

# The basal clades of modern birds

Joel Cracraft

Department of Ornithology, American Museum of Natural History  
Central Park West at 79th Street, New York, NY 10024 U.S.A.

*E-mail:* JLC@amnh.org

Julia Clarke

Department of Geology and Geophysics, Yale University  
P.O. Box 208109, New Haven, CT 06520-8109 U.S.A.

*E-mail:* julia.clarke@yale.edu

## *Abstract*

This paper synthesizes the available evidence, including morphological, molecular and biochemical data, regarding the relationships among the basal lineages of modern birds (Neornithes). Both older and more recent data support the monophyly of the Neornithes as well as its basal sister clades, the Palaeognathae and Neognathae. Within the latter, congruence in morphological and molecular data supports a monophyletic Galloanserae (Galliformes + Anseriformes) as the sister group of all other neognaths (Neoaves). There is no consilience among different kinds of evidence that allows identification of basal relationships within the Neoaves. Conflicts in the literature have arisen for many reasons: (1) investigators have favored their evidence to the exclusion of other forms of data; (2) taxon samples of molecular studies have been inadequate, and thus artifacts of rooting have resulted; and (3) there have been misunderstandings about character homology in morphological studies.

## *Keywords*

Neornithes, avian evolution, avian phylogeny, Galloanserae, total evidence.

## Appendix 1: Character matrix

## Appendix 2: Character list

Available at <http://www.peabody.yale.edu/collections/vp/>

---

© 2001 Joel Cracraft and Julia Clarke. All rights reserved.

From *New Perspectives on the Origin and Early Evolution of Birds: Proceedings of the International Symposium in Honor of John H. Ostrom*.  
J. Gauthier and L. F. Gall, eds. New Haven: Peabody Mus. Nat. Hist., Yale Univ. ISBN 0-912532-57-2.

© 2001 Peabody Museum of Natural History, Yale University. All rights reserved.

## Appendix 1: Character matrix

Matrix of characters and character coding used in this paper (see text for details).

	10	20	30	40	44
Outgroup	0 0 0 2 0 0 0 0 0 0	0 ? 0 0 0 0 0 1 0 0	0 0 0 0 0 0 0 0 0 0	0 <sub>1</sub> 0 0 0 0 0 0 0 0 0	0 0 0 <sub>1</sub> 0
<i>Hesperornithes</i>	0 ? 0 0 <sub>1</sub> 1 1 0 0 0 1 1	0 ? 0 0 0 0 0 0 0 0 <sub>1</sub>	? 0 0 0 0 0 0 ? 0 0	0 0 0 0 0 0 1 0 0 0	0 0 ? 0
<i>Ichthyornis</i>	0 ? 0 0 <sub>1</sub> ? ? ? ? ? ?	? ? ? ? ? ? ? 0 0 0	? ? 0 0 0 ? 0 ? 0 ?	? 0 0 0 0 0 0 0 0 0	0 0 ? 0
Tinamous	1 1 1 2 0 0 0 0 0 0	1 0 1 1 1 1 0 1 0 1 1	1 1 1 1 1 1 0 0 1 1	1 0 0 0 0 0 0 0 0 0	0 0 2 1
Ratites	1 1 1 2 0 0 0 0 0 0	1 0 1 1 1 1 0 1 0 1 1	1 0 <sub>1</sub> 1 1 1 1 0 0 0 <sub>1</sub>	1 0 0 0 0 0 0 0 0 0	0 0 2 1
Galliforms	1 1 1 1 1 1 1 1 1 1	1 1 1 0 1 1 0 1 1 1	1 1 1 1 1 1 1 1 1 1	1 1 1 1 1 1 1 1 1 1	1 1 0 1
Anseriforms	1 1 1 1 1 1 1 1 1 1	1 1 0 0 1 1 0 1 1 1	1 0 1 1 1 1 1 1 1 1	1 1 1 1 1 1 1 1 1 1	1 1 0 1
Neoaves	1 1 1 1 1 1 1 1 1 1	1 1 0 0 <sub>1</sub> 0 <sub>1</sub> 0 <sub>1</sub> 0 1 1 1 1	1 0 <sub>1</sub> 1 1 1 1 1 1 1 1	1 0 0 0 0 0 0 0 0 0	0 0 0 <sub>1</sub> 0 <sub>1</sub>

## Appendix 2: Character list

- Teeth on maxilla and dentary: (0) present, (1) absent. Though the presence/absence of teeth shows significant homoplasy in theropods, and especially avialan theropods (Chiappe et al., 1999), basal enantiornithines and close outgroups to neornithines have teeth.
- Coronoid bone: (0) present, (1) absent.
- Bony mandibular symphysis: (0) absent, (1) present.
- Dentary, caudal development: (0) with no separate dorsal rami, (1) weakly forked posteriorly into dorsal and ventral rami, (2) strongly forked (ordered). *Note:* This character is based on two of Cracraft (1986). A strongly forked dentary appears present in *Confuciusornis* and is weakly forked in some nonavian theropods (Chiappe et al. 1999). Thus, a strongly forked dentary is considered a synapomorphy of a more inclusive avialan clade. The dentary in *Hesperornis* and *Ichthyornis*, on the other hand, was apparently slightly forked (or unforked posteriorly). A strongly forked dentary, with dorsal and ventral rami approximately equal in distal extent, thus appears to be apomorphic within neornithines.
- Extensive articulation between the vomer and pterygoid: (0) present, (1) absent.
- Palatines and pterygoids: (0) sutured, (1) segmented (articulated).
- Palatines (0) pterygoid and vomer exclude the palatines from the midline, (1) palatines not excluded, meet at midline and contact basisphenoid rostrum.
- Palatines contact: (0) maxillae only, (1) premaxillae. *Note:* See Witmer and Martin (1987). This and the previous character have the same known distribution for the taxa included in this analysis and may not be independent.
- Vomers contact premaxillae: (0) present, (1) absent. *Note:* See Witmer and Martin (1987).
- Ventral, “zygomatic” process of the squamosal: (0) long, laterally adjacent to the quadrate rostr dorsally (1) short—noncontacting. *Note:* A long ventral process on the squamosal contacting the quadrate rostr dorsally is present in nonavian theropod outgroups as well as *Confuciusornis*. This condition is unknown in *Ichthyornis*, in *Hesperornis* it appears to be short.
- Eustachian tubes (ossified): (0) absent, (1) present.
- Eustachian tubes: (0) open laterally, (1) open at midline. *Note:* This and the previous character cannot be scored so as to express phylogenetic information without some ambiguity. Thus, without the discovery of additional information from fossils with ossified eustachian tubes, the primitive condition (whether lateral or at the midline) for Neornithes cannot be specified. Because of the apparent lack of ossified eustachian tubes in outgroups, the zero state does not imply laterally located tubes are primitive.
- Alaparasphenoidalis is inflated by the rostral tympanic diverticulum: (0) absent, (1) present. *Note:* Scored following Witmer’s (1990) revision of Cracraft (1986).
- Skull with highly pneumatic bone posterior to the articulation with the quadrate. *Note:* Witmer (1990) reviewed this character (Cracraft 1986) and considers it a synapomorphy of Palaeognathae, noting, however that this character is also present in most gruiforms.
- Increased extent of tympanic pneumaticity: (0) absent, (1) present. *Note:* Three characters related to the communication of the contralateral dorsal tympanic

## Appendix 2, continued.

- diverticula within the dermal skull roof were described by Witmer (1990, characters 12 to 14). Presently, all have the same taxic distribution, and may not be independent, thus they are here scored as a single character. Scoring them as separate characters did not effect the results of the analysis.
16. Rostral maxillary sinus: (0) present, (1) reduced or absent. *Note:* Scored following Witmer (1990).
  17. Caudal maxillary sinus (0) present, (1) absent. *Note:* Scored following Witmer (1990).
  18. Quadrate, development of intercotylar incisure between prootic and squamosal cotylae: (0) absent, (1) present. *Note:* Information provided by new specimens has made it clear that a double (prootic and squamosal) quadrate articulation is synapomorphic for a more inclusive clade than Neornithes. A double articulation is found in other Ornithurae (Witmer 1990) and in Mesozoic avialans such as *Confuciusornis* (Chiappe et al. 1999). However, an incisure between the prootic and squamosal cotylae, apparently related to the passage of the dorsal tympanic diverticulum (Witmer 1990), is not present in *Hesperornis*, *Ichthyornis* or the Palaeognathae. In *Confuciusornis* (Chiappe et al. 1999), and within Neognathae, these two cotyla are clearly separated by the incisure.
  19. Quadrate with three mandibular condyles (caudal articular surface added): (0) absent, (1) present. *Note:* After Gauthier (1986). Although the morphology of the caudal condyle is highly variable within Neornithes, this group does not possess a condition like the nonneornithine avialan outgroups. Dzerzhinsky (1995) and Livezey (1997) considered the loss of the caudal condyle a synapomorphy of Galloanseres. However, rather than score the caudal condyle as lost, which results in scoring the condition in Galloanseres the same as that in nonneornithine theropods, the present character is preferred; the synapomorphic condition repeatedly noted for Galloanseres is encompassed by character 38 in the present analysis.
  20. Number of ankylosed synsacral vertebrae greater than 10: (0) absent, (1) present. *Note:* The synsacrum of modern birds consists of 11 to 23 ankylosed vertebrae (Verheyen 1960, in Chiappe 1996). The only Mesozoic avialan with more than 10 ankylosed vertebrae is *Hesperornis regalis*, whereas *Baptornis advenus*, traditionally considered basal to Hesperornithiformes, has but 10 (Chiappe 1996). *Ichthyornis dispar* also has 10 (Marsh 1880).
  21. Gastralria: (0) present, (1) absent. *Note:* See Cracraft (1986) and Gauthier (1986).
  22. Uncinate processes fused to ribs: (0) absent, (1) present. *Note:* Fused processes are not present in loons, grebes, penguins, Anhimidae and *Apteryx*, and are occasionally unfused in other ratites (Gauthier 1986). Variation in this character across taxa may be affected by skeletal preparation artifacts.
  23. Deltopectoral crest of humerus: (0) projects dorsally, (1) with cranial deflection.
  24. Humerus with pneumatic foramen perforating shaft: (0) absent, (1) present. *Note:* Pneumatic foramina in Mesozoic avialans such as *Confuciusornis* or *Enantiornis leali* do not enter the humeral shaft, perforating an enlarged deltopectoral crest and ventral tubercle respectively (Chiappe et al. 1999). Even if these foramina were considered homologous, pneumatic foramina are absent in Hesperornithiformes and *Ichthyornis* and thus would be optimized unambiguously as a synapomorphy for Neornithes.
  25. Cranioventrally directed flange or tubercle developed on ischium demarcating caudal end of fenestra ("obturator foramen") associated with the passage of obturator nerve between the ischium and pubis: (0) absent, (1) present. *Note:* Cracraft (1986) considered an "obturator foramen" a synapomorphy of Neornithes. However, primitively, the obturator nerve perforates the pubis through what is traditionally referred to in the nonneornithine literature as an "obturator foramen." The obturator nerve is located between the ischium and pubis in early tetanuran dinosaurs and retains this position in neornithines. The neornithine condition has generally been considered nonhomologous with the obturator process of other tetanurans. The nonavialan tetanuran process was probably lost at the base of Avialae but certainly is absent thereafter (Gauthier 1986). An osseous flange-like projection of the ischium is present in at least one dromeosaur specimen (Norell and Makovicky 1997), though its homology with that in Neornithes is uncertain. There is only a slight ventral extension ("flange") on the ischial surface in *Patagopteryx*, thus a condition like that of Neornithes is clearly lacking (Chiappe 1996:218). No flange is discernable in either *Hesperornis* (Marsh 1880) or *Ichthyornis* (contra Marsh 1880). The foramen is decidedly more conspicuous in Neornithes because the pubis closely parallels the ischium, the two bones being in contact in many taxa, although not in all (in many neornithines the ischial flange closely parallels

## Appendix 2, continued.

- but does not directly contact the pubis, yet an opening, the “foramen,” is nevertheless demarcated).
26. Ilium lengthened anteriorly so that it overlaps bases of at least one set of ribs: (0) absent, (1) present. *Note:* This character (from Gauthier 1986) could be alternatively described as the retention of the ribs of at least one thoracic vertebrae that has become incorporated into the synsacrum.
  27. Ilium and ischium: (0) unfused posteriorly, (1) fused posteriorly, thus the “ilioischiatric fenestra” is closed. *Note:* See Cracraft (1986). The feature is secondarily derived in some ratites.
  28. Calcaneum, (0) small, unfused to ascending process, (1) large, fused to ascending process. *Note:* See McGowan (1984, 1985).
  29. Supratendinal bridge on tibiotarsus (0) absent, (1) present. *Note:* This character is reversed in some ratites, parrots, and owls (Gauthier 1986).
  30. Tarsometatarsus, cristae and sulci hypotarsi: (0) absent, (1) present. *Note:* This character describes the condition of the “hypotarsus” of various authors. In more basal avialans, after the complete fusion of the distal tarsals, a flat, discrete, slightly protruding surface arises in the area of the hypotarsus, but no sulci or medial or lateral cristae are apparent. What is referred to as the hypotarsus of modern birds is a modification of the proximal metatarsal surface constraining the passage of the flexor tendons of the pedal digits. A posterior projection is present in the enantiornithine *Lectavis brevicola* (Chiappe 1993), *Patagopteryx deferraris*, and very slightly in *Hesperornithiformes*, yet there are no hypotarsal crests or sulci. The condition is best scored as missing data for *Ichthyornis* inasmuch as the tarsometatarsi identified as being from that taxon are not associated with any material referable to *Ichthyornis*, and a tarsometatarsus is not represented in the type material (Clarke 1999).
  31. Tarsometatarsus, proximal vascular foramina: (0) absent or only one, (1) two or more. *Note:* This character is modified from previous authors. A single foramen between metatarsi III and IV is present in *Patagopteryx* (Chiappe 1996), and though this foramen is quite reasonably homologous with those of neornithines, none is present in *Hesperornis*, and the condition of *Ichthyornis* is coded as missing data.
  32. Ectethmoid: (0) present, (1) absent or weakly developed. *Note:* Ericson (1996) reviewed the character absence or presence of the ectethmoid (Cracraft 1988), suggesting (a) the presence of a ectethmoid in some galliform and anseriform taxa (e.g., Megapodidae, *Chauna*) as well as (b) the loss of the ectethmoid in a few other neognath taxa (citing Phoenicopterigidae and Eurypygididae) negated this character’s usefulness. This is not true inasmuch as characters do not have to be 100% consistent on a tree. Moreover, the usefulness of this character will ultimately be judged once other basal neognaths are identified.
  33. Rostropterygoid articulation (Weber 1993): (0) absent, (1) present. *Note:* This character is equivalent in terms of coding to “basipterygoid processes on side of parasphenoid rostrum,” which has been postulated as a synapomorphy of Galloanseres by Cracraft (1988), Dzerzhinsky (1995), Livezey (1997) and Ericson (1996). On the basis of embryological observations, Weber (1993) suggests this may be a neomorph and nonhomologous with other avian basipterygoid processes. Whether this is true or not requires additional analysis.
  34. Basiparasphenoid plate is inflated, rounded and broad: (0) absent, (1) present. *Note:* Postulated as a synapomorphy by Cracraft (1988). Ericson (1996) claims this character is too variable within Galloanseres and occurs elsewhere in neognaths, yet a broad, rounded plate is present in galliforms and is shared with anseriforms, most prominently by anhimids. The extent to which a similar condition may exist in other neognaths is relevant for monophyly of Galloanseres only if those taxa are at the base of the neognath tree; the character needs further study.
  35. Well-marked depression on posterolateral side of basiparasphenoid plate containing numerous foramina for arteries and cranial nerves: (0) absent, (1) present. *Note:* Postulated as a synapomorphy by Cracraft (1988). Ericson (1996) notes that a similar depression is found in some other neognaths, and suggests the depression is related to an inflated basiparasphenoid plate and hence should not be considered independent of character 34. He recognized that this observation is not constant, which suggests the phylogenetic independence of these two characters.
  36. Palatines long and thin, especially anteriorly, poorly developed posteriorly, and widely separated anteriorly: (0) absent, (1) present. *Note:* Postulated to be a synapomorphy by Cracraft (1988). Ericson (1996: 197) questioned this character by claiming “the statement that anseriforms and galliforms have long and thin palatines, is not generally valid.” Yet it seems to be valid. It is true, as Ericson states, that the interpreta-

## Appendix 2, continued.

tions of Gingerich (1973; and also Witmer and Martin 1987) indicate the palatines of *Hesperornis* are long and thin. The condition postulated here as derived is more clearly described by adding the phrase “widely separated anteriorly.” The palatines of tinamids and neognaths in general are broad and are relatively closer together at their anterior end, a condition not generally shared by galliforms and anseriforms.

37. Dorsally projecting process on quadrate anterior to quadrate–prootic articulation (attachment for m. adductor mandibulae externum, pars profundus): (0) absent or very poorly developed, (1) present and well developed. *Note:* Postulated to be a synapomorphy by Cracraft (1988) and by Livezey (1997, his character 49). Ericson (1996) cites variability within Galloanseres and rejects this character as a synapomorphy. Yet, the fact that it varies in some individual skeletons, or even if it is found in some other neognath taxa, does not exclude it from being a shared derived character.
38. External (lateral) mandibular condyle of quadrate relatively large and oriented lateromedially: (0) absent, (1) present. *Note:* Postulated to be a synapomorphy of Galloanseres by Cracraft (1988). Dzerzhinsky (1995) and Livezey (1997) considered the loss of the caudal condyle a synapomorphy of Galloanseres. Ericson (1996) suggests this and the next two characters are not independent. If a more detailed analysis of anseriform and galliforms shows they *always* covary as discrete character states, then they might be treated as a single character. The results of this study would not change using either approach to coding.
39. Articular surface of mandible having single centrally located ridge oriented anteroposteriorly: (0) absent, (1) present. *Note:* Postulated to be a synapomorphy by Cracraft (1988) and by Livezey (1997, his character 26). Ericson (1996) suggested that this character is also present in *Hesperornis*, *Baptornis* and *Ichthyornis*, but reexamination of specimens of *Ichthyornis* and *Hesperornis* at the Yale Peabody Museum did not confirm this supposition; the central ridge of the articular surface is oriented laterally (contra the illustration in Gingerich 1973), a condition not observed in Galloanseres.
40. Posteromedial and lateral walls of articular surface of mandible: (0) present, (1) absent. *Note:* Postulated to be a synapomorphy by Cracraft (1988).
41. Long, dorsally oriented internal articular process on mandible: (0) absent, (1) present. *Note:* Postulated to be a synapomorphy by Cracraft (1988) and by Livezey (1997, his character 25). Ericson (1996) again cites processes he considers equivalent in several disparate neognath taxa (Turnicidae, Cuculidae and several passeriform families); that this character might exhibit homoplasy within neornithines does not negate it as a local synapomorphy of Galloanseres.
42. Long, curving retroarticular process strongly compressed lateromedially: (0) absent, (1) present. *Note:* Postulated to be a synapomorphy by Cracraft (1988) and by Livezey (1997, his character 20). Despite the fact that other taxa might have a lengthened retroarticular process (Ericson 1996), none has the long, flattened shape characteristic of Galloanseres.
43. Parental care: (0) primarily females, (1) biparental, (2) primarily males. *Note:* See McKittrick (1992). McKittrick considered the absence of parental care as the plesiomorphic condition for Archosauria, and although crocodylians do not brood their eggs, they tend them and often lay next to the nest and engage in a variety of post-hatching behaviors related to “rearing” (Cott 1971). The female is considered to be the primary caregiver, though both parents are said to participate. Thus, whether this behavior is considered primarily female or biparental, the palaeognath condition with primarily male caregiving would be derived, as would this condition elsewhere in neognaths (McKittrick 1992). None of those latter taxa, however, are likely to be at the base of the neornithine tree.
44. First synsacral vertebra heterocoelous, or saddle-shaped: (0) absent, (1) present. *Note:* Gauthier (1986) considered heterocoelous articulations extending into the posterior thoracic vertebrae a possible synapomorphy of neornithines following previous authors. Martin (1987) has argued that the heterocoelous thoracics in *Hesperornithes* are probably convergent with those of neornithines as they are absent in *Enaliornis*, which he considered the basalmost member of this clade. The relationship of *Enaliornis* to *Hesperornis* and *Baptornis* needs to be reviewed. The present character does not require a phylogeny of *Hesperornithes* since all of these taxa, as well as *Ichthyornis*, lack heterocoelous first synsacral vertebrae. Although the morphology of the cranial articular surface varies within neornithines, the distribution of the character within taxa included in this analysis constrains the optimization of the derived condition to the base of Neornithes.