



The fossil record of galliform birds: comments on Crowe et al. (2006)

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In a recent article, Crowe et al. (2006) analyzed the interrelationships of galliform birds, combining molecular sequence data with morphological characters from a study by Dyke et al. (2003). They calibrated the resulting phylogeny with fossil galliforms and concluded that “basal lineages of galliforms diverged prior to the Cretaceous/Tertiary (K-T) Event and that the subsequent cladogenesis was influenced by the break-up of Gondwana” (Crowe et al., 2006, p. 495; note that this statement refers to putatively “basal” crown group Galliformes, not to the existence of early Cretaceous stem lineage representatives). Unfortunately, however, several of the statements concerning fossil Galliformes are erroneous and the calibration of the molecular data is based on incorrectly assigned fossil taxa.

Crowe et al.’s (2006, p. 506) assumption of a maximum age of 123 million years for the origin of crown group Galliformes clearly is a profound overestimation. This age is about that of the Chinese Jehol Biota and other early Cretaceous sites that yielded numerous fossil birds, none of which can be shown to be part of Neornithes, let alone being a crown group representative of any extant avian taxon. Crown group Neornithes are unknown until the late Cretaceous, about 70 million years ago (e.g., Clarke et al., 2005), and a “ghost lineage” of more than 50 million years is extremely unlikely given the fact that all of the diverse and fairly abundant early Cretaceous birds belong to non-neornithine taxa.

Crowe et al. (2006, p. 503) noted that “research based on analyses of mtDNA sequences by Van Tuinen and Dyke (2004) [...] using the ages of some of the above-mentioned fossil galliforms as calibration anchorpoints has produced molecular clock phylogenies that also suggest that the gamebirds originated on Gondwana”. However, they do not mention that Mayr (2005) showed that at least six of the nine “internal fossil-based

anchorpoints” used by van Tuinen and Dyke (2004) for their calibration of galliform molecular clocks were based on incorrectly identified taxa (e.g., the Quercymegapodiidae are stem-group Galliformes, not Megapodiidae; *Paleortyx* [used to calibrate “Crown Odontophoridae”] is not a member of the New World Odontophoridae; “*Gallus bravardi*”, used to calibrate “Crown *Gallus*”, is a peafowl of the genus *Pavo*). *Contra* Crowe et al. (2006, p. 502), Megapodiidae were not recorded from the Paleogene of Europe, and the Quercymegapodiidae were considered to be stem group Galliformes in the original description (Mourer-Chauviré, 1992).

Although Mayr and Weidig (2004) detailed that the very incompletely known early Eocene taxon *Amitabha* described by Gulas-Wroblewski and Wroblewski (2003) cannot even be convincingly shown to be a galliform bird, a view not challenged by subsequent authors, this taxon was used by Crowe et al. (2006, p. 506) to calibrate the divergence between “New World quails and non-numidine phasianids”.

Crowe et al. (2006) further used the earliest undisputed galliform bird, *Gallinuloides wyomingensis* from the early Eocene of North America, to calibrate “stem phasianoids”. Concerning phylogenetic placement of this species, they followed Dyke (2003) who, based on examination of the poorly preserved holotype, concluded that *G. wyomingensis* is the sister taxon of the Phasianidae, i.e., within crown group Galliformes. However, Mayr and Weidig (2004) detailed that the characters listed by Dyke (2003) as evidence for this hypothesis are in fact not visible in the holotype of *G. wyomingensis* and absent in a new specimen of this species from the type locality. Crowe et al. (2006, p. 505) note that Mayr and Weidig (2004) identified *Gallinuloides* as a stem group galliform “based largely on its possession of a cup-like scapular articulation facet on the coracoid (a plesiomorphic character within neornithines that is also present in Anseriformes)”. They did not mention that Mayr and Weidig (2004) listed eight

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additional characters that support a position of *Gallinuloides* at least outside a clade including Cracidae, Numididae, Odontophoridae and Phasianidae, and that the gallinuloidid *Paraortygoides* (Mayr, 2000, 2006) has also been considered a stem group galliform by Dyke and Gulas (2002). Instead, they refer to an analysis by “Lindow et al. (in review)”, which, based on the character matrix of Dyke et al. (2003), “once again places *Gallinuloides* with the crown Galliformes and basal to the phasianoids” (Crowe et al., 2006, p. 505).

Because this study has not yet been published, it is not possible to evaluate this new character evidence. However, the character matrix of Dyke et al. (2003), on which the analysis of Dyke (2003) is based, exhibits numerous incorrect character codings, as unfortunately is the case with several other studies authored by Dyke (Mayr, 2001a,b; Mayr and Weidig, 2004). For example, a cup-like cotyla scapularis, which is invariably present in all anseriform birds, has been coded as present for *Anseranas* only but incorrectly coded as absent for the other anseriform outgroup taxa included in the study (*Anas*, *Dendrocygna*, *Chauna*, *Anhima*; Dyke et al., 2003, character 37). Not surprisingly, thus, this character does not affect the position of *Gallinuloides* in the analysis, as it is optimized as an autapomorphy of *Anseranas* and not as a plesiomorphic feature of all anseriform birds and stem group Galliformes (e.g., Mourer-Chauviré, 1992).

Crowe et al. (2006, p. 503) note that the taxa included in their analysis “were scored for the 102 [...] characters employed by Dyke et al. (2003)”. Unfortunately, they neither provide their data matrix nor do they comment on whether character scoring has been taken unmodified from Dyke et al. (2003). This is so much the more unfortunate, as some taxa that were not included in the analysis of Dyke et al. (2003) must have been newly scored by Crowe et al. (2006) (e.g., *Xenoperdix*, *Leipoa*, *Penelopina*, *Peliperdix*, *Dendroperdix*, etc.). Character coding of these taxa cannot be checked and it is to be hoped that Crowe et al. (2006) corrected the erroneous scoring in the data matrix of Dyke et al. (2003) who, for example, incorrectly coded a spur on the tarsometatarsus of the male as present for Tetraoninae, *Perdix* and *Arborophila* (Dyke et al., 2003, character 86), the feathered head of the Crested Argus (*Rheinardia ocellata*) as “largely naked” (Dyke et al., 2003, character 101), and eye-spots (ocelli) on the feathers as present for *Pavo* and *Argusianus* (Dyke et al., 2003, character 96), although these occur on the tail coverts in *Pavo* but on the secondaries in *Argusianus* and are thus non-homologous; ocelli are further incorrectly coded as present in *Afropavo*. Although the distribution of a spur is correctly shown by Crowe et al. (2006, fig. 10), this character seems to have been a posteriori mapped onto the phylogeny and it is thus not possible to evaluate its coding for the analysis.

In summary, the molecular estimates for galliform divergences resulting from Crowe et al.’s (2006) study are severely flawed by an uncritical use of fossil taxa for calibration of the data, and the results of the combined analyses should at least be taken with caution until the underlying character matrix is available. The fossil record does not support a Cretaceous divergence of crown group Galliformes [see Mayr and Weidig, 2004 who did not state that “stem galliforms originated only after the Cretaceous-Tertiary mass extinction event” (*contra* Crowe et al., 2006, p. 502)]. Even the presence of Late Cretaceous stem lineage Galliformes has not yet been convincingly established, and, without exception, all pre-Oligocene Galliformes described so far are outside the crown group (see also Mourer-Chauviré, 1992). Many of the late Paleogene and Neogene taxa assigned to Phasianidae further have to be revised in the light of the new hypotheses concerning galliform inter-relationships before they can be used as calibration points to date molecular analyses.

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