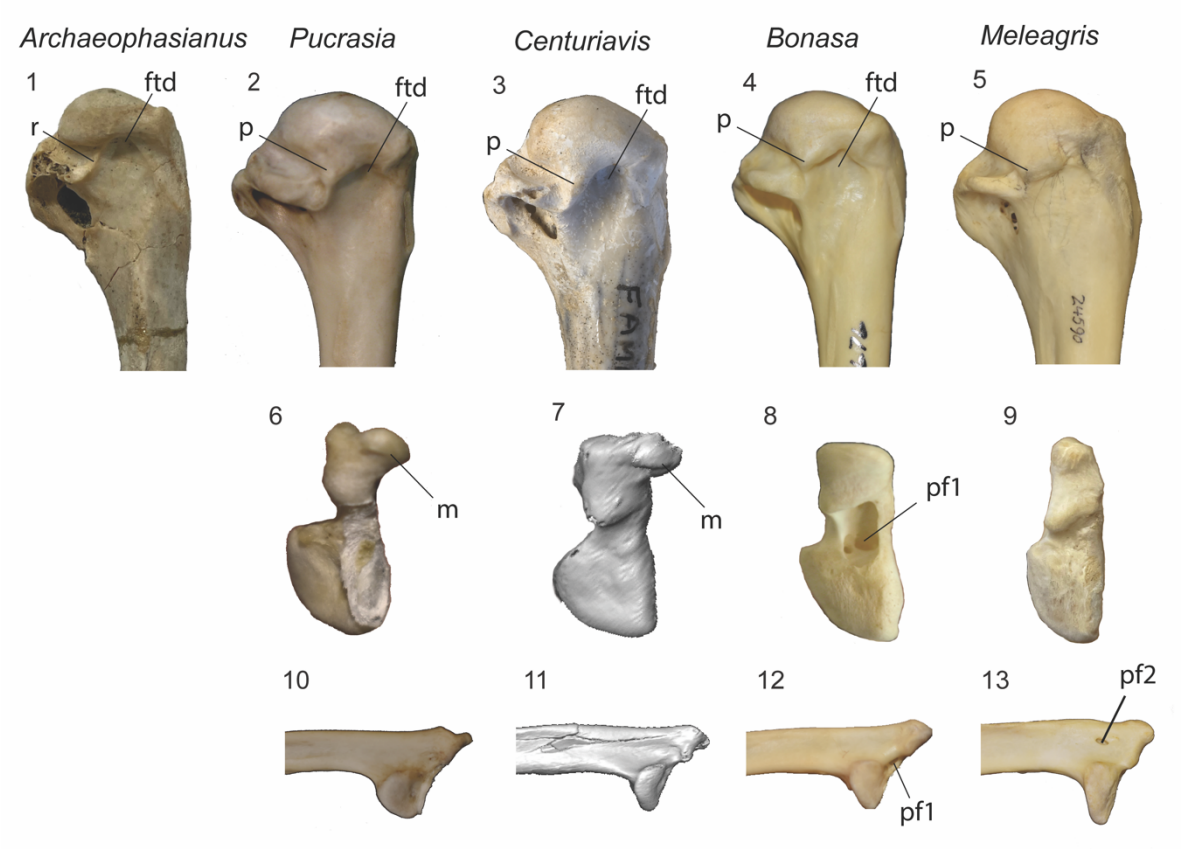



**Figure 5**. Comparison of humerus and scapula of Galliformes. (**1-5**) Proximal end of right humerus is caudal view, (**6-9**) omal end of right scapula in omal view, (**10-13**) omal end of right scapula is lateral view in of (**1**) *Archaeophasianus mioceanus* (YPM VP 909), (**2,6,10**) *Pucrasia macrolopha* (AMNH SKEL 17676), (**3,7,9**) *Centuriavis lioae* (AMNH FARB 8629) (**4,8,12**) *Bonasa umbellus* (AMNH SKEL 21616), and (**5,9,13**) *Meleagris gallopavo* (AMNH SKEL 24590). Images (**7**) and (**11**) were taken from a CT rendering of the scapula. Abbreviations: ftd=fossa tricipitalis dorsalis, m=medial deflection of acromion, p=projection of articular surface of the caput humeri; pf1=pneumatic foramen opening between the acromion and facies articularis humeralis, pf2=pneumatic foramen at base of acromion, dorsal to facies articularis humeralis, r=weak ridge separating the fossa pneumotricipitalis dorsalis from the incisura capitis. Not to scale.

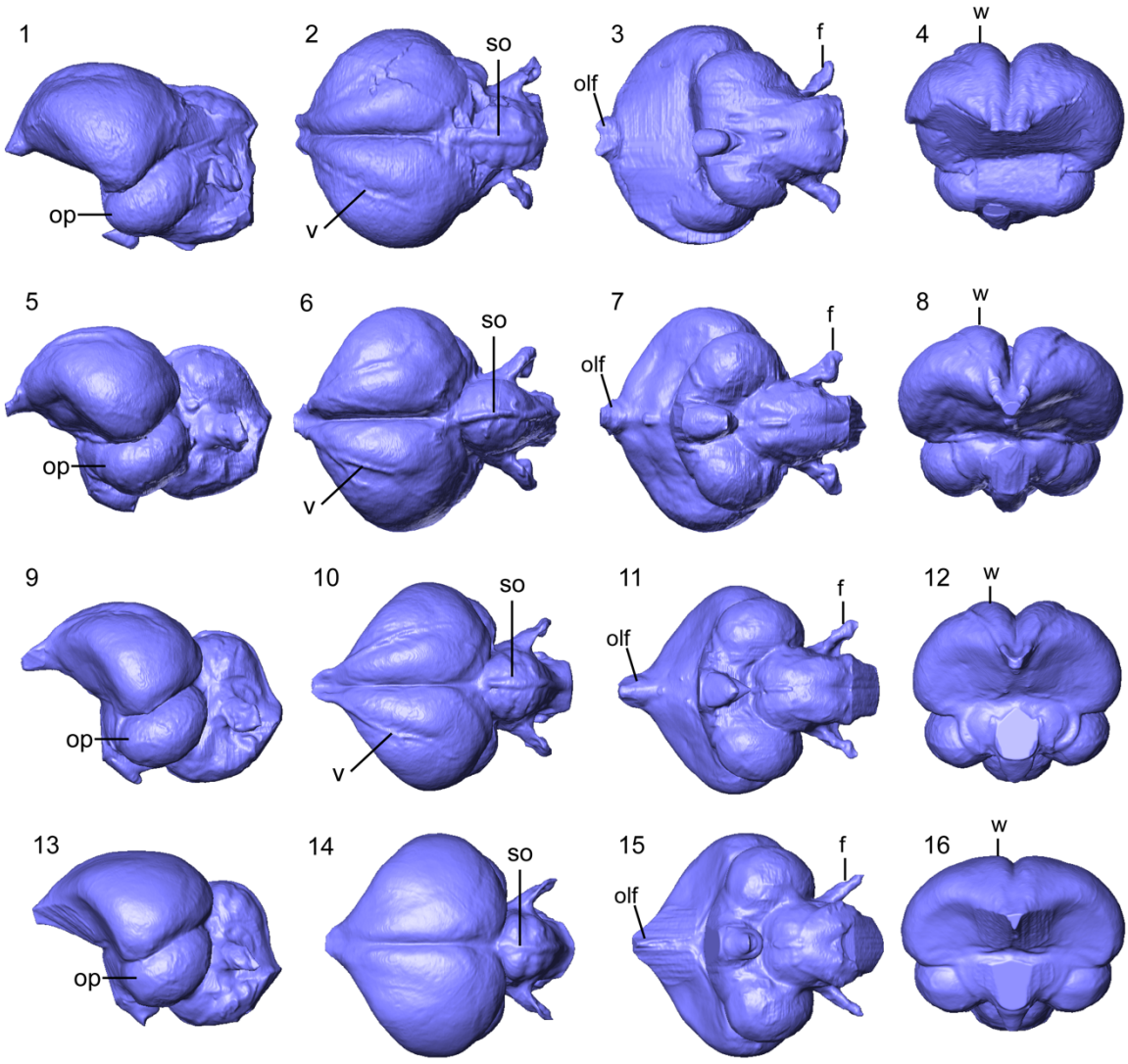
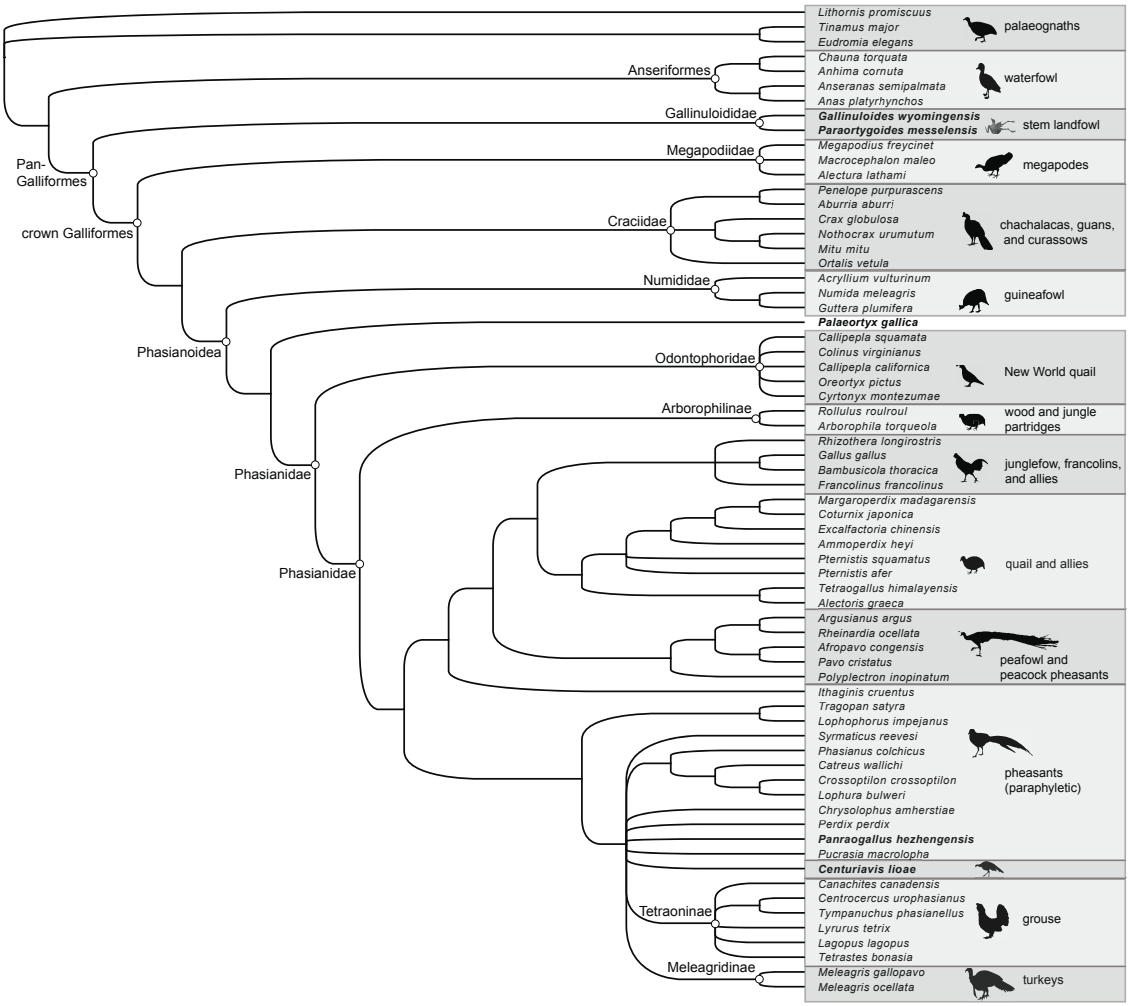



**Figure 6**. Brain endocasts of North American Galliformes: *Centuriavis lioae* (AMNH FARB 8629) in (**1**) lateral, (**2**) dorsal, (**3**) ventral, and (**4**) rostral view. *Meleagris gallopavo* (OUVC 10599) in (**5**) lateral, (**6**) dorsal, (**7**) ventral, and (**8**) rostral view. *Bonasa umbellus* (AMNH SKEL 21616) in (**9**) lateral, (**10**) dorsal, (**11**) ventral, and (**12**) rostral view. *Colinus virginianus* (Odontophoridae, AMNH SKEL 2310) in (**13**) lateral, (**14**) dorsal, (**15**) ventral, and (**16**) rostral view. Abbreviations: f=flocullar fossa, olf=olfactory bulb, op=optic lobe, so=sulcus olfactorius, v=vallecula, w=Wulst.




1199

1200 **Figure 7**. Strict consensus of 3,642 MPTs of 478 steps from parsimony analysis of 137

1201 morphological characters, applying a backbone constraint based on the molecular study of

1202 Hosner et al. (2017). Fossil taxa are indicated in bold.

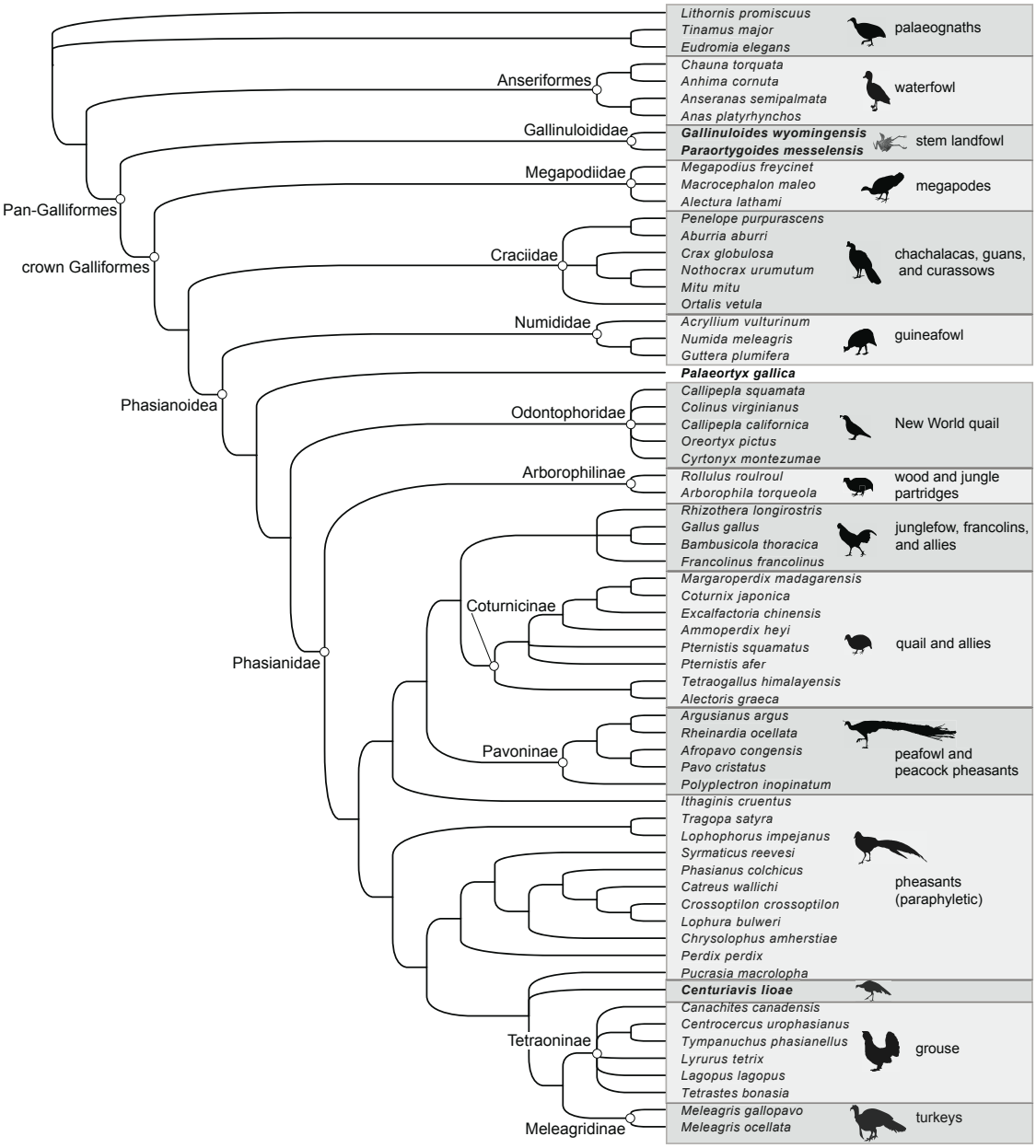



**Figure 8**. Strict consensus of 1,808 MPTs of 474 steps from parsimony analysis of 137 morphological characters, excluding the fossil taxon *Panraogallus* and applying a backbone constraint based on the molecular study of Hosner et al. (2017). Fossil taxa are indicated in bold.

1209 TABLE 1 – Measurements (mm) from *Centuriavis lioae* holotype and referred material.

| Element | Dimension | AMNH FARB 8629 (holotype) | AMNH FARB 8628 | AMNH FARB 8627 |
|---|---|---|---|---|
| Skull | length | 60.0 | | |
| Scapula | length to acromion | 78.9 | | |
| | length to facies articularis humeralis | 69.7 | | |
| Coracoid | maximum length | 60.6 | | |
| | length to midpoint of facies articularis sternalis | 56.0 | | |
| Humerus | maximum length | 79.8 | 70.5 | |
| | proximal width | 21.3 | 19.3 | |
| | midshaft width | 8.9 | 8.0 | |
| | midshaft breadth | 7.8 | 6.3 | |
| | distal width | 17.1 | 15.6 | |
| Ulna | maximum length | 81.1 | | |
| Radius | maximum length | 70.3 | | |
| Tarsometatarsus | maximum length | | | 70.2 |
| | proximal width | | | 13.0 |
| | midshaft width | | | 6.1 |
| | midshaft breadth | | | 12.5 |

1210