

S20-1 Supra-generic cladistics of landfowl (Order Galliformes)

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Abstract Molecular and organismal evidence bearing on the evolutionary relationships of gamebirds within the order Galliformes is reviewed. The monophyly of most traditionally recognized supra-generic taxa is supported, but the Phasianini (pheasants) and Perdicipini (partridges and quails) are shown to be polyphyletic. Contrary to DNA-DNA hybridization data, New World quails (Odontophoridae) did not branch off the galliform evolutionary tree before the guineafowl (Numididae), but rather immediately after; and the cracids (Cracidae) and megapodes (Megapodiidae) are not sister groups of one another. Evidence is presented to support the notion of very early divergence among species currently confined to the New World, Africa and southeast Asia. Evidence from mtDNA sequences (cytochrome *b* and D-loop), proteins (ovomucoids), life history, behavior, and bones and feathers is analyzed phylogenetically in three ways: separately, combined and combined but differentially weighted. Separate analysis always produces less well-resolved trees than those suggested by combined data; and deweighting putatively less informative evidence undermines rather than enhances phylogenetic signal. Furthermore, analysis of combined data produces a tree with a novel, but biogeographically meaningful, topology, with organismal and molecular information more useful at respective more basal and more terminal branches of the tree.

Key words Galliformes, Phylogeny, Combined vs separate vs deweighted evidence

1 Introduction

The phylogeny of the pheasant, quail and turkey order Galliformes is reconstructed for 102 in-group taxa listed in Crowe et al. (1992, Appendix 3) and rooted on two representatives of the Anseriformes, a duck (*Cairina moschata*) and a screamer (*Chauna torquata*). Exemplars represent all putative supra-generic taxa and 55 traditionally recognized genera (after del Hoyo et al., 1994). Character data include a combination of 949 phylogenetical informants, from morphology and behavior ($n = 47$), ovomucoid amino acids ($n = 47$), and gene sequences in mitochondrial cytochrome *b* and D-loop ($n = 522, 333$ respectively). Raw data matrices for these three sources of character variation are available from the senior author or from the web site of the Percy FitzPatrick Institute.

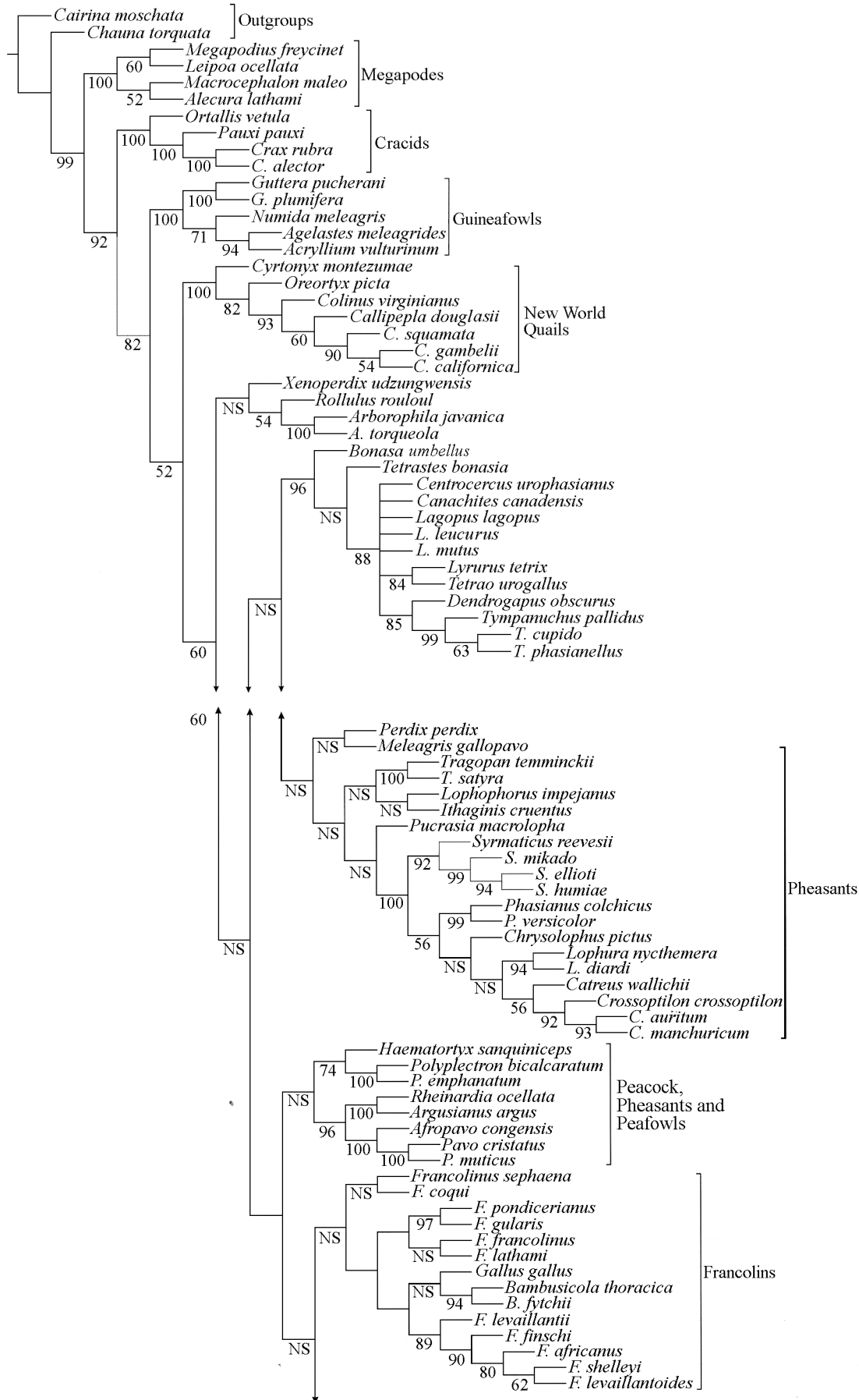
2 Methods

Phylogenetic analyses were conducted using WinClada ver. 0.9.99m8.1 BETA (Nixon, 2000). The searching strategy employed was the Ratchet Island Hopper (1 000 iterations; 2 trees to hold; $\pm 10\%$ characters to sample; and amb. poly. = option), with organismal characters as additive and all molecular characters nonadditive. Bootstrap

analyses were conducted with 1 000 replicates.

3 Results and discussion

Analysis of the combined dataset of characters yielded two equally parsimonious trees (CI = 0.21, 7 296 steps), of which a strict consensus application required the collapsing of five nodes, all within the tetraonine grouse (Fig. 1). Traditionally recognized supra-generic taxa supported by this consensus tree with $\geq 50\%$ bootstrap support are: (1) the Superfamily Phasianoidea, including all galliforms except the megapodes and cracids; (2) the megapodes (Megapodiidae); (3) the cracids (Cracidae); (4) the guineafowls (Numididae); and (4) the New World quails (Odontophoridae). Resolution within the Phasianidae is not well supported. Within the phasianids, the grouse (Tetraoninae), the gallo-pheasant subset of the pheasants (Phasianinae, including *Syrmaticus*, *Phasianus*, *Chrysolophus*, *Lophura*, *Catreus* and *Crossoptilon*), and the pavonine peafowl (Pavonini, including *Rheinardia*, *Argusianus*, *Afropavo* and *Pavo*) are supported. However, although grouping with the gallo-pheasants, the basal pheasant assemblage of Johnsgard (1986), excluding the junglefowls (*Gallus* spp.) and peacock-pheasants (*Polyplectron* spp.), does not have “significant” ($\geq 50\%$)



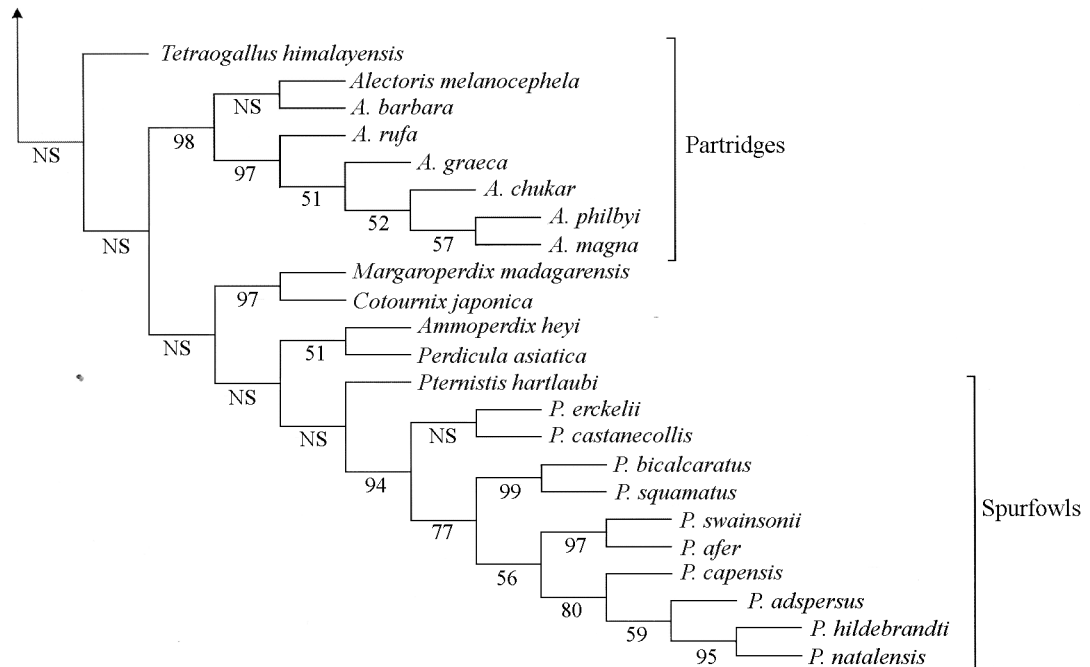


Fig. 1 (page 355 and above) Phylogenetic relationships of galliform birds

Tree based on maximum parsimony analysis of a combination of 949 phylogenetically informative morphological-behavioral, ovomucoid amino acid, and mitochondrial cytochrome *b* and D-loop characters. Numbers at nodes are bootstrap values (NS = not supported by bootstrap values of ≥ 50).

bootstrap support.

The monophyly of several traditionally recognized groupings is not supported. The megapodes and cracids which comprise the order Craciformes or superfamily Cracoidea are paraphyletic with respect to one another. Partridges (tribe *Perdicini*) are highly polyphyletic. The grey partridge (*Perdix perdix*) groups with the wild turkey (*Meleagris gallopavo*) or with the pheasants when the turkey is excluded. The sister taxon of the Madagascan partridge (*Margaroperdix madagarensis*) is the common quail (*Coturnix coturnix*), and that of the sand partridge (*Ammoperdix heyi*) is the bush quail (*Perdicola argoondah*). The francolins (*Francolinus* spp., *sensu* Hall, 1963) comprise at least two distantly related clades: (1) true francolins, including *Dendroperdix*, *Peliperdix*, *Francolinus* and *Scleroptila*, and (2) spurfowls, including *Pternistis* (also Crowe et al., 1992; Bloomer and Crowe, 1998).

Contrary to DNA-DNA hybridization results (Sibley and Ahlquist, 1985, 1990; Sibley, 1994) and those of 'culled' DNA sequences of mitochondrial cytochrome *b* from a small set of exemplar taxa (Kornegay et al., 1993), the New World quails, although basal within the Phasianoidae, are not basal relative to the guinea-fowls. Noteworthy among the other novelties is the placement of the red junglefowl (*Gallus gallus*) with bamboo partridges (*Bambusicola* spp.), within a clade dominated by "francolins" and "partridges" and outside of clades including pheasants (cf., Fumihito et al., 1995; Kimball et al., 1999). Other novel groupings include the association of the recently discovered African "partridge" *Xenoperdix udzungwensis* (Dinesen et al., 1994) with

Asiatic "partridges" (*Rollulus rouloul* and *Arborophila* spp.), and the crimson-headed wood partridge (*Haematortyx sanquineus*) with the peacock-pheasants (*Polyplectron*).

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