# the TIMETREE of LIFE

edited by **S. BLAIR HEDGES** and **SUDHIR KUMAR**
foreword by James D. Watson

# Shorebirds (Charadriiformes)

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## Abstract

The Order Charadriiformes is a major clade of shorebirds and consists of 19 families, ~90 genera, and 366 species. In DNA sequence trees three major clades representing suborders are recognizable: the Scolopaci (sandpipers and allies), Lari (gulls and allies, plus buttonquail), which form a group, and the Charadrii (plovers and allies). The latest divergence time estimates, incorporating uncertainties in phylogenetic trees and fossil dates, suggest that the Charadriiformes originated in the Cretaceous, about 93 million years ago (Ma), and that charadriiform families radiated mostly in the late Cretaceous (93–66 Ma) but also in the Paleogene (66–23 Ma).

Shorebirds are a diverse cosmopolitan group that forms the monophyletic Order Charadriiformes. They represent one of the largest clades in birds with 366 species classified traditionally in 19 families (*1*). The order can be divided into three major clades (*2–4*): Scolopaci (sandpipers, jacanas, painted snipes, seedsnipes, and Plains-wanderer), Lari (Crab Plover, coursers and pratincoles, gulls, terns, skimmers, and alcids), and Charadrii (plovers, oystercatchers, Ibisbill, stilts, avocets, sheathbills, and Magellanic Plover) (Fig. 1). Here we review the phylogenetic relationships and estimates of divergence times of the families of shorebirds.

Relationships among taxa and even which taxa should be included in the Charadriiformes has proved difficult in the past, due in part to convergent acquisition of traits involved in exploitation of a range of ecological niches (*4*). Phylogenies derived from an extensive data set of morphological and skeletal characters (*5*) lack resolution at various nodes, and the topologies change depending on how characters are coded and which ones are excluded from analyses (*5–8*). In addition to their incongruence,

these trees place the Alcidae as the closest relative of all other Charadriiformes. The three major clades of shorebirds were first detected in DNA–DNA hybridization studies (*9*), in which Charadrii and Lari (including Alcidae) formed a group, closest to Scolopaci, and the buttonquails (Turnicidae), traditionally classified in their own Order Turniciformes, were closest to the rest of the Lari. Phylogenetic analysis of a very large data set of 2954 morphological characters also led to this topology (*10*), but placed the Plains-wanderer (Pedionimidae), jacanas (Jacanidae), and painted snipes (Rostratulidae) outside the Scolopaci, and buttonquails as the closest relative to a group including shorebirds and rails (part of Gruiformes). DNA-sequencing studies subsequently altered this arrangement by joining the Lari and Scolopaci as closest relatives (*2–4, 11, 12*). Additionally, DNA sequence-based phylogenies placed buttonquails as the closest relatives to Lari (*2–4, 12*). Recent phylogenies of 90 recognized genera of charadriiforms showed that plovers and noddies are not monophyletic assemblages, and the enigmatic Egyptian Plover *Pluvianus* is not a plover (*2, 12*), and hence deserves to be placed in its own separate Family Pluvianidae. Similarly, gray and golden plovers *Pluvialis*



**Fig. 1** A Red Knot (*Calidris canutus*), Family Scolopacidae, from Delaware Bay, New Jersey, USA. Credit: M. Peck.
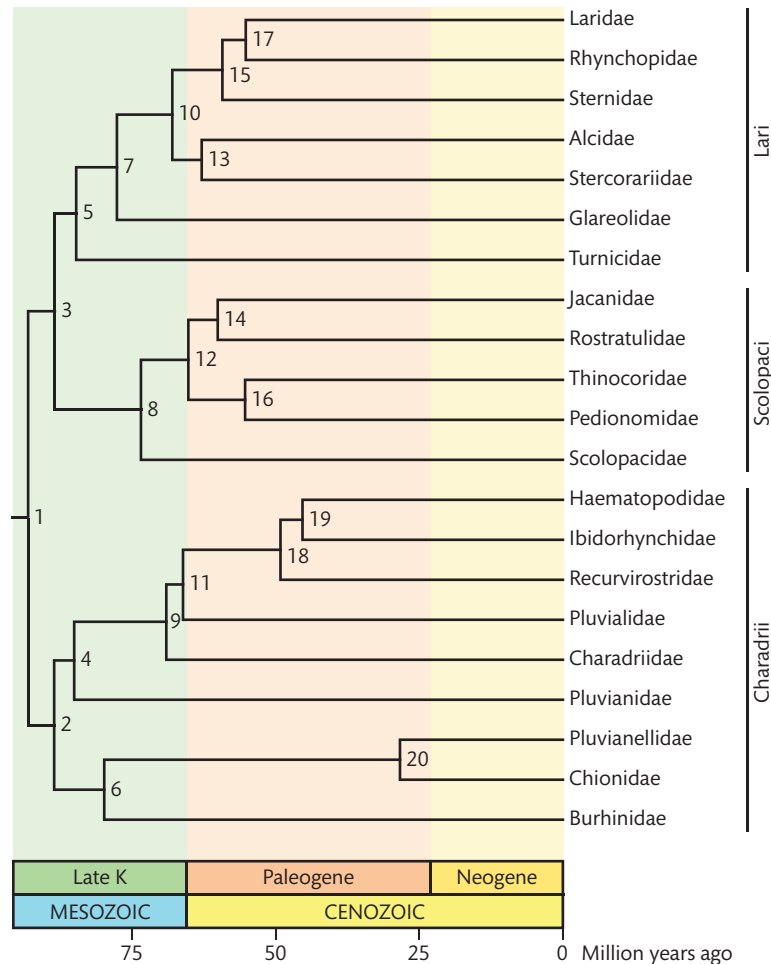
**Fig. 2** A timetree of shorebirds (Charadriiformes). Divergence times are from Table 1. *Abbreviation*: K (Cretaceous).

are also considered here in their own family Pluvialidae as they form a distinct lineage more closely related to oystercatchers (Haematopidae), Ibisbill (Ibidorhynchidae), and stilts and avocets (Recurvirostridae) than to typical plovers (Charadriidae) (*2, 12*). A multiple gene phylogeny of the terns (*13*) found 11 clades that were each classified in separate genera, expanding on the seven or 10 genera recognized previously (*14, 15*). Parallel evolution and retention of ancestral morphological states was inferred when they were mapped on a multigene phylogeny of the shanks (*16*). The phylogenetic affinities of sandgrouse (*Pterocles*) have been debated over a century (*10*). Morphological characters suggest a closer relationship between sandgrouse and pigeons (Columbiformes) (*10*), and DNA studies do not support a close relationship between *Pterocles* and shorebirds (*2, 4, 12*).

Estimates of divergence time within shorebirds (Table 1) based on analyses of mitochondrial DNA sequences (*2, 4, 17–20*) agree that the group originated in the Cretaceous, and some lineages have survived the Cretaceous–Paleogene mass extinction. However, other studies that included fewer shorebird lineages, and used different time constraints based on the fossil record or other molecular time estimates (*21, 22*) have suggested younger ages for the origin of Charadriiformes. We opted to show a timetree (Fig. 2) based in the most comprehensive study for the group, which includes members of all families and 93% of all genera, and used 14 fossil dates as internal constraints within Charadriiformes to properly account for uncertainties in fossil ages (*2*). Additionally, the minimum age of the root was taken from a study of vertebrates in which additional external fossil ages

**Table 1.** Divergence times (Ma) and their confidence/credibility intervals (CI) among shorebirds (Charadriiformes).

| Timetree | | Estimates | | | | | |
|---|---|---|---|---|---|---|---|
| | | Ref. (*2*) | | Ref. (*4*) | | Ref. (*18*) | |
| Node | Time | Time | CI | Time | CI | Time | CI |
| 1 | 93.1 | 93.1 | 102–85 | – | – | 81.7 | 94–69 |
| 2 | 88.6 | 88.6 | 98–80 | 65.6 | 79–51 | 75.6 | 88–62 |
| 3 | 88.5 | 88.5 | 98–80 | 75.8 | 80–66 | – | – |
| 4 | 85.1 | 85.1 | 95–76 | – | – | – | – |
| 5 | 84.7 | 84.7 | 94–76 | 71.8 | 78–61 | – | – |
| 6 | 79.9 | 79.9 | 90–70 | 54.0 | 67–42 | – | – |
| 7 | 77.6 | 77.6 | 87–69 | 45.2 | 56–37 | 64.5 | 78–51 |
| 8 | 73.4 | 73.4 | 83–64 | 63.8 | 70–57 | 63.4 | 77–48 |
| 9 | 69.0 | 69.0 | 79–60 | 32.8 | 44–22 | 62.4 | 77–47 |
| 10 | 68.0 | 68.0 | 77–60 | 36.0 | 44–25 | 51.8 | 67–38 |
| 11 | 66.1 | 66.1 | 76–57 | – | – | – | – |
| 12 | 65.2 | 65.2 | 75–56 | 52.1 | 60–45 | 49.5 | 64–32 |
| 13 | 62.9 | 62.9 | 72–55 | – | – | 45.6 | 59–31 |
| 14 | 60.1 | 60.1 | 70–51 | 45.8 | 54–38 | – | – |
| 15 | 59.3 | 59.3 | 68–51 | 24.4 | 33–17 | – | – |
| 16 | 55.3 | 55.3 | 66–46 | 52.1 | 60–45 | – | – |
| 17 | 55.2 | 55.2 | 64–47 | 22.7 | 33–16 | – | – |
| 18 | 49.2 | 49.2 | 59–40 | 13.9 | 22–7 | 45.4 | 64–30 |
| 19 | 45.3 | 45.3 | 56–36 | 19.1 | 28–12 | – | – |
| 20 | 28.3 | 28.3 | 37–21 | 19.0 | 29–12 | – | – |

*Note*: Node times in the timetree are from ref. (*2*). Ref. (*4*) provides results from a combined analysis of the nuclear *RAG1* gene and three mitochondrial genes, and ref. (*18*) provides results from the analyses of partial mtDNA genome sequences.

had been employed (*19*). The common ancestor of the Charadriiformes is estimated to have occurred between 85 and 102 Ma, with a mean estimate of 93 Ma. The much older age of the common ancestor than estimated in (*4*) is because the age of the root was previously fixed at 78 Ma, which in turn was based on a molecular age calculated from mtDNA genome sequences (*23*). Similarly, in an admittedly conservative approach in which calibrations of 62 Ma for the divergence of storks and penguins and 66 Ma for the origin of the Anseriformes (*24–26*) were used as minimal fossil anchor-points, the Charadriiformes was estimated to have originated about 69 Ma (*22*).

The three suborders of Charadriiformes diverged in the late Cretaceous 98–79 Ma, with a mean estimate of ~88 Ma. Fourteen ancestors of extant lineages were estimated to have occurred before the Mesozoic–Cenozoic boundary (66 Ma). Ten existing families and the two monogeneric lineages that need to be elevated to family status (Pluvialidae and Pluvianidae) also predated this boundary (Fig. 2). Diversification of genera, however, predominantly occurred after the asteroid impact, from the Paleocene to the mid-Miocene (66–15 Ma) (*4*). The survival of so many lineages dating from an origin in the late Cretaceous (*22, 23, 27, 28*) may explain why it has been historically difficult to determine the limits of the Charadriiformes, as many ancient forms have disparate morphologies as they adapted to a wide range of ecological niches over vast timescales.

## Acknowledgments

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