



Feraequornithes: a name for the clade formed by *Procellariiformes*, *Sphenisciformes*, *Ciconiiformes*, *Suliformes* and *Pelecaniformes* (Aves)

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Abstract

Recent genomic data sets have resolved many aspects of higher-level phylogenetic relationships of birds. Eleven phylogenomic studies provide congruent support for a clade formed by *Procellariiformes*, *Sphenisciformes*, *Ciconiiformes*, *Suliformes* and *Pelecaniformes*. This clade is here named ‘*Feraequornithes*’ following the rules and requirements of the *PhyloCode*.

Key words

Aequornithes, clade names, PhyloCode, phylogenetic nomenclature, rankless taxonomy

Introduction

The resolution of the avian tree of life has proceeded steadily since the first use of nuclear DNA markers in avian systematics in the late 1990s. With the analysis of phylogenomic data sets, many aspects of higher-level relationships of birds were congruently resolved by independent data sets (Ericson et al. 2006; Hackett et al. 2008; McCormack et al. 2013; Jarvis et al. 2014; Burleigh et al. 2015; Prum et al. 2015; Reddy et al. 2017; Kuhl et al. 2021). One recently clarified group is a large clade of aquatic and semi-aquatic birds (Ericson et al. 2006; Hackett et al. 2008; Burleigh et al. 2015; Prum et al. 2015; Kimball et al. 2019; Kuhl et al. 2021), which was named *Aequornithes* (Mayr 2011). *Aequornithes* (Fig. 1) includes the divers (*Gaviidae*), storm-petrels (*Hydrobatidae*, *Oceanitidae*), albatrosses (*Diomedidae*), petrels (*Procellariidae*) including diving-petrels (*Pelecanoides*

spp.), penguins (*Spheniscidae*), storks (*Ciconiidae*), frigatebirds (*Fregatidae*), darters (*Anhingidae*), cormorants (*Phalacrocoracidae*), gannets and boobies (*Sulidae*), herons (*Ardeidae*), ibises (*Threskiornithidae*), pelicans (*Pelecanidae*), Shoebill (*Balaenicipitidae*), Hamerkop (*Scopidae*) and the extinct stem representatives of these clades.

These studies have further shown that ‘*Pelecaniformes*’ and ‘*Ciconiiformes*’, as traditionally circumscribed (e.g. Storer 1971; Howard and Moore 1991), represent non-monophyletic groups. There is now robust evidence that herons, ibises, pelicans and allies form a clade; that the frigatebirds, darters, cormorants, gannets and boobies form another clade, and that the storks represent a third clade. These three clades are now known as *Pelecaniformes*, *Suliformes* and *Ciconiiformes*, respectively (Yuri et al.

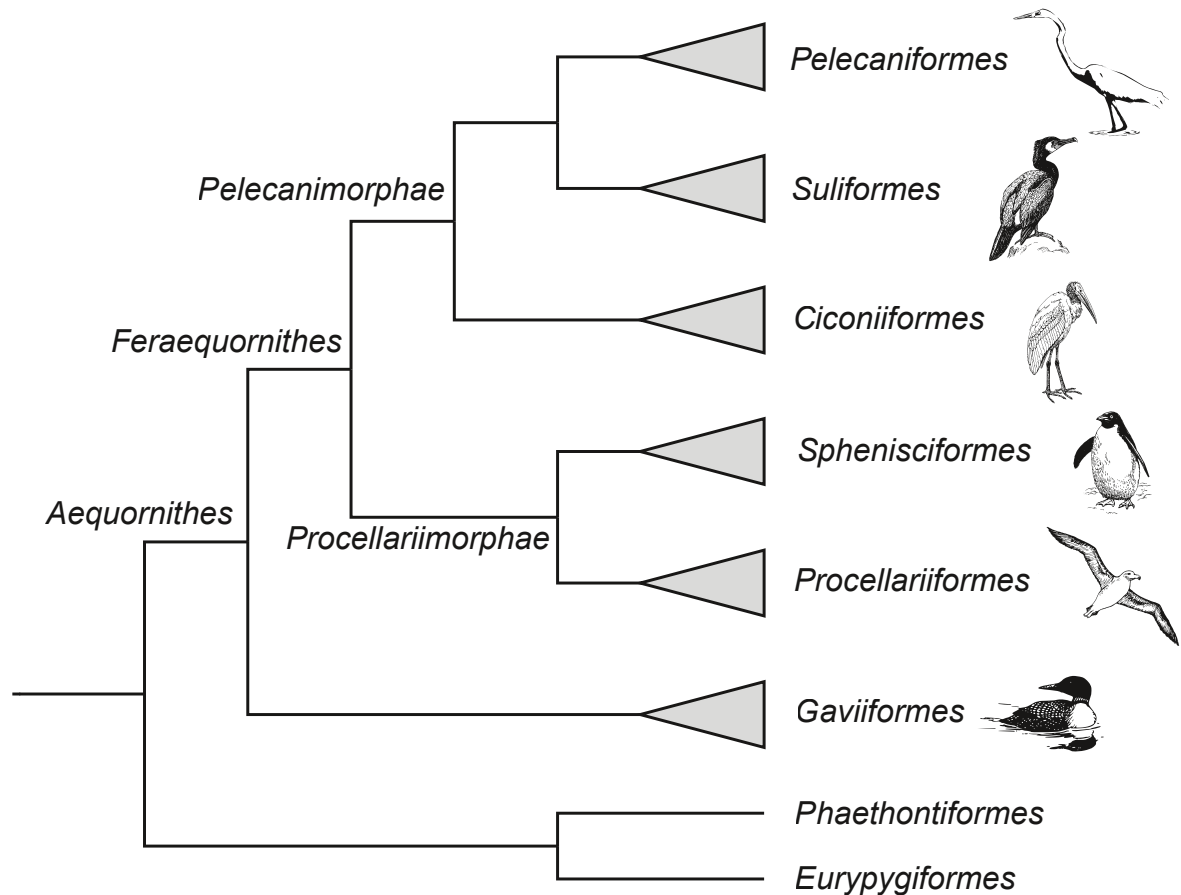


Figure 1. Consensus phylogeny of aquatic and semi-aquatic birds (based on Hackett et al. 2008, Burleigh et al. 2015, Prum et al. 2015, Reddy et al. 2017, Kimball et al. 2019, Kuhl et al. 2021). All bird vignettes are in the public domain (<https://publicdomain-vectors.org>).

2013; Mayr 2017; Kimball et al. 2019; Kuhl et al. 2021), although Cracraft (2013) used the name *Pelecaniformes* for a group that combines all three clades. A sister group relationship of *Procellariiformes* and *Sphenisciformes* is also well-supported (Hackett et al. 2008; McCormack et al. 2013; Jarvis et al. 2014; Burleigh et al. 2015; Kuramoto et al. 2015; Prum et al. 2015; Reddy et al. 2017; Kimball et al. 2019; Kuhl et al. 2021), and this clade has been named *Procellariimorphae* (Livezey and Zusi 2007).

Evidence for a clade formed by *Procellariiformes*, *Sphenisciformes*, *Ciconiiformes*, *Suliformes* and *Pelecaniformes* consists of multiple phylogenomic data sets generated in eleven studies, and is summarized in Table 1. This clade has not been named yet, unlike many other novel clades that are now widely supported (Sangster 2005a, 2005b; Mayr 2011; Suh et al. 2011; Ericson 2012; Yuri et al. 2013; Prum et al. 2015).

The stability of taxonomic names above the superfamily rank has long been problematic because their availability and priority was not governed by any nomenclatural code. In the mid 1980s, taxonomists began proposing, discussing and using phylogenetic definitions for clade names (e.g. Gauthier 1986; Rowe 1987; De Queiroz and Gauthier 1992; Bryant 1994; Lee 1996; Padian et al. 1999). This grew out of the recognition that the current rank-based systems of nomenclature (e.g. ICZN 1999) are poorly suited to regulate the names of clades. These

discussions about phylogenetic nomenclature have led to the development of the *PhyloCode* which went through several preliminary versions that appeared online between 2000 and 2019. The publication of the *PhyloCode* (v6; Cantino and De Queiroz 2020), which came into effect in June 2020 with the publication of the companion volume *Phylonoms* (De Queiroz et al. 2020) and the RegNum online database (Cellinese and Dell 2020), now provides an opportunity to formalize and stabilize clade names. The *PhyloCode* provides rules for the express purpose of naming clades through explicit reference to phylogeny (Cantino and De Queiroz 2020). The purpose of this note is to define a name for the clade formed by *Procellariiformes*, *Sphenisciformes*, *Ciconiiformes*, *Suliformes* and *Pelecaniformes* following the rules and requirements of the *PhyloCode*.

***Feraequornithes*, new clade name**

RegNum registration number: 416

Definition. The least-inclusive crown clade containing *Pelecanus onocrotalus* Linnaeus, 1758 (*Pelecaniformes*) and *Procellaria aequinoctialis* Linnaeus, 1758 (*Procel-*

Table 1. Phylogenomic support for the clade formed by *Procellariiformes*, *Sphenisciformes*, *Ciconiiformes*, *Suliformes* and *Pelecaniformes*. ML, maximum likelihood; PP, posterior probability; MRP, matrix representation with parsimony; SH-aLRT, Shimodaira-Hasegawa approximate likelihood ratio test.

Source	Data type(s)	Support
Hackett et al. (2008)	19 nuclear loci	94% ML bootstrap
McCormack et al. (2013)	1541 ultra-conserved elements	100% ML bootstrap; 1.0 PP
Jarvis et al. (2014)	8251 exon loci, 2516 intron loci, 3769 ultra-conserved elements	100% exaML bootstrap
Burleigh et al. (2015)	25 nuclear loci, mitochondrial DNA	73% ML bootstrap
Kuramoto et al. (2015)	30 retroposon presence/absence loci	P < 0.001
Prum et al. (2015)	259 anchored nuclear loci	1.0 PP
Suh et al. (2015)	2118 retroposon presence/absence loci	(not given)
Reddy et al. (2017)	54 nuclear loci	≥ 95% ML bootstrap
Liu et al. (2018)	63 nuclear protein-coding loci	99% ML bootstrap
Kimball et al. (2019)	supertree	100% MRP bootstrap
Kuhl et al. (2021)	noncoding 3-prime untranslated region (3'UTR) sequences (2.5 million analyzable patterns)	100% (SH-aLRT)

lariiformes). This is a minimum-crown-clade definition. Abbreviated definition: min crown ∇ (*Pelecanus onocrotalus* Linnaeus, 1758 & *Procellaria aequinoctialis* Linnaeus, 1758).

Etymology. Coined from a combination of *Aequornithes* with the Latin adverb *ferè*, meaning “almost” or “near”, in reference to the fact that the clade includes almost all *Aequornithes* except *Gaviiformes*.

Reference phylogeny. For the purpose of applying the definition of *Feraequornithes*, Figure 3 in Kuhl et al. (2021) should be regarded as the primary reference phylogeny. Figure 1 in Prum et al. (2015) may be regarded as a secondary reference phylogeny.

Composition. *Feraequornithes* includes the herons (*Ardeidae*), ibises (*Threskiornithidae*), pelicans (*Pelecanidae*), Shoebill (*Balaenicipitidae*), Hamerkop (*Scopidae*), frigatebirds (*Fregatidae*), darters (*Anhingidae*), cormorants (*Phalacrocoracidae*), gannets and boobies (*Sulidae*), storks (*Ciconiidae*), storm-petrels (*Hydrobatidae*, *Oceanitidae*), albatrosses (*Diomedidae*), petrels (*Procellariidae*) including diving petrels (*Pelecanoides* spp.), and penguins (*Spheniscidae*). This clade comprises 310–350 extant species, listings of which are given in Dickinson and Remsen, (2013) and Gill et al. (2020). Accounts of extinct groups (*Diomedoididae*, *Plotopteridae*) are provided by Olson and Hasegawa (1979), De Pietri et al. (2010), Mayr and Smith (2012), Mayr (2017) and Mayr et al. (2021).

Diagnostic apomorphies. Members of this clade possess long, slit-like nostrils in juveniles (Mayr 2017). These are absent in extant *Sphenisciformes* and *Procellariiformes*, but occur in adults of long-beaked fossil stem group *Sphenisciformes* (Ksepka et al. 2008; Mayr et al. 2017). Possibly correlated with the latter trait, the beak of adult birds of most representatives of the clade exhibits furrows along its lateral surfaces, which begin at the rostral end of the nostril (these furrows are absent in the *Ciconiidae*

and weakly developed in the *Ardeidae*). Kuramoto et al. (2015) listed eight apomorphic retroposons (Chicken Repeat 1 insertions), which are found on chromosomes 1, 1A, 2, 5 and 20.

Comment. *Pelecanus onocrotalus* Linnaeus, 1758 and *Procellaria aequinoctialis* Linnaeus, 1758 were selected as reference taxa, because these are the type species of the genera *Pelecanus* and *Procellaria*, respectively. A node-based (minimum-crown-clade) definition was selected because there is very strong, congruent support for the basal dichotomy within *Feraequornithes* in recent molecular analyses (Hackett et al. 2008; McCormack et al. 2013; Jarvis et al. 2014; Burleigh et al. 2015; Kuramoto et al. 2015; Prum et al. 2015; Suh et al. 2015; Reddy et al. 2017; Kimball et al. 2019; Kuhl et al. 2021).

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