

Phylogeny of shorebirds, gulls, and alcids (Aves: Charadrii) from the cytochrome-*b* gene: parsimony, Bayesian inference, minimum evolution, and quartet puzzling

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Abstract

Charadrii shorebirds, gulls, and alcids have exceptional diversity in morphology, behaviour, and life-history traits. A phylogenetic framework is necessary to fully understand the relationships among these birds. Despite several attempts to resolve the phylogeny of the Charadrii, none have comprehensively utilized molecular sequence data. Complete and partial cytochrome-*b* gene sequences for 90 Charadrii and five *Falconidae* species (as outgroup taxa) were obtained from GenBank and aligned. We analysed the resulting sequence using parsimony, Bayesian inference, minimum evolution, and quartet puzzling methods. Posterior probabilities, decay indices, and bootstrapping provide strong support for four major lineages consisting of gulls, alcids, plovers, and sandpipers, respectively. The lowest structure of the tree differs significantly from all previous hypotheses of Charadrii phylogeny in placing the plovers at the base of the tree before the sandpipers and gulls; a posterior support towards a large clade of gulls and alcids. The parsimony, Bayesian, and minimum evolution results provide strong evidence for this phylogenetic hypothesis. This is further corroborated by non tree based measures of support and conflict (Locus plot). The quartet puzzling trees are poorly resolved and inconsistent.

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1. Introduction

The Charadrii (shorebirds, gulls, and alcids) display exceptional diversity in their ecology, behaviour, and breeding systems (Bonser and Oring, 2002; Ligon, 1996; Rensvold and Sackley, 1987; Sackley et al., 2000). Phylogenetic comparative studies have begun to reveal relationships between sexual selection, breeding systems, migration, parental care, breeding density, and sexual size dimorphism. Despite advances in our knowledge of the life-history evolution of the group, the phylogeny itself remains unresolved.

The earliest studies of Charadrii classification differed markedly from contemporary views. The close relationships of sandpipers, plovers, mystacinids, and gulls were recognized by Linnaeus (1758) in his group the *Circidae*, but he also included cranes, herons, and

rails in this group whilst excluding the gulls and alcids. The addition of the alcids initially proved elusive, being regarded as relations of the pelagicus until Sharpe (1867) grouped them with the gulls based on palatal paper. Quoy (1892) proposed a classification of the Order Charadriiformes that reunited already current relations including sandpipers, plovers, gulls, and alcids. Despite this apparent intuition, the *haradrii* (Kittlitz) were later grouped with the plovers and sandpipers because of their superficial similarity to thick-knee (*Elanus*), whilst the gulls and alcids were still excluded (e.g., Sharpe, 1896). Subsequent classifications involved minor amendments to previous schemes with a significant contribution coming from a series of detailed anatomical papers by Lusk (e.g., 1915, 1922). The extensive taxonomic works on the Charadrii have yielded surprising insight into the evolutionary history of the group. For example, Hall (1969) presented a “tentative phylogeny” based on color patterns of the downy young, which closely resembles the more recent DNA–DNA hybridization phylogeny of Sibley and Ahlquist

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