Morphological and molecular support for nonmonophyly of the Galloanserae

Per G. P. Ericson
Department of Vertebrate Zoology, Swedish Museum of Natural History
P.O. Box 50007, SE-104 05 Stockholm, Sweden
E-mail: per.ericson@nrm.se

Thomas J. Parsons
U.S. Armed Forces DNA Identification Laboratory
Armed Forces Institute for Pathology
1413 Research Blvd., Rockville, MD 20850 U.S.A.
E-mail: parsons@afip.osd.mil

Ulf S. Johansson
Department of Vertebrate Zoology, Swedish Museum of Natural History
P. O. Box 50007, SE-104 05 Stockholm, Sweden

Department of Zoology, University of Stockholm
SE-106 91 Stockholm, Sweden
E-mail: ulf.johansson@nrm.se

Abstract
This paper discusses morphological and molecular data bearing on the earliest evolution of the Neornithes. Phylogenetic analyses of basal neornithine groups frequently result in poorly resolved trees, most likely caused by rapid branching events in the Cretaceous and early Tertiary. Although data that efficiently resolve the earliest history of modern birds are few, a consensus opinion about their basal phylogeny has emerged in recent years. Two major splits within Neornithes are postulated. The first occurs when the palaeognathous birds branch off from the rest (the Neognathae), and the second when the Anseriformes and Galliformes split from all other neognaths. Morphological data presented by Livezey (1997) supporting this second dichotomy are combined with additional data from Ericson (1997) and re-analyzed. In addition, a new data set consisting of nucleotide sequences from the nuclear, single-copy gene c-*myc* is analyzed separately and in combination with the morphological data. Neither analyses support the suggested anseriform–galliform relationship. Instead, the Anseriformes group with the Ciconiiformes, Phoenicopteriformes and Charadriiformes, that is, a clade of wading birds.

Keywords
Neornithes, Palaeognathae, Neognathae, Anseriformes, Galliformes, phylogeny, skeletal morphology, nucleotide sequences, c-*myc*.

Appendix: Data matrix

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

© 2001 Per G. P. Ericson, Thomas J. Parsons and Ulf S. Johansson. 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: Data matrix

Data matrix for the analysis of the pooled morphological data sets of Ericson (1997) and Livezey (1997). Below the character numbers are indicated the numbers in the original data sets. Character descriptions, codings and polarities are as in the original publications.

					5					10					15					20					25
	E2	E4	E5	E6	E8	E9	E10	E11	E13	E14	E16	E17	E19	E20	E21	E22	E23	E24	E25	E26	E27	E28	E29	E30	E32
Tinamiformes	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Charadriiformes	1	0	0	1	1	1	0	0	0	0	1	0	0	0	1	1	0	1	1	0	0	1	0	0	0
Ciconiiformes	0/1	0	0	0/1	2	1	0	0	0/1	0/1	1	0	0	0	1	0	0	0	0/1	0/1	0	0	0	0	0
Phoenicopteriformes	1	1	0	1	2	1	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Galliformes	1	0	0	0/1	1	0	0/1	0	0	0	1	0	0/1	0	1	0	0	0	0	0	0	0	1	0/1	0
Anhima	1	0	0	1	2	0	0	0	0	0	1	1	1	0	1	0	1	0	0	1	0	0	0	0	0
Chauna	1	0	0	1	2	0	0	0	0	0	1	1	1	0	1	0	1	0	0	1	0	0	0	0	0
Anseranas	1	0	0	1	2	0	0	1	0	0	1	1	1	1	1	0	0	0	0	1	1	0	0	0	0
Anatidae	1	0	1	1	2	0	0	1	0	0	1	1	1	1	1	0	0	0	0	0	1	0	0	0	0

					30					35					40					45					50
	E33	E34	E35	E36	E37	E38	E39	E40	E41	E42	E43	E44	E45	E46	E47	E48	E49	E50	E51	E52	E53	E54	E56	E57	E58
Tinamiformes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Charadriiformes	0	1	0	0	1	0	1	2	1	0	1	1	1	0	0	0	0	0	1	0	0	1	0	0	0
Ciconiiformes	0	1	0	0	0	0	1	1/2	1	0	0	0/1	1/2	0/2	0/1	0	0	0	0	0	0	1	0	0	0
Phoenicopteriformes	0	1	0	0	1	0	1	2	1	0	0	1	1	0	0	1	0	0	0	0	0	1	0	0	0
Galliformes	0/1	0	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0
Anhima	0	0	0	0	1	0	1	2	1	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0
Chauna	0	0	0	0	1	0	1	2	1	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0
Anseranas	0	0	0	0	1	1	1	2	1	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0
Anatidae	0	0	0	0	0	1	1	2	1	0	0	1	1	0	0	1	0	0	0	0	0	1	0	0	0

					55					60					65					70					75
	E59	E60	E61	E62	E63	E64	E65	E67	E68	E69	E70	E71	L1	L2	L3	L4	L5	L6	L7	L8	L9	L10	L11	L12	L13
Tinamiformes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Charadriiformes	0	1	1	1	0	1	0	0/1	0	0	0	0	0	0	0/1	0	0	0	2/3	0	0/1	0	0	0	0
Ciconiiformes	0	1	1	1	0	1	0	1	0	0	0	0	0/1	0	0/1	0	0	0	3	0	0/1	0	0	0	0
Phoenicopteriformes	0	1	1	1	0	1	0	0	0	0	0	0	0	1	1	0	0	0	3	0	0	0	0	0	0
Galliformes	0	0	0	0	0	0	0	0	0	0	0/1	0	1	0	0	1	0	0	1	1	0	0	0	0/1	0
Anhima	0	1	1	1	0	2	0	0	0	1	0	0	1	0	0	1	1	1	1	2	0	0	1	0	1
Chauna	0	1	1	1	0	2	0	0	0	1	0	0	1	0	0	1	1	1	1	2	0	1	0	0	1
Anseranas	0	1	1	1	0	1	0	0	0	1	0	0	1	1	1	0	2	0	1	3	1	0	0	1	0
Anatidae	0	1	1	1	0	1	0	0	0	1	0	0	1	1	1	0	2	0	1	3	1	0	0	0	0

					80					85					90					95					100
	L14	L15	L16	L17	L18	L19	L20	L21	L22	L23	L24	L25	L27	L28	L29	L30	L31	L32	L33	L34	L35	L36	L37	L38	L39
Tinamiformes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Charadriiformes	0	0	0	0/1	0	0	0	0	0	0	0	0	0/1	0	0	0/1	0	0	0/1	0	0/1	0/1	0	0	0
Ciconiiformes	0	0	0	0/1	0	0	3	0	0	0	0	0	0	1	0	0	0	0	0/1	0	0/1	0/1	0	2	0
Phoenicopteriformes	2	0	0	0	0	0	2	0	0	0	0	1	0	0	0	0	1	0	0	0	0	1	0	2	0
Galliformes	0	0/1	0	0	0	1	1	0	0	0	1	1	0	1	0	0	0	0	0	0	0/1	1	0	0	0
Anhima	0	1	0	0	0	1	2	0	0	0	1	1	0	1	0	0	0	0	0	0	1	1	0	1	1
Chauna	0	1	0	0	0	1	2	0	0	0	1	1	0	1	0	0	0	0	0	0	1	1	0	1	1
Anseranas	0	0	1	1	1	1	2	0	1	1	1	1	1	1	0	1	1	0	1	1	1	1	1	2	1
Anatidae	1	0	1	1	1	1	2	1	1	1	1	1	1	1	0/1	1	1	1	1	1	1	1	1	2	1

Appendix, continued.

					105					110					115				120					125
	L40	L41	L42	L43	L44	L45	L46	L47	L48	L49	L50	L51	L52	L53	L54	L55	L56	L57	L58	L59	L60	L61	L62	L63	L64
Tinamiformes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Charadriiformes	0	1	1	1	1	0	1	2	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0/1	0	0
Ciconiiformes	0	1	1	1	1	0	1	2	0	0	0	0	0	0	0/1	0	0/1	0	0	0	0	0	0/1	0	1
Phoenicopteriformes	0	1	1	1	1	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Galliformes	0	1	0	1	1	0	0	2	0/1	1	0	1	0	0	0/1	0	0	0	0	0	1	1	1	0	1
Anhima	0	1	0	1	1	1	0	1	0	2	0	1	1	1	0	0	1	1	1	0	0	0	0	1	1
Chauna	0	1	0	1	1	1	0	1	0	2	0	1	1	1	0	0	1	1	1	0	0	0	0	1	1
Anseranas	1	1	1	1	1	2	0	1	1	1	1	1	1	1	1	1	1	1	0	1	0	0	0	0	1
Anatidae	1	1	1	1	1	2	0	1	1	1	1	1	1	1	0	1	1	1	0	2	0/1	0	0	0	0/1

					130					135					140				145					150
	L65	L66	L67	L68	L69	L70	L71	L72	L73	L74	L75	L76	L77	L78	L79	L80	L81	L82	L83	L84	L85	L86	L87	L88	L89
Tinamiformes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Charadriiformes	0	0	1	1	0/1	0	0/1	0	0	0	0/1	0	0	1	0	0	0	1	0	0	0/1	0	0	0/1/2	0
Ciconiiformes	0/1	0/1	1	1	1	0	0/1	0	0	0	0/1	0	0	1	0/1	0/1	0	1	0	0	0	0	0	1/2	0
Phoenicopteriformes	0	0	1	0	0	0	1	0	0	0	1	0	0	1	0	0	0	1	0	0	1	0	0	2	0
Galliformes	0	1	1	1	0/1	0/1	0	0	0	0/1	0	0	0	1	2	0	0	0	0	0	0	0	0	0/1	1
Anhima	1	1	0	1	0	1	1	1	1	0	1	1	1	1	2	1	0	1	0	1	0	1	1	1	0
Chauna	1	1	0	1	0/1	1	1	1	1	0	1	1	1	1	2	1	0	1	0	1	0	1	1	1	0
Anseranas	1	0	1	1	0	1	1	0	0	0	1	0	0	1	1	1	0	1	0	0	1	1	1	1	0
Anatidae	0	0/1	0	0	1	0	0/1	0	0	0	1	0	0	1	0	1	1	1	1	0	1	1	1	0/1	0

					155					160					165					170
	L90	L91	L92	L93	L94	L95	L96	L97	L98	L99	L100	L101	L102	L103	L104	L105	L106	L107	L108	L109
Tinamiformes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Charadriiformes	0	0	0	0	0/1	0	0/1	1	0	0	0	0	0/1	0	0	0	0	0	0	0
Ciconiiformes	0	1	0	0	0	0	1	1	0	0	0	0	0/1	0	0	0	0	0	0	0
Phoenicopteriformes	0	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0
Galliformes	1	1	0	0	0	0	1	0/1	0	0/1	0	0	0/1	0	0	0	0	0	0	0
Anhima	1	1	0	0	0	1	1	0	1	1	1	0	1	1	0	1	1	0	0	0
Chauna	1	1	0	0	0	1	1	0	1	1	1	1	1	1	1	0	1	1	0	1
Anseranas	1	1	0	1	0	1	1	0	0	1	0	0	1	2	0	0	0	0	1	0
Anatidae	0	0	1	0	1	1	0	1	0	1	0	0	0	2	0	0	0	0	0	0

					175					180					184
	L110	L111	L112	L113	L114	L115	L116	L117	L118	L119	L120	L121	L122	L123
Tinamiformes	0	0	1	2/3	2	0	0	0	0	0	0	0	0/1	0
Charadriiformes	0	0	0	2	1	0	0	1	1	0	0/1	0	1/2	0
Ciconiiformes	0	0	0	2	2	0/1/2	0	1	1	0	0	0	2	0
Phoenicopteriformes	1	0	0	2	2	3	0	1	1	0	0	0	1	0
Galliformes	0	0/1	0	0/2	0	0/1	0	0	0	0	0	0	2	0
Anhima	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Chauna	0	0	0	0/2	0	1	1	0	0	0	0	0	0	0
Anseranas	0	0/1	0	0/2	0	2	0	0	0	1	0	0	0	0
Anatidae	0	1	0	0	0	3	0	0	0	1	1	1	0	1