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A Phylogenetic Analysis of Extinct and Extant Pan-Alcidae (Charadriiformes: Aves)

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Abstract

Pan-Alcidae is a clade of birds consisting of the crown-clade Alcidae and the extinct Mancallinae. They include 24 extant species, 1 recently extinct species, and a fossil record extending as far back as the Eocene. All extinct and extant Pan-alcid diversity exhibit an exclusively Holarctic distribution with the majority of extant diversity found in the Pacific. The relationships of the Pan-Alcidae have been a long-standing subject of debate. Early systematic hypotheses placed Pan-Alcidae as close relatives of various water birds, however modern phylogenetic hypotheses have supported their placement within Charadriiformes. Their exact placement within Charadriiformes has yielded multiple hypotheses with further difficulty found in resolving the relationships within the clade itself. Until recently, most work on Pan-Alcidae systematics focused primarily on extant diversity, neglecting to include data from their robust fossil record. By performing molecular, morphological, and combined analyses of Pan-Alcidae and a dense outgroup of Charadriiformes representatives, this study proposes hypotheses for the relationships of extinct and extant species. A novel hypothesis is proposed for the placement of the extinct *Aethia rossmoori* among the *Brachyramphus*. This relationship makes *A. rossmoori* the earliest known fossil from this lineage and extends the *Brachyramphus* lineage's fossil record into the Late Miocene. Additionally, all analyses support the placement of *Pseudocepphus teres* as sister to the *Cepphus* extending their temporal and geographic range to include the Middle to Late Miocene Atlantic. A Bayesian total-evidence dating analysis estimated a divergence of Alcidae from other Charadriiformes during the Early Eocene. The divergence of the major Alcidae clades (the Fraterculinae and Alcinae) was estimated to have occurred during the Oligocene. Of 29 fossil Pan-

Alcidae species, 6 were inferred to be sampled ancestors. Notably, *Mancalla cedrosensis* was inferred to be a direct ancestor of *Mancalla californiensis* providing a novel hypothesis for their previously supported close relationship.

MONTCLAIR STATE UNIVERSITY

A Phylogenetic Analysis of Extinct and Extant Pan-Alcidae (Charadriiformes: Aves)

by

Alexandria A. DiGiacomo

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Introduction

With over 360 species, the Charadriiformes comprise a prominent fraction of the world's aquatic bird diversity and represent a major player in marine ecosystems (Baker, *et al*. 2007; Livezey 2010; Paton *et al*. 2003). Unique within Charadriiformes are the pelagic Pan-Alcidae, a clade of small to medium-sized birds with reduced tails, short wings, and primarily dark plumage (del Hoyo, *et al*. 1996; Johnsgard 1987; Moum, *et al*. 1994; Smith 2011). The Pan-Alcidae are commonly referred to as "auks" or "alcids" and are composed of the crown clade Alcidae and the extinct Mancallinae (Smith 2014; Smith and Clarke 2015). All Pan-alcids are geographically confined to the northern hemisphere and exhibit a circumpolar distribution (del Hoyo, *et al*. 1996; Moum, *et al*. 1994; Smith and Clarke 2011,2015). They are best known for their use of wing-propelled diving to fly underwater during prey pursuit and have evolved numerous structural adaptations which allow them to fly both aerially and aquatically (Pereira and Baker 2008; Smith 2013,2014; Smith and Clarke 2011). The most prominent of these modifications include reduced forelimbs, elongated and robust bodies, and truncated tails (del Hoyo, *et al*. 1996; Mayr 2016; Smith and Clarke 2014; Smith and Mayr 2013). Additionally, all Pan-Alcidae exhibit some amount of dorsoventral compression of the radius, ulna, and humerus which distinguishes them from all other Charadriiformes (Smith, *et al*. 2007; Smith and Mayr 2013).

While all extant alcids are volant, the Mancallinae and the recently extinct Great Auk were both flightless (Mayr 2016; Smith 2011). The loss of flight in these taxa is notable as they are two of only four Cenozoic avian taxa which evolved as flightless wing-propelled divers (Ando and Fordyce 2014). Current systematic hypotheses support independent occurrences of flight loss in these lineages (Smith 2011). Research has suggested the loss of flight seen in Pan-Alcidae may be due in part to the absence of terrestrial predators (Mayr 2016). Eliminating the requirement for flight to escape predation may have decreased evolutionary pressures towards the small size and wing proportions necessary for flight (Mayr 2016). Consequently, their maximum size was likely only constrained by the mechanics for wing-propelled diving and obligate on-shore reproduction (Smith 2016). Furthermore, it may have allowed for an increased rate of evolution in modifications associated with wing-propelled diving (Mayr 2016).

Within Pan-Alcidae are 24 extant and one recently extinct species which can be broadly divided into the Alcinae and Fraterculinae (American Ornithologists' Union 1998; Klenova 2015; Smith 2011; Weir and Mursleen 2013). Extant alcid diversity includes the true auks, auklets, dovekies, guillemots, murres, murrelets, and puffins (American Ornithologists' Union 1998; Smith 2013; Smith and Clarke 2011,2015). The murrelets are the most speciose of the alcids and include the Long-billed Murrelet (*Brachyramphus perdix*), Marbled Murrelet (*Brachyramphus marmoratus*), Kittlitz's Murrelet (*Brachyramphus brevirostris*), Craveri's Murrelet (*Synthliboramphus craveri*), Japanese Murrelet (*Synthliboramphus wumizusume*), and Ancient Murrelet (*Synthliboramphus antiquus*). Also amongst the murrelets are the Scripps's Murrelet (*Synthliboramphus scrippsi*) and Guadalupe Murrelet (*Synthliboramphus hypoleucus*) which until 2012 were considered one species referred to as the Xantus's Murrelet (American Ornithologists' Union 1998; del Hoyo, *et al*. 1996; Birt, *et al*. 2012). The next largest group within Alcidae is the auklets including the Cassin's Auklet (*Ptychoramphus aleuticus*), Least Auklet (*Aethia pusilla*), Parakeet Auklet (*Aethia psittacula*), Whiskered

Auklet (*Aethia pygmaea*), and Crested Auklet (*Aethia cristatella*) (American Ornithologists' Union 1998; del Hoyo, *et al*. 1996; Smith 2014). Among the puffins are the Rhinoceros Auklet (*Cerorhinca monocerata*), Atlantic Puffin (*Fratercula arctica*), Tufted Puffin (*Fratercula cirrhata*), and Horned Puffin (*Fratercula corniculate)* (American Ornithologists' Union 1998; del Hoyo, *et al*. 1996). The guillemots include the Black Guillemot (*Cepphus grylle),* Spectacled Guillemot (*Cepphus carbo*), and Pigeon Guillemot (*Cepphus Columba*) (American Ornithologists' Union 1998; del Hoyo, *et al*. 1996). The murres include two extant species: the Common Murre (*Uria aalge*) and Thick-billed Murre (*Uria lomvia*) (American Ornithologists' Union 1998; del Hoyo, *et al*. 1996). The remaining two groups possess only one extant species each: the Dovekie (*Alle alle*) and the true auks' Razorbill (*Alca torda*) (American Ornithologists' Union 1998; del Hoyo, *et al*. 1996). Though not extant, one other notable modern alcid is the Great Auk (*Pinguinus impennis*) which went extinct as recently as the 1840s (Moum, *et al*. 2002).

The relationships of extant alcids have long been a topic of debate and accordingly the focus of considerable research. The convergent morphology of alcids and other waterbirds led early hypotheses to place them as close relatives to penguins (Spheniscidae), loons (Gaviidae), ducks (Anatidae), grebes (Podicipedidae), and diving petrels (Pelecanoididae) (Linnaeus 1758; Vigors 1825; Brandt 1837; Swainson 1837; Baird 1858; Coues 1868; Smith 2011; del Hoyo, *et al*. 1996; American Ornithologists' Union 1998). Though these hypotheses persisted into the 20th century (Verheyen 1958; Smith 2011), the advent of modern phylogenetic methods as well as the inclusion of molecular data have provided strong support for placement of the alcids within

Charadriiformes. Recent work places Alcidae as a monophyletic family within Charadriiformes though their precise relationships to other members of the order has been debated (American Ornithologists' Union 1998; Ridgeway 1919; Sibley and Ahlquist 1990; Strauch 1978; Mickevich and Parenti 1980; Björklund 1994; Chu 1995; Ericson, *et al*. 2003; Paton, *et al*. 2003; Paton and Baker 2006; Baker, *et al*. 2007; Fain and Houde 2007; Mayr 2011; Chu 1998; Cracraft, *et al*. 2004; Livezey 2010; Livezey and Zusi 2007; Mayr 2016). Prior studies of Charadriiformes have proposed a range of systematic placements for the Alcidae including as part of *Laridae* (Sibley and Ahlquist 1990; American Ornithologists' Union 1998), sister to all other Charadriiformes families (Strauch 1978; Mickevich and Parenti 1980; Björklund 1994; Chu 1995), sister to the gulls *Laridae* (Chu 1998; Cracraft, *et al*. 2004), sister to the skuas *Stercoraridae* (Ericson, *et al*. 2003; Paton, *et al*. 2003; Paton and Baker 2006; Baker, *et al*. 2007; Fain and Houde 2007; Smith 2011; Yang, *et al*. 2017; Mayr 2011), and sister to the clade containing the gulls *Laridae*, terns *Sternidae*, and skimmer *Rynchopidae* (Livezey and Zusi 2007; Prum, *et al*. 2015).

Alcid systematics has been further complicated by their unresolved interspecific relationships. As the only extant member of its lineage, determining the relationship of the Dovekie to other alcids has been particularly problematic. Hypotheses range from placing the Dovekie as sister to the Razorbill *Alca* (Moum, *et al*. 1994; Friesen, *et al*. 1996), the murres *Uria* and Razorbill *Alca* (Friesen, *et al*. 1996), the guillemots *Cepphus*, auklets *Aethia*, and murrelets *Brachyramphus* (Chu 1998), and the Great Auk *Pinguinus* and Razorbill *Alca* (Moum, *et al*. 2002; Baker, *et al*. 2007). The relationships within the *Aethia* has been equally challenging. Monophyly of the auklets, including *Aethia* and

Ptychoramphus, has been strongly supported by recent analyses (Friesen, *et al.* 1996; Moum, *et al.* 1994; Pereira and Baker 2008; Smith 2011,2014; Smith and Clarke 2014; Thomas, *et al.* 2004). However, studies including the auklets have failed to resolve their relationships and continue to yield polytomies and low nodal support (Pereira and Baker 2008; Thomas, *et al*. 2004; Friesen, *et al*. 1996; Moum, *et al*. 2002; Smith 2014).

To date, research in alcid systematics has focused heavily on resolving the relationships of extant alcids with comparatively few studies seeking to resolve the relationships between extinct and extant taxa. This exclusion of extinct taxa neglects to take advantage of the substantial fossil record available for the lineage. With approximately 17,000 referred specimens, Pan-Alcidae has the most abundant fossil record within Charadriiformes (Smith 2013; Smith and Clarke 2011; Smith and Mayr 2013). Currently described alcid fossils range in age from the Eocene through the Holocene, a record spanning over 30 million years (Smith 2013,2016; Smith and Clarke 2011,2015; Smith and Mayr 2013). The oldest fossil attributed to the Pan-Alcidae lineage is a fragmentary humerus from approximately 34 mya (Smith 2016; Smith and Clarke 2015). As with this early representative, 97% of the Pan-Alcidae fossil record is composed of incomplete or fragmentary specimens making the dorsoventral compression seen only in Pan-Alcidae vital to assigning specimens to the clade (Smith and Clarke 2011,2015). As with many lineages, the early record for Pan-Alcidae represents the most incomplete portion of their fossil record (Smith 2011). However, they exhibit a robust record from the Neogene with numerous fossils known from Pliocene formations and at least 13 species identified in Miocene formations (Smith 2013).

The abundance of available fossil data attributed to Pan-Alcidae is unique among the Charadriiformes, creating the opportunity to better understand both the evolution of the lineage and seabirds as a whole (del Hoyo, *et al*. 1996; Smith and Clarke 2015). Prior studies in phylogenetic inference have demonstrated that integrating paleontological data with neontological data produces better resolved relationships, more accurate divergence time estimates, and ultimately a better understanding of macroevolutionary trends (Arcila, *et al*. 2015; Donoghue, *et al*. 1989; Herrera and Dávalos 2016; Pyron 2011,2015; Slater, *et al*. 2012; Smith and Turner 2005; Smith 2016; Etienne and Apol 2009). These findings reinforce the need for increased focus on incorporating fossil data in studies of Pan-Alcidae evolution, especially as more than half of known alcid diversity is extinct (Smith 2016). A comprehensive analysis of Pan-Alcidae relationships could clarify longstanding questions about the lineage's biogeographic history and the evolution of their unique and diverse morphology (Smith and Clarke 2011).

Though Pan-Alcidae has a sizable fossil record, a large portion of specimens remained undescribed until recently (Olson 1985; Smith 2014). Studies over the past two decades have made strides in reviewing these undescribed specimens and assigning them to taxonomic units (Wijnker and Olson 2009; Smith, *et al*. 2007; Smith 2011,2013; Smith and Clarke 2011). In the past 10 years alone at least 15 new fossil species of Pan-Alcidae have been described including 3 species of *Alca* and 2 species of *Aethia* (Smith 2014; Smith and Clarke 2011, 2015). As this taxonomic review has progressed, efforts have been made to simultaneously analyze extinct and extant Pan-Alcidae relationships. However, studies incorporating alcid fossil data have been largely limited to parsimony analyses and fail to take advantage of the advances in maximum likelihood and Bayesian methods. Consequently, alcid systematics can benefit from additional analyses using varied methods.

Though incorporating fossil taxa in Pan-alcid research has shed new light on their evolutionary history, it has also highlighted their more confounding relationships. The Mancallinae have been of particular interest both because they are nonvolant and because limited work has been done to assess their relationships with the remainder of Pan-Alcidae. Early work on the Mancallinae proposed they are likely sister to all other alcids though some researchers suggested they may be more closely related to a genus within the Alcinae (Olson 1985). Recent analyses supported their placement as sister to all other Pan-Alcidae; however, work on the subject is limited and additional research is needed to assess these findings and resolve polytomies within the clade (Smith 2011, 2014; Smith and Clarke 2011, 2015). As in analyses of extant species, there has been difficulty in resolving the interspecific relationships of both the auklets and the dovekies which is compounded by the proportions of missing data in their extinct representatives (Smith 2013,2014). In addition to interspecific relationships, systematic studies have faced difficulty in recovering consistent hypotheses for early divergences in the Pan-Alcidae lineage. Among these are the intergeneric relationships of *Cepphus*, *Brachyramphus*, and *Synthliboramphus* (Pereira and Baker 2008; Moum, *et al.* 1994; Smith 2014; Thomas, *et al.* 2004).

Without a well-supported hypothesis of Pan-Alcidae relationships our understanding of early alcids and the origins of the lineage remain lacking. The study described herein takes advantage of recent advancements in alcid taxonomy and phylogenetic models to propose a hypothesis of extinct and extant Pan-Alcidae relationships. This study incorporates 23 extant and 29 fossil species of alcids with an outgroup of 28 extant and 3 extinct Charadriiformes. Through a combination of parsimony, maximum likelihood, and Bayesian analyses, this study seeks to investigate the placement of the Mancallinae and the problematic relationships of early alcids such as *Aethia rossmoori* and *Pseudocepphus teres*. Further analyses using exclusively molecular data provide strongly supported hypotheses of extant Charadriiformes relationships. These along with a morphology-based analysis and the combined analyses allow for comparison of molecular, morphology, and combined results. Additionally, this study proposes a hypothesis of alcid divergence times including between alcid genera and of Pan-Alcidae from other Charadriiformes.

Materials and Methods

Taxonomy guidelines

Analysis included 31 outgroup species, 29 extinct species of Pan-Alcidae, and 23 extant species of alcids. Species taxonomy for extant Alcidae follow those outlined by the 7th edition Checklist of North American Birds, its subsequent supplements, and the Check-List of Japanese Birds (American Ornithologists' Union 1998; Ornithological Society of Japan 2012; Banks, *et al.* 2006; Chesser, *et al.* 2013). *Synthliboramphus hyploeucus* is treated as Xantus's murrelet as per the 7th edition Checklist of North American Birds prior to the 53rd supplement and accordingly represents the now delimited Scripps's Murrelet *Synthliboramphus scrippsi* and Guadalupe Murrelet *Synthliboramphus hypoleucus* (American Ornithologists' Union 1998).

Morphological character data

Morphology character data were drawn from previously published sources and combined to compile a matrix of 291 binary and 62 multistate characters for 83 species (Smith 2011,2014; Smith and Clarke 2011,2015). Data include 232 osteology, 43 integumentary, 2 reproductive and diet, 24 myology, and 52 feather microstructure characters. Character descriptions are the same as those of Smith (2013).

Molecular data

Previously published sequence data were retrieved from GenBank for 5 mitochondrial (CO1, CYTB, ND2, ND5, ND6), 2 ribosomal RNA (12S, 16S), and 1 nuclear gene (RAG 1). Accession numbers are listed in Appendix 1. Sequences were aligned using the MUSCLE package in Geneious version 11.0.5 (Edgar 2004a; Edgar 2004b; https://www.geneious.com, Kearse, *et al*. 2012). Aligned sequences were concatenated to generate an alignment of 9941 base pairs in length.

Stratigraphic age range data

Stratigraphic age ranges were compiled for all included fossil species using the Paleobiology database. Data were downloaded on January 4, 2018 using a search for the following taxa names: Mancalla, Miocepphus, Uria, Ptychoramphus, Miomancalla, Pinguinus, Alcodes, Alle, Australca, Aethia, Brachyramphus, Cepphus, Cerorhinca, Fratercula, Pseudocepphus, and Synthliboramphus. Date ranges were confirmed in original publications for any species which had under three concurring entries and for any records which disagreed with other records for that taxon. Included in Appendix 2 is a table of species and citations of the original publications from which age range data were detailed. Changes and additions to the data downloaded from Paleobiology Database are described in Appendix 3.

Phylogenetic analysis

Parsimony analysis

A combined analysis of morphology and molecular data was performed using PAUP* version 4.0a (Swofford 2002). Analysis was performed using the bootstrap method with fast-heuristic search with the following criteria: 1000 bootstrap replicates, fast stepwise addition search, accelerated transformation optimization, all characters were equally weighted and unordered, gaps were treated as “missing”, multistate characters were treated as polymorphism, and branches were collapsed if maximum branch length equals zero. Descriptive tree statistics (including CI, RI, RC, and HI), bootstrap support values, and a 50% majority-rule consensus tree with other compatible groups were calculated in PAUP* (Swofford 2002). All multistate characters were treated as unordered as prior studies using the morphology data set used in this study showed no difference in tree topology when multistate characters were treated as ordered or unordered (Smith and Clarke 2015). Trees were rooted on *Charadrius wilsonia* and *Charadrius vociferous a priori* based on prior analyses of Charadriiformes (Baker, *et al*. 2007; Paton, *et al*. 2003; Strauch 1978; Sibley and Ahlquist 1990; Fain and Houde 2004,2007; Cracraft, *et al*. 2004; Chu 1995; Ericson, *et al*. 2003). Heuristic parsimony analysis failed to run.

Maximum likelihood analysis

Maximum likelihood analysis was performed on a molecular dataset for extant Charadriiformes, a morphology dataset for extant taxa, and a combined dataset of morphological and molecular data for extinct and extant Charadriiformes. Analysis of datasets was performed using RaxML version 8.2.10 (Stamatakis 2014) and the CIPRES

Science Gateway (Miller, *et al*. 2010). For the molecular analysis, data were partitioned by gene resulting in 8 partitions. For the combined analysis, data were partitioned into morphology and individual genes resulting in a total of 9 partitions. Analysis included rapid bootstrap analysis of 1000 replicates and subsequent search for best scoring maximum likelihood tree. Nucleotide substitution was modeled using a General Time Reversible model with a Gamma distribution for site rate heterogeneity (GTR+Γ). The MK model of substitution was implemented for morphology data (Lewis 2001).

Bayesian analysis

Bayesian analysis was performed for a molecular dataset and a combined dataset of molecular and morphology data using MrBayes v3.2.6 (Ronquist, *et al*. 2012) and the CIPRES Science Gateway (Miller, *et al*. 2010). Nucleotide substitution was modeled using a General Time Reversible model with a Gamma distribution for site rate variation and a proportion of invariable sites (GTR+I+Γ). Analysis was run using BEAGLE (Ayres, *et al*. 2012). Molecular and morphology data were partitioned as described in the above maximum likelihood methods. The command blocks used for both the combined and molecular analyses are included in Appendix 4.

Bayesian total-evidence dating analysis

A Bayesian total-evidence dating analysis was performed to assess phylogenetic relationships and divergence dates. The multistate morphology matrix described above was reduced to generate a matrix of 291 binary characters. Morphological data of extant and extinct species, molecular data for extant and one recently extinct species, and stratigraphic range data for fossil species was integrated in an analysis performed using RevBayes version 1.0.7 (Höhna, *et al.* 2014; Höhna, *et al.* 2016). The Mk model was used for morphological character data including a Jukes-Cantor model of character substitution (Lewis 2001). Morphology substitution rates vary across sites according to a Gamma distribution and branch rates are based on a strict morphological clock. Nucleotide substitution was modeled using a General Time Reversible model with a Gamma distribution for site rate heterogeneity (GTR+Γ). Molecular branch rates were modeled based on an uncorrelated relaxed molecular clock. A uniform distribution was placed on the stratigraphic age range data to inform the likelihood of fossil observation. The Fossilized-Birth Death model was incorporated as a prior distribution for time trees and uses exponential priors for speciation, extinction, and fossilization rates (Heath, *et al*. 2014). Subsequently, a maximum clade credibility tree was generated in RevBayes version 1.0.7 (Höhna, *et al.* 2014; Höhna, *et al.* 2016).

Results

Molecular phylogenetic analysis

Maximum likelihood and Bayesian analyses of molecular data from extant alcids, the extinct *Pinguinus impennis*, and outgroup taxa provided predominantly congruent phylogenies (Figures 1-2). Bayesian analysis yielded a largely well-supported phylogeny with 42 nodes yielding ≥0.95 Bayesian posterior probability (BPP) and 46 nodes yielding ≥0.9 BPP (Figures 2). Analyses supported monophyly of the major Alcidae clades including the Alcinae (true auks, dovekie, murres, murrelets, and guillemots) and Fraterculinae (auklets and puffins). Both analyses also recovered their sub-clades: the Alcini (*Alca*, *Pinguinus*, *Alle,* and *Uria*), the Cepphini (*Cepphus*), the Aethiini (*Aethia* and *Ptychoramphus*), and the Fraterculini (*Cerorhinca* and *Fratercula*). *Alle alle* was recovered as sister to *Pinguinus impennis* and *Alca torda. Uria* was recovered as sister to

Alle, Pinguinus, and *Alca* forming the Alcini. *Synthliboramphus* was placed sister to the Alcini with *Cepphus* sister to a clade containing the Alcini and *Synthliboramphus* with both relationships yielding ≥0.98 BPP. *Brachyramphus* was recovered as sister to all other Alcinae taxa with 100% bootstrap support (BS) and 1.0 BPP. Relationships among the puffins were congruent with all nodes yielding 100% BS and 1.0 BPP.

Within the Alcidae, molecular analyses disagreed only in the placement of *Aethia* species. Maximum likelihood analysis places *A. psittacula* as sister to *A. cristatella* and *A. pygmaea*. *A. pusilla* was recovered as sister to the all other *Aethia* with 100% BS (Figure 1). Contrastingly, Bayesian analysis places *A. pusilla* as sister to *A. psittacula* and *A. pygmaea* with 1.0 BPP. *A. cristatella* was recovered as sister to all other *Aethia* with 1.0 BPP (Figure 2). Analyses were congruent in the placement of *Ptychoramphus aleuticus* as sister to all *Aethia* species with the relationship yielding 100% BS and 1.0 BPP.

Both molecular analyses placed the skuas (*Stercorarius longicaudus* and *Stercorarius skua*) as sister to a monophyletic Alcidae with the Bayesian analysis yielding 1.0 BPP. A clade containing the gulls, terns, skimmer, and *Anous tenuirostris* was recovered as sister to the skuas and Alcidae with 100% BS and 1.0 BPP. Within this clade, all relationships were congruent excluding the placement of *A. tenuirostris.*

Combined phylogenetic analysis

Parsimony, maximum likelihood, and Bayesian analyses of combined molecular and morphology data yielded largely unresolved phylogenies (Figures 3-5). All analyses supported a monophyletic Pan-Alcidae. Parsimony analysis yielded a tree of 16,146 steps (CI=0.356, RI=0.514, RC=0.183, HI=0.647, 2954 parsimony informative characters;

Figure 3). Pan-Alcidae was inferred to be sister to a clade containing the skuas, gulls, skimmer, and terns and all major Pan-Alcid clades were recovered (Alcini, Cepphini, Alcinae, Fraterculini, Aethiini, and Fraterculinae). *Miocepphus blowi* was placed as sister to *Alca minor* within the clade containing *Pinguinus* and *Alca* in disagreement with a monophyletic clade containing only *Alca* and *Pinguinus*. Notably, all *Miocepphus* taxa were recovered within the Alcinae. *Pinguinus impennis* was placed as sister to *Alca stewarti* and *Alca torda* providing support for the relationship inferred through both molecular analyses. Furthermore, the Mancallinae supraspecific terminal was placed as sister to the crown-clade Alcidae, supporting previously published hypotheses (Smith 2011, 2014; Smith and Clarke 2011, 2015).

Maximum likelihood analysis yielded a tree in which most of the major clades of alcids were recovered including the Fraterculini, Aethiini, Fraterculinae, and Cepphini (Figure 4). The skuas, *Stercorarius longicaudus* and *Stercorarius skua*, were recovered as sister to all Pan-Alcidae contradicting the parsimony results but supporting this study's molecular results and previously published hypotheses (Ericson, et al. 2003; Paton, et al. 2003; Paton and Baker 2006; Baker, et al. 2007; Fain and Houde 2007; Smith 2011; Yang, et al. 2017; Mayr 2011). As with the parsimony analysis, a close relationship between the *Alca* and *Pinguinus impennis* was supported with the *P. impennis* recovered as sister to *Alca ausonia*. The Mancallinae supraspecific terminal was placed as sister to the crown-clade Alcidae, supporting both the parsimony analysis and previously published hypotheses (Smith 2011, 2014; Smith and Clarke 2011, 2015).

Bayesian combined analysis recovered *Stercorarius longicaudus* and *Stercorarius skua* as sister to all Pan-Alcidae supporting the hypothesis of the maximum likelihood combined analysis and both molecular analyses (Figure 5). Results also support the monophyly of the Aethiini, Fraterculini, Fraterculinae, and Cepphini. However, the placement of the Mancallinae supraspecific terminal as sister to *Uria* challenges both the monophyly of the Alcini and Alcinae as well as their placement as sister to all other Pan-alcids. Results supported the close relationships of *Pinguinus* and *Alca* inferred by all previous analyses.

All combined analyses (Figures 2-5) placed *Miocepphus blowi* within the Alcinae as a close relative of *Alca* and *Pinguinus.* Additionally, *Alle alle* was recovered as sister to a clade containing *Uria, Alca,* and *Pinguinus* contradicting the molecular hypotheses. *Aethia rossmoori* was consistently recovered within or as sister to *Brachyramphus* placing them outside the clade containing all other *Aethia* species. All analyses recovered a clade including *Ptychoramphus aleuticus* and all *Aethia,* excluding the previously mentioned *A. rossmoori*. Furthermore, *Pseudocepphus teres* was recovered as sister to all other *Cepphus* with the Bayesian analysis yielding high support for the relationship (≥0.99 BPP). Analyses did not yield any congruence in the intergeneric relationships of *Cepphus, Synthliboramphus,* and *Brachyramphus.*

Morphological phylogenetic analysis

A maximum likelihood analysis of Mancallinae and skua morphology data was performed to focus on the interspecific relationships of the Mancallinae (Figure 6). Analysis of morphology data recovered *Mancalla californiensis* as sister to *Mancalla cedrosensis. Mancalla lucasi* was found as sister to *M. californiensis* and *M. cedrosensis. Mancalla vegrandis* was recovered as sister to all other *Mancalla* taxa. *Miomancalla howardi* was recovered as sister to all other Mancallinae yielding support of 100% BS.

An additional analysis of extant alcids, *Pinguinus impennis,* and outgroup taxa was performed using only morphology data (Figure 7). The morphology-based analysis placed a clade containing the skuas, gulls, terns, and skimmer as sister to all Pan-Alcidae and recovered most of the major alcid clades including the Cepphini, Fraterculini, Aethiini, and Fraterculinae. The placement of *Cepphus* as sister to all other Alcidae is notable as it yielded strong bootstrap support (100% BS) and infers the currently defined Alcini and Alcinae to be polyphyletic. As with all other analyses, *Alca* was recovered as sister to *Pinguinus* with high bootstrap support (98% BS). Contradictory to the molecular analyses but similar to the combined data analyses, *Alle alle* was recovered as sister to the *Alca, Uria,* and *Pinguinus*. The interspecific relationships of *Aethia* again contradict all other analyses.

Total-evidence dating analysis yielded a tree in which 9 fossil taxa were inferred to be sampled ancestors (Figure 8). All node ages are indicated in Figure 8A with 95% HPD represented in Figure 8B. Notably, the crown-clade Alcidae was recovered as sister to all other Charadriiformes with a divergence date of approximately 52 mya. The Mancallinae were recovered as sister to all Charadriiformes with an inferred divergence date of approximately 69 mya. Tree topology was in partial agreement with combined analyses. *Pinguinus* was again placed as sister to *Alca*. *Alle alle* was recovered as sister to a clade containing *Alca, Pinguinus* and *Uria* but excluding *Uria brodkorbi*. *Aethia rossmoori* was again recovered as sister to *Brachyramphus.* Differences include the placement of *Uria brodkorbi* outside the clade containing both extant *Uria* representatives with 0.74 BPP (Figure 8C). *Pseudocepphus teres* was not recovered as sister to the *Cepphus*, but instead was placed as sister to all other Alcinae excluding

Miocepphus bohaski. *Ptychoramphus aleuticus* was recovered within the clade containing *Aethia* supporting a relationship between the taxa.

Discussion

Phylogenetic relationships

The maximum likelihood and Bayesian analyses of molecular data yielded predominantly congruent, well-resolved trees. Both analyses yielded a monophyletic Alcidae sister to the skuas in support of previously published hypotheses (Ericson, et al. 2003; Paton, et al. 2003; Paton and Baker 2006; Baker, et al. 2007; Fain and Houde 2007; Smith 2011; Yang, et al. 2017; Mayr 2011). Molecular results further provided support for Alcinae and Fraterculinae as well as their sub-clades: the Alcini, Cepphini, Aethiini, and Fraterculini. Notably, both analyses recovered *Alle alle* as sister to *Alca* and *Pinguinus.* Though this result contradicts some previous studies (Pereira and Baker 2008; Strauch 1985; Thomas, *et al.* 2004), it is supported by numerous molecular hypotheses (Baker, *et al.* 2007; Moum, *et al.* 1994; Moum, *et al.* 2002; Pereira and Baker 2008; Smith and Clarke 2014; Thomas, *et al.* 2004). As the placement of *Alle alle* has been consistently problematic and this study did not yield universally high support, further work should be performed to resolve this relationship and may benefit from the inclusion of additional molecular data. The interspecific relationships of the Aethiini also remain enigmatic with numerous disagreements between analyses. However, both analyses recovered *Aethia* and *Ptychoramphus* as a monophyletic clade providing support for previous hypotheses (Friesen, *et al.* 1996; Moum, *et al.* 1994; Pereira and Baker 2008; Thomas, *et al.* 2004).

The parsimony, maximum likelihood, and Bayesian combined analyses were congruent in the recovery of a monophyletic Pan-Alcidae. The molecular analyses, combined maximum likelihood analysis, and combined Bayesian analysis supported the placement of skuas as the closest relative of the Pan-Alcidae. This result is consistent with numerous prior studies and was well supported in most analyses of this study (≥80% BS; ≥0.8 BPP) (Ericson, et al. 2003; Paton, et al. 2003; Paton and Baker 2006; Baker, et al. 2007; Fain and Houde 2007; Smith 2011; Yang, et al. 2017; Mayr 2011). Only the morphology and combined parsimony analysis disagreed with this relationship. The results of these analyses proposed a clade containing skuas, gulls, terns, and the skimmer as sister to the Alcidae, but both yielded low support (<50% BS) for the relationship.

The parsimony, maximum likelihood, and Bayesian combined analyses were discordant regarding interspecific Alcidae relationships and early divergences. However, consistent placement of specific fossil taxa provides interesting and novel hypotheses for Pan-Alcidae evolutionary history and relationships. As in molecular analyses, *Ptychoramphus* and *Aethia*, excluding *Aethia rossmoori,* were consistently recovered as a monophyletic clade with unresolved interspecific relationships. Notably all analyses placed the extinct *A. rossmoori* within or as sister to the *Brachyramphus*. As previous analysis recovered *A. rossmoori* in a polytomy at the base of the Alcidae, the placement of the taxon with *Brachyramphus* provides a novel hypothesis for their relationship within the Alcidae (Smith 2014). The inclusion of *A. rossmoori* as a close relative of *Brachyramphus* would extend the lineage's fossil record in California from the Early Pleistocene/Pliocene to the Late Miocene. However, nodal support for *A. rossmoori's* recovered placement within *Brachyramphus* is low. This poor support may in part be due to the large amount of missing data for both *A. rossmoori* and the extinct *Brachyramphus* species, *B. dunkeli* and *B. pliocenum* (Table 1). Furthermore, the 18 morphology characters for which *A. rossmoori* could be scored were unscored in both extinct *Brachyramphus*. While more focused analysis may further our understanding of *A. rossmoori's* placement, the identification of additional specimens would be invaluable to clarifying their phylogenetic position. However, as the holotype for *A. rossmoori* is based exclusively on a right ulna, referral of further specimens will be difficult.

Combined analyses yielded insight into the relationships of extinct and extant Cepphini. Among extant Cepphini, relationships were congruent between both molecular analyses, the combined Bayesian analysis, and the combined maximum likelihood analysis. Relationships of extinct Cepphini were predominantly congruent, with only the parsimony analysis in disagreement. Notably, the placement of the extinct *Cepphus olsoni* as sister to *Cepphus carbo* was recovered in the maximum likelihood and Bayesian analyses with 91 BS/0.98 BPP providing a strongly supported hypothesis for the fossil taxon's placement. All combined analysis methods recovered the extinct *Pseudocepphus teres* as sister to all extinct and extant *Cepphus* species. Bayesian support for this relationship was strong yielding a value of 0.99 BPP. Furthermore, this relationship is consistent with a previous analysis including the taxon by Smith and Clarke (2014). The well supported relationships of *C. olsoni* and *P. teres* with extant Cepphus may have significant implications in the lineage's historical biogeography. Currently, *Cepphus* exhibits a predominantly Pacific distribution with only the Black Guillemot (*Cepphus grylle*) represented in the Northern Atlantic. Similar to extant *Cepphus* distribution, *C. olsoni* is known from the Pacific dating as early as the Late Miocene (Wijnker and Olson

2009). Contrastingly, *P. teres* is known from a Middle to Late Miocene formation in Atlantic off the coast of Maryland (Wijnker and Olson 2009). The inclusion of *P. teres* as part of the Cepphini provides evidence for the clade's presence in both the Atlantic and Pacific since at least the Late Miocene.

As with their only extant representative, placing the four extinct dovekie species proved difficult. Of the *Miocepphus*, only *M. blowi* exhibited approximately consistent placement and was inferred to be a close relative of the clade containing *Alca* and *Pinguinus*. Previously published hypotheses recovered the *Miocepphus* as part of the Alcinae (Smith and Clarke 2011,2014). However, only the parsimony analysis in this study recovered all *Miocepphus* species within the Alcinae. It should be further noted that support values for *Miocepphus* relationships exhibited extremely low support values (≤33% BS/≤0.42 BPP). This difficulty may be partly due to the taxa's high proportions of missing data. Furthermore, of 353 total morphology characters only 5.4% (19 characters) were coded in all four taxa providing little information by which the taxa can be directly compared. In support of the likely impact of missing data of *Miocepphus* placement, the only species with consistent placement, *M. blowi*, had the lowest proportion of missing morphology data at 67.1% missing. *M. bohaski*, *M. mcclungi*, and *M. mergulellus* had higher proportions with 81.3%, 89.2% and 85.3% missing respectively (Table 1). The phylogenetic placement of the only extant dovekie, *Alle alle*, was congruent among the combined analyses with all results placing *Alle* sister to the clade containing *Alca, Pinguinus,* and *Uria*. This result contrasts that of the molecular analyses and yielded low support for all combined analyses. Furthermore, as this placement of *Alle* is congruent with that of the morphology-based analysis of Alcidae, it may be a result of the inclusion of morphology data rather than an accurate relationship. As past studies including the *Miocepphus* have relied heavily on parsimony methods and results from this study were discordant when maximum likelihood and Bayesian methods were used, our understanding of the interspecific relationships of the genus may benefit from further work utilizing varied phylogenetic methods.

Results for the relationship of the Mancallinae to the rest of Pan-Alcidae partially agreed with the only two prior studies which included the taxa (Chandler 1990; Smith 2011; Smith and Clarke 2014). In agreement with prior studies, the parsimony and maximum likelihood analyses placed the Mancallinae sister to the crown-clade Alcidae with the maximum likelihood analysis yielding relatively strong support (88% BS). However, support for this placement was not universal among analyses, with the Bayesian analysis recovering the Mancallinae within the Alcinae as sister to *Uria*. All Mancallinae exhibit a distinguishing scar on their humerus neighboring their primary pneumotricipital fossa (Smith 2011). This unique osteological feature enabled the use of a supraspecific terminal for the clade thereby reducing the proportion of missing morphology data from 64.6%-88.4% for individual taxa to 39.7% for the combined terminal (Table 1). However, even with increased available data for the terminal node, the phylogenetic placement of the Mancallinae with respect to all other alcids was unresolved. Despite the disagreement in results, both systematic hypotheses proposed in this study support the popular hypothesis of two independent flight loss events in the Pan-Alcidae.

As in prior studies, the relationships between *Cepphus, Synthliboramphus,* and *Brachyramphus* and of these genera to other Alcidae were unresolved. Only the molecular analyses and the combined Bayesian analysis agreed, placing *Synthliboramphus* sister to the clade *Alle*, *Uria*, *Alca,* and *Pinguinus.* The results of these analyses place *Brachyramphus* sister to all other Alcinae with *Synthliboramphus* sister to *Cepphus* and the Alcini. Support for these relationships was strong in the molecular Bayesian analysis (≥0.98 BPP) and relatively high in the molecular maximum likelihood analysis (≥86% BS). The relationship was further supported by the combined Bayesian analysis. However, the parsimony and maximum likelihood combined analyses yielded hypotheses contradicting both this placement and each other. Difficulty resolving these relationships is consistent with past studies and further highlights the sizable gap in our understanding of the early alcid divergences and radiation.

Total-evidence dating analysis

A Bayesian total-evidence dating analysis was performed in an effort to further our understand of the divergences of Pan-Alcidae from other Charadriiformes and of the major Alcidae clades. Unlike in the combined analyses, the Mancallinae were recovered as sister to all crown clade Charadriiformes implying a paraphyletic Pan-Alcidae. Results estimate they diverged from Charadriiformes during the Late Paleocene (59 mya; 95% HPD 51.05-65.57 mya). The crown clade Alcidae were recovered as sister to all other Charadriiformes. The Alcidae are estimated to have diverged from other Charadriiformes approximately 52 mya. The divergence of Alcidae had a 95% HPD spanning from the Early Paleocene to the Middle Eocene (42.13-62.23 mya) refuting claims of an origin predating the K-T boundary (Baker, *et al.* 2007). The two major Alcidae clades, the Fraterculinae and Alcinae, are inferred to have diverged during the Oligocene (28.67 mya; 95% HPD 22.52-35.8 mya). As the oldest described alcid fossil is from approximately 34 mya, an Early Eocene origin of Alcidae implies a 20 million year ghost lineage. Further analysis of the divergence will be required to assess this result. The discovery and continuing referral of additional fossil specimens may provide insight into this early period of alcid evolution. The inferred radiation and subsequent diversification of auks beginning in the Early Oligocene is consistent with their progressively denser Neogene fossil record.

Of the 29 fossil Pan-alcids included in this analysis, 6 species were inferred to be sampled ancestors: *Alca ausonia, Cepphus olsoni, Brachyramphus pliocenum, Aethia barnesi, Miocepphus mcclungi,* and *Mancalla cedrosensis.* However, the Bayesian support for all but the relationship of *Cepphus olsoni* to *Cepphus* was <0.75 BPP. Analysis yielded support of 0.78 BPP for the placement of *C. olsoni* as a direct ancestor of the *Cepphus* warranting further investigation into this possible relationship. As both this study and the only previously published phylogenetic analysis of Mancallinae species recovered *Mancalla cedrosensis* and *Mancalla californiensis* as sister taxa, the recovered placement of *M. cedrosensis* as a direct ancestor of *M. californiensis* provides a unique and novel perspective on their relationship (Smith 2011). If supported through further analysis, this relationship would have interesting implications for the lineage's biogeographic history. *M. cedrosensis* has been identified in localities from Baja California (Mexico) and San Diego (CA, USA) while *M. californiensis* has been identified in San Diego (CA, USA), Los Angeles (CA, USA), and Orange (CA, USA). The disparity in total range with a common midpoint may indicate a possible Northward trend.

Though the Bayesian dating analysis can provide insight into the divergence of major Pan-Alcidae clades, there are numerous disagreements in phylogenetic relationships between this and the other analyses performed in this study. As before, disparities are seen for many interspecific relationships and early alcid relationships. The presence of rogue taxa, such as *Miocepphus mcclungi* and *Miocepphus bohaski*, combined with high proportion of missing data for many fossil taxa may play a role in this poor resolution. Additionally, the limited sequence data currently available may limit our ability to better resolve extant relationships. Consequently, our understanding of alcid relationships, divergence times, historical biogeography, and morphological evolution would benefit from additional sequencing, fossil discovery and description, and further analyses emphasizing the placement of poorly supported taxa.

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Appendix 1: GenBank Accession Numbers and References

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Ingroup GenBank Accession Numbers

Taxa	**12S rDNA**		**16S rDNA**		**CO1**	
Aethia cristatella	EF373064	[n]	EF380278	[n]	EF380315	[n]
Aethia psittacula	EF373077	[a]	EF380290	[n]	EF380327	[n]
Aethia pusilla	EF380303	[n]	EF380279	[n]	EF380316	[n]
Aethia pygmaea	EF380304	[n]	EF380280	[n]	EF380317	[n]
Alca torda	EF373065	[a]	EF380281	[n]	EF380318	[n]
Alle alle	AJ242684	[k]	EF380282	[n]	EF380319	[n]
Brachyramphus brevirostris	EF373070.2	[n]	EF380284	[n]	EF380321	[n]
Brachyramphus marmoratus	EF380306	[n]	EF380285	[n]	EF380322	[n]
Brachyramphus perdix	EF380307.1	[n]	EF380286	[n]	EF380323	[n]
Cepphus carbo	EF380308	[n]	EF380287	[n]	EF380324	[n]
Cepphus columba	X76349	[j]	DQ674610	[d]	EF380325	[n]
Cepphus grylle	AJ242688	[k]			DQ433470	[h]
Cerorhinca monocerata	EF373072	[a]	EF380289	[n]	EF380326	[n]
Fratercula arctica	DQ385279	[l]	DQ385296	[l]	DQ385177	[l]
Fratercula cirrhata	EF380309	[n]	EF380291	[n]	EF380329	[n]
Fratercula corniculata	EF380310	[n]	EF380292	[n]	EF380328	[n]
Pinguinus impennis †	AJ242685	[k]	MF188888			
Ptychoramphus aleuticus	EF373103	[a]	EF380293	[n]	EF380330	[n]
Synthliboramphus antiquus	EF373111	[a]	EF380294	[n]	EF380331	[n]
Synthliboramphus craveri	EF380311	[n]	EF380295	[n]	EF380332	[n]
Synthliboramphus hypoleucus					DQ434184	[h]
Synthliboramphus wumizusume	EF380312	[n]	EF380296	[n]	EF380333	[n]
Uria aalge	DQ485794	[d]	DQ485832	[d]	EF380334	[n]
Uria lomvia	AJ242687	[k]	EF380299	[n]	EF380336	[n]

Taxa	**cytb**		**ND2**		**ND5**	
Aethia cristatella	U37087	[e]	EF373219	[a]		
Aethia psittacula	U37296	[e]	EF373235	[a]		
Aethia pusilla	U37104	[e]	EF380337	[n]		
Aethia pygmaea	U37286	[e]	EF380338	[n]		
Alca torda	U37288	[e]	EF373220	[a]	AJ242683	[k]
Alle alle	U37287	[e]	EF373221	[a]	AJ242684	[k]
Brachyramphus brevirostris	U37289	[e]	EF373227	[a]		
Brachyramphus marmoratus	U37290	[e]	EF380340	[n]		
Brachyramphus perdix	U37291	[e]	EF380341	[n]		
Cepphus carbo	U37292	[e]	EF380342	[n]		
Cepphus columba	U37293	[e]	EF373229	[a]		
Cepphus grylle	U37294	[e]			AJ242688	[k]
Cerorhinca monocerata	U37295	[e]	EF373230	[a]		
Fratercula arctica	U37297	[e]	DQ385092	[l]	DQ385160	[l]
Fratercula cirrhata	U37298	[e]	EF380343	[n]		
Fratercula corniculata	U37299	[e]	EF380344	[n]		
Pinguinus impennis †	AJ242685	[k]	MF188888	[w]	AJ242685	[k]
Ptychoramphus aleuticus	U37302	[e]	EF373261	[a]		
Synthliboramphus antiquus	U37303	[e]	EF373269	[a]	AP009042	[p]
Synthliboramphus craveri	U37304	[e]	EF380345	[n]		
Synthliboramphus hypoleucus	U37305	[e]				
Synthliboramphus wumizusume	U37306	[e]	EF380346	[n]		
Uria aalge	U37307	[e]	EF380348	[n]	AJ242686	[k]
Uria lomvia	U37308	[e]	EF373273	[a]	AJ242687	[k]

Taxa	**ND6**		**RAG-1**	
Aethia cristatella	X73928	[j]	EF373165	[a]
Aethia psittacula	X73925	[j]	EF373179	[a]
Aethia pusilla	X73926	[j]	EF380266	[n]
Aethia pygmaea	X73927	[j]	EF380267	[n]
Alca torda	X73916	[j]	AY228788	[m]
Alle alle	X73915	[j]	EF373166	[a]
Brachyramphus brevirostris	X73922	[j]	EF373172	[a]
Brachyramphus marmoratus	X73923	[j]	EF380269	[n]
Brachyramphus perdix			EF380270	[n]
Cepphus carbo			EF380271	[n]
Cepphus columba	X73918	[j]	EF373173	[a]
Cepphus grylle	X73917	[j]		
Cerorhinca monocerata			EF373174	[a]
Fratercula arctica	X73929	[j]	AY228787	[m]
Fratercula cirrhata	X73931	[j]	EF380273	[n]
Fratercula corniculata	X73930	[j]	EF380272	[n]
Pinguinus impennis †	AJ242685	[k]		
Ptychoramphus aleuticus	X73924	[j]	EF373204	[a]
Synthliboramphus antiquus	X73920	[j]	EF373212	[a]
Synthliboramphus craveri			EF380274	[n]
Synthliboramphus hypoleucus	X73921	[j]		
Synthliboramphus wumizusume	X73919	[j]	EF380275	[n]
Uria aalge	X73913	[j]	EF380276	[n]
Uria lomvia	X73914	[j]	EF373216	[a]

Outgroup GenBank Accession Numbers

Taxon	12S rDNA	16S rDNA	CO1
Anous tenuirostris	EF373066 [a]		JQ174031.1 [u]
Bartramia longicauda	EF373069 [a]		AY666283 [g]
Calidris subruficollis	EF373114 [a]		AY666178 [g]
Charadrius vociferous	DQ385269 [l]	DQ385286 [l]	DQ385167 [l]
Charadrius wilsonia			AY666175 [h]
Chlidonias leucopterus	EF373073 [a]		EU525340.1
Creagrus furcatus	EF373076 [a]		
Cursorius temminckii	DQ385277 [l]	DQ385294 [l]	DQ385175 [l]
Gelochelidon nilotica	AY631347 [b]		DQ434167 [h]
Glareola maldivarum	EF373083 [a]		AB843529.1 [q]
Gygis alba	EF373084 [a]		JQ174973.1 [u]
Hydrophasianus chirurgus	EF373085 [a]		
Larosterna inca	AY631328 [b]		
Larus marinus	EF373088 [a]		DQ433757 [h]
Numenius minutus	EF373095 [a]		KF009548.1 [*]
Onychoprion anaethetus	AY631332 [b]		DQ433203 [h]
Pagophila eburnea	EF373097 [a]		DQ433862 [h]
Phaetusa simplex	AY631329 [b]		FJ028004.1 [t]
Rhinoptilus chalcopterus	EF373105 [a]		
Rhodostethia rosea	EF373106 [a]		DQ434048 [h]
Rissa tridactyla	DQ385280 [l]	DQ385297 [l]	DQ385178 [l]
Rynchops niger	DQ385281 [l]	DQ385298 [l]	DQ385179 [l]
Stercorarius longicaudus	EF373109 [a]		DQ434147 [h]
Stercorarius skua	DQ385278 [l]	DQ385295 [l]	DQ385176 [l]
Sternula superciliaris	AY631352 [b]		EU525527.1 [v]
Stiltia isabella	EF373110 [a]		
Thalasseus maximus	DQ674571 [d]	DQ674609 [d]	DQ434165 [h]
Xema sabini	EF373116 [a]		AY666205.1 [s]

Taxon	**cytb**		**ND2**		**ND5**	
Anous tenuirostris	EF373119	[a]	EF373223	[a]		
Bartramia longicauda	EF373122	[a]	EF373226	[a]		
Calidris subruficollis	EF373162	[a]	EF373272	[a]		
Charadrius vociferous	DQ385218	[l]	DQ385082	[l]	DQ385150	[l]
Charadrius wilsonia						
Chlidonias leucopterus	EF373124	[a]	EF373231	[a]		
Creagrus furcatus	EF373127	[a]	EF373234	[a]		
Cursorius temminckii	DQ385226	[l]	DQ385090	[l]	DQ385158	[l]
Gelochelidon nilotica	AY631311	[b]	AY631383	[b]		
Glareola maldivarum	EF373133	[a]	EF373241	[a]		
Gygis alba	AY631290	[b]	EF373242	[a]		
Hydrophasianus chirurgus	EF373135	[a]	EF373243	[a]	AF146627	[o]
Larosterna inca	AY631292	[b]	AY631364	[b]		
Larus marinus	AJ508140	[i]	EF373246	[a]		
Numenius minutus	EF373145	[a]	EF373253	[a]		
Onychoprion anaethetus	AY631296	[b]	AY631368	[b]		
Pagophila eburnea	EF373147	[a]	EF373255	[a]		
Phaetusa simplex	AY631293	[b]	AY631365	[b]		
Rhinoptilus chalcopterus	EF373154	[a]	EF373263	[a]		
Rhodostethia rosea	EF373155	[a]	EF373264	[a]		
Rissa tridactyla	DQ385229	[l]	DQ385093	[l]	DQ385161	[l]
Rynchops niger	DQ385230	[l]	DQ385094	[l]	DQ385162	[l]
Stercorarius longicaudus	U76820	[c]	EF373267	[a]		
Stercorarius skua	DQ385227	[l]	DQ385091	[l]	DQ385159	[l]
Sternula superciliaris	AY631316	[b]	AY631388	[b]		
Stiltia isabella	EF373159	[a]	EF373268	[a]		
Thalasseus maximus	AY631309	[b]	AY631381	[b]		
Xema sabini	EF373164	[a]	EF373275	[a]		

Taxon	**ND6**	**RAG-1**	
Anous tenuirostris		EF373168	[a]
Bartramia longicauda		EF373171	[a]
Calidris subruficollis		EF373215	[a]
Charadrius vociferous		AF143736	[f]
Charadrius wilsonia		KM001593.1	[r]
Chlidonias leucopterus		EF373175	[a]
Creagrus furcatus		EF373178	[a]
Cursorius temminckii		AY228780	[m]
Gelochelidon nilotica		EF373184	[a]
Glareola maldivarum			
Gygis alba		EF373185	[a]
Hydrophasianus chirurgus		EF373186	[a]
Larosterna inca		EF373190	[a]
Larus marinus		AY228799	[m]
Numenius minutus		EF373195	[a]
Onychoprion anaethetus			
Pagophila eburnea		EF373198	[a]
Phaetusa simplex		EF373200	[a]
Rhinoptilus chalcopterus		EF373205	[a]
Rhodostethia rosea		EF373206	[a]
Rissa tridactyla		AY228785	[m]
Rynchops niger		AY228784	[m]
Stercorarius longicaudus		EF373208	[a]
Stercorarius skua		AY228783	[m]
Sternula superciliaris		EF373210	[a]
Stiltia isabella		EF373211	[a]
Thalasseus maximus			
Xema sabini		EF373217	[a]

Appendix 2: Stratigraphic Age Data References

Taxon	**References** (See following chart for full reference information)
Aethia barnesi	36
Aethia rossmoori	19; 36
Aethia storeri	36
Alca ausonia	1; 16; 47
Alca carolinensis	34
Alca grandis	14; 16; 38; 47
Alca minor	34
Alca olsoni	34
Alca stewarti	25
Boutersemia belgica	17
Brachyramphus dunkeli	45
Brachyramphus pliocenum	18; 45
Cepphus olsoni	23
Cerorhinca minor	20; 27
Cerorhinca reai	45
Fratercula dowi	7; 8; 9
Laricola elegans	37
Mancalla californiensis	15; 18; 30; 31
Mancalla cedrosensis	20; 23; 27; 35
Mancalla lucasi	35
Mancalla vergrandis	35
Miocepphus blowi	13
Miocepphus bohaskai	13
Miocepphus mcclungi	2; 13; 43; 47; 50
Miocepphus mergulellus	13
Miomancalla howardi	35
Miomancalla wetmorei	21; 23
Miomancalla wetmorei	35
Nupharanassa bulotorum	11
Pinguinus alfrednewtoni	49
Pinguinus impennis	3; 4; 5; 6; 10; 12; 24; 26; 28; 32; 33; 39; 41; 42; 44; 46; 48; 51
Pseudocepphus teres	13
Synthliboramphus rineyi	45
Uria brodkorbi	22

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5	C. Mourer-Chauvire. 1999. Influence de l'homme prehistorique sur la repartition de certains oiseaux marins: L'exemple du grand pingouin Pinguinus impennis. 67(4):273-279
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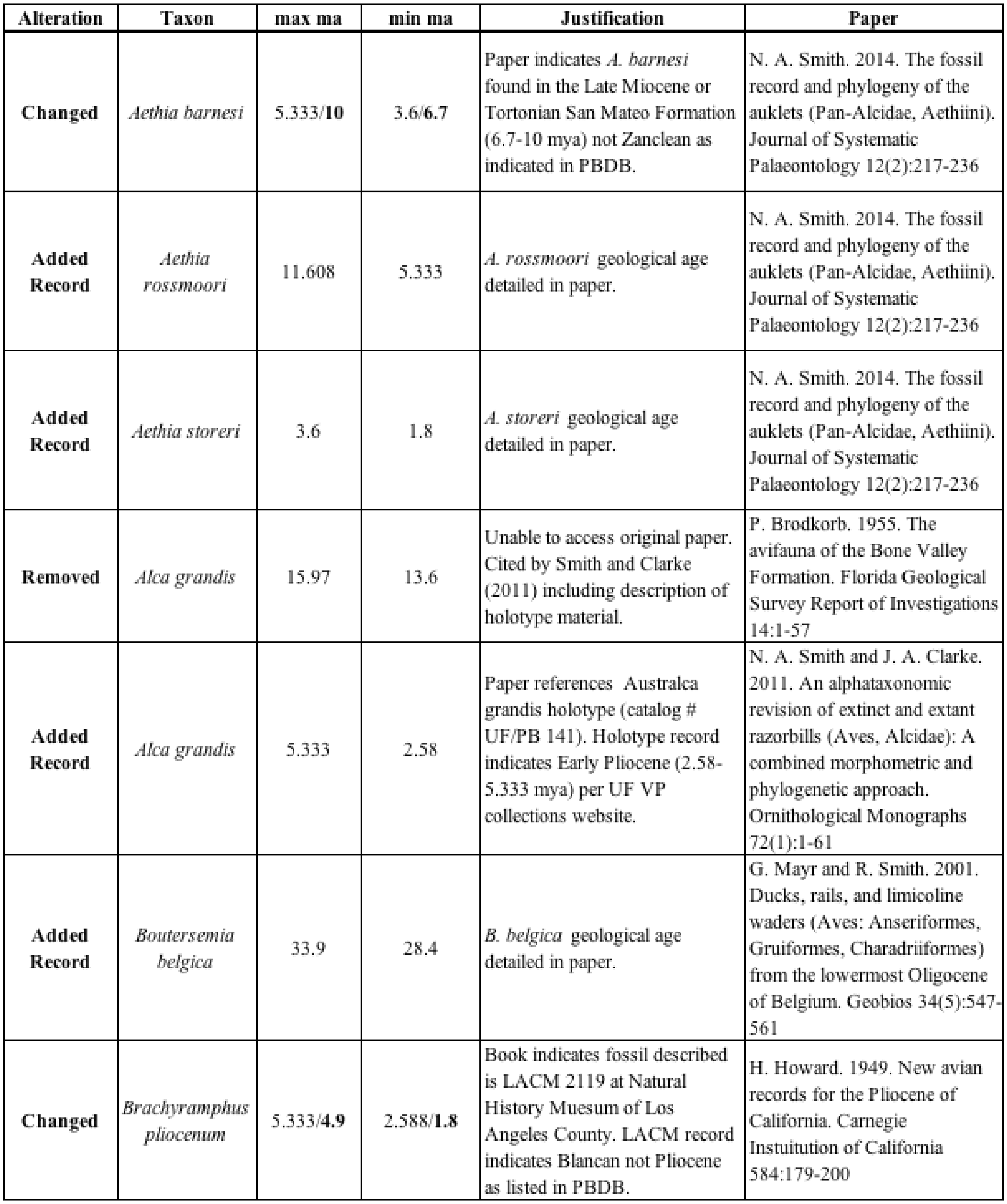
Appendix 3: Alterations to Stratigraphic Age Data from Paleobiology Database

Records from PBDB which were updated and records added from additional literature review are indicated. When records were corrected based on the original paper the change is formatted as the original PBDB entry / the updated age in bold (Original/**Corrected**).



Alteration	Taxon	max ma	min ma	Justification	Paper
Changed	*Aethia barnesi*	5.333/**10**	3.6/**6.7**	Paper indicates *A. barnesi* found in the Late Miocene or Tortonian San Mateo Formation (6.7-10 mya) not Zanclean as indicated in PBDB.	N. A. Smith. 2014. The fossil record and phylogeny of the auklets (Pan-Alcidae, Aethiini). Journal of Systematic Palaeontology 12(2):217-236
Added Record	*Aethia rossmoori*	11.608	5.333	*A. rossmoori* geological age detailed in paper.	N. A. Smith. 2014. The fossil record and phylogeny of the auklets (Pan-Alcidae, Aethiini). Journal of Systematic Palaeontology 12(2):217-236
Added Record	*Aethia storeri*	3.6	1.8	*A. storeri* geological age detailed in paper.	N. A. Smith. 2014. The fossil record and phylogeny of the auklets (Pan-Alcidae, Aethiini). Journal of Systematic Palaeontology 12(2):217-236
Removed	*Alca grandis*	15.97	13.6	Unable to access original paper. Cited by Smith and Clarke (2011) including description of holotype material.	P. Brodkorb. 1955. The avifauna of the Bone Valley Formation. Florida Geological Survey Report of Investigations 14:1-57
Added Record	*Alca grandis*	5.333	2.58	Paper references Australca grandis holotype (catalog # UF/PB 141). Holotype record indicates Early Pliocene (2.58-5.333 mya) per UF VP collections website.	N. A. Smith and J. A. Clarke. 2011. An alphataxonomic revision of extinct and extant razorbills (Aves, Alcidae): A combined morphometric and phylogenetic approach. Ornithological Monographs 72(1):1-61
Added Record	*Boutersemia belgica*	33.9	28.4	*B. belgica* geological age detailed in paper.	G. Mayr and R. Smith. 2001. Ducks, rails, and limicoline waders (Aves: Anseriformes, Gruiformes, Charadriiformes) from the lowermost Oligocene of Belgium. Geobios 34(5):547-561
Changed	*Brachyramphus pliocenum*	5.333/**4.9**	2.588/**1.8**	Book indicates fossil described is LACM 2119 at Natural History Muesum of Los Angeles County. LACM record indicates Blancan not Pliocene as listed in PBDB.	H. Howard. 1949. New avian records for the Pliocene of California. Carnegie Insutuition of California 584:179-200

Alteration	Taxon	max ma	min ma	Justification	Paper
Changed	*Cepphus olsoni*	5.333/**11.65**	3.6/**5.333**	Paper indicated fossil is from late Miocene (5.333-11.65) not Zanclean as listed in PBDB.	H. Howard. 1982. Fossil birds from Tertiary marine beds at Oceanside, San Diego County, California, with discriptions of two species of the genera Uria and Cepphus (Aves: Alcidae). Contributions in Science, Natural History Museum of Los Angeles County 341:1-15
Added Record	*Laricola elegans*	24.1	23.6	*L. elegans* geological age detailed in paper.	N.A. Smith. 2015. Sixteen vetted fossil calibrations for divergence dating of Charadriiformes (Aves, Neognathae). Palaeontologia Electronica 18.1.4FC.
Added Record	*Mancalla cedrosensis*	7.246	5.333	Paper references Howard (1971) fossil record from Late Miocene.	N. A. Smith. 2011. Taxonomic revision and phylogenetic analysis of the flightless Mancallinae (Aves, Pan-Alcidae). ZooKeys 91:1-116
Changed	*Mancalla vergrandis*	3.6/**5.333**	2.588/**0.781**	Paper indicates fossil is from "Middle Pliocene to Early Pleistocene (Zanclean-Calabrian)" not Piacenzian as listed in PBDB.	N. A. Smith. 2011. Taxonomic revision and phylogenetic analysis of the flightless Mancallinae (Aves, Pan-Alcidae). ZooKeys 91:1-116
Added Record	*Miomancalla wetmorei*	7.246	3.6	Confirmed dates for entry: H. Howard. 1976. A new species of flightless auk from the Miocene of California (Alcidae: Mancallinae). Smithsonian Contributions to Paleobiology, Washington, DC: Smithsonian Institution\r\n (27):141-146	N. A. Smith. 2011. Taxonomic revision and phylogenetic analysis of the flightless Mancallinae (Aves, Pan-Alcidae). ZooKeys 91:1-116
Added Record	*Nupharanassa bulotorum*	33.9	28.1	*N. bulotorum* geological age detailed in paper.	D. T. Rasmussen, S. L. Olson, and E. L. Simons. 1987. Fossil Birds from the Oligocene Jebel Qatrani Formation, Fayum Province, Egypt. Smithsonian Contributions to Paleobiology 62:1-20
Changed	*Pseudocepphus teres*	15.97	13.82/**5.333**	Paper states *P. teres* fossil from "Middle Miocene Calvert Formation and Upper Miocene St Mary's Formation in Calvert and St Mary's counties, Maryland." extending PBDB's listed Langhian age.	E. Wijnker and S. L. Olson. 2009. A revision of the fossil genus Miocepphus and other Miocene Alcidae (Aves: Charadriiformes) of the western North Atlantic Ocean. Journal of Systematic Palaeontology 7(4):471-487
Changed	*Uria brodkorbi*	11.62/**12.5**	7.246/**9.4**	Paper states fossil from "Formation and age. -Sisquoc Formation, late Miocene, Clarendonian land mammal age" not Tortonian as listed in PBDB.	H. Howard. 1981. A new species of murre, genus Uria, from the Late Miocene of California (Aves: Alcidae). Bulletin of the Southern California Academy of Sciences 80(1):1-12

Appendix 4: Combined Bayesian analysis command block

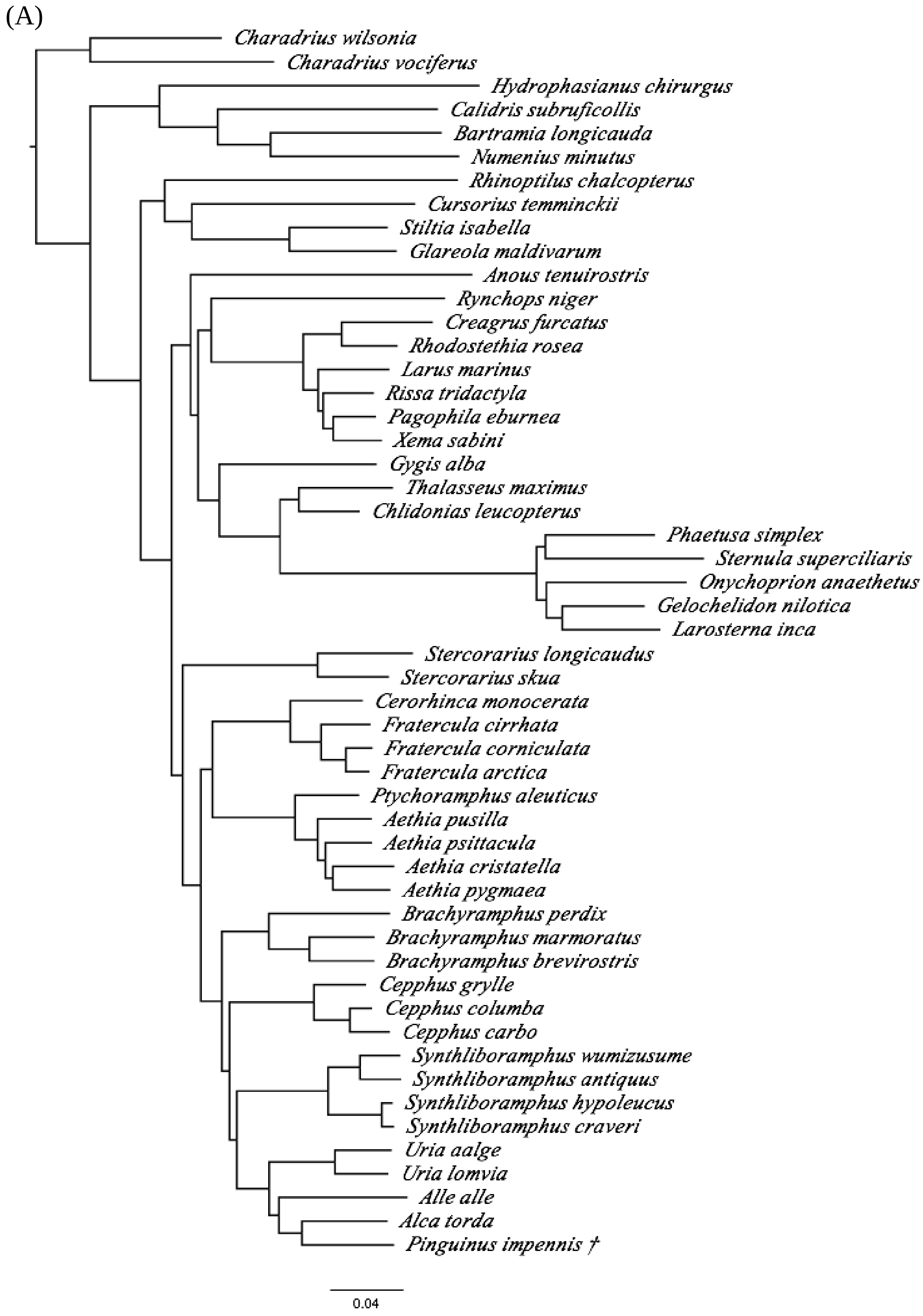
```
BEGIN MRBAYES;

       CHARSET 12S = 1 - 698;
       CHARSET 16S = 699 - 1735;
       CHARSET CO1 = 1736 - 2815;
       CHARSET ND2 = 2816 - 3813;
       CHARSET ND5 = 3814 - 5632;
       CHARSET ND6 = 5633 - 6154;
       CHARSET RAG1 = 6155 - 8896;
       CHARSET cytb = 8897 - 9941;
       CHARSET morphology = 9942 - 10294;

partition favored = 9: 12S, 16S, CO1, ND2, ND5, ND6, RAG1,
cytb, morphology;

set partition = favored;

lset applyto=(9) coding=variable;

prset applyto=(9) symdirihyperpr=fixed(infinity)
ratepr=variable;


lset applyto=(1,2,3,4,5,6,7,8) nst=6 rates=invgamma;

prset applyto=(1,2,3,4,5,6,7,8) revmatpr=dirichlet(1,2,1,1,2,1)
statefreqpr=dirichlet(2,2,2,2) pinvarpr=uniform(0,1)
ratepr=variable;

prset applyto=(all) brlenspr=unconstrained:exponential(1.0)
shapepr=exponential(1.0);

unlink shape=(all) statefreq=(all) revmat=(all);

outgroup Charadrius_vociferus;

mcmc ngen=25000000 samplefreq=1000 printfreq=10000 nchains=4
nruns=2;

sumt nruns=2 burninfrac=.25 contype=Allcompat;
sump nruns=2 burninfrac=.25;

quit;
```

Molecular Bayesian analysis command block

```
BEGIN MRBAYES;

       CHARSET 12S = 1 - 698;
```

```
	CHARSET 16S = 699 - 1735;
	CHARSET CO1 = 1736 - 2815;
	CHARSET ND2 = 2816 - 3813;
	CHARSET ND5 = 3814 - 5632;
	CHARSET ND6 = 5633 - 6154;
	CHARSET RAG1 = 6155 - 8896;
	CHARSET cytb = 8897 - 9941;

partition favored = 8: 12S, 16S, CO1, ND2, ND5, ND6, RAG1,
cytb;

set partition = favored;


lset applyto=(1,2,3,4,5,6,7,8) nst=6 rates=invgamma;

prset applyto=(1,2,3,4,5,6,7,8)
revmatpr=dirichlet(1,2,1,1,2,1)
statefreqpr=dirichlet(2,2,2,2) pinvarpr=uniform(0,1)
ratepr=variable;

prset applyto=(all)
brlenspr=unconstrained:exponential(1.0)
shapepr=exponential(1.0);

unlink shape=(all) statefreq=(all) revmat=(all);

outgroup Charadrius_vociferus;

mcmc ngen=25000000 samplefreq=1000 printfreq=10000
nchains=4 nruns=2;

sumt nruns=2 burninfrac=.25 contype=Allcompat;
sump nruns=2 burninfrac=.25;

quit;


END;
```

Figures and Tables



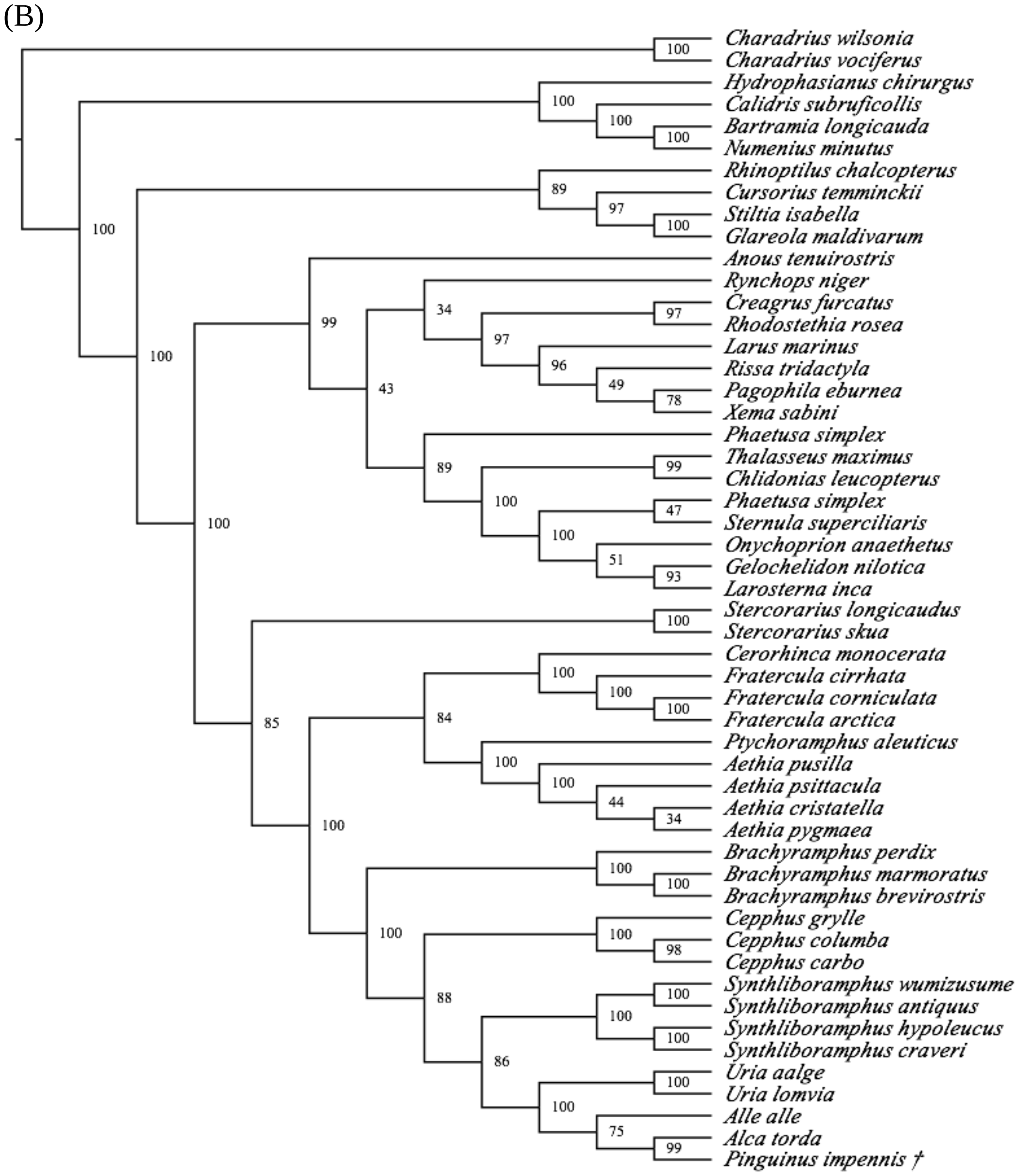
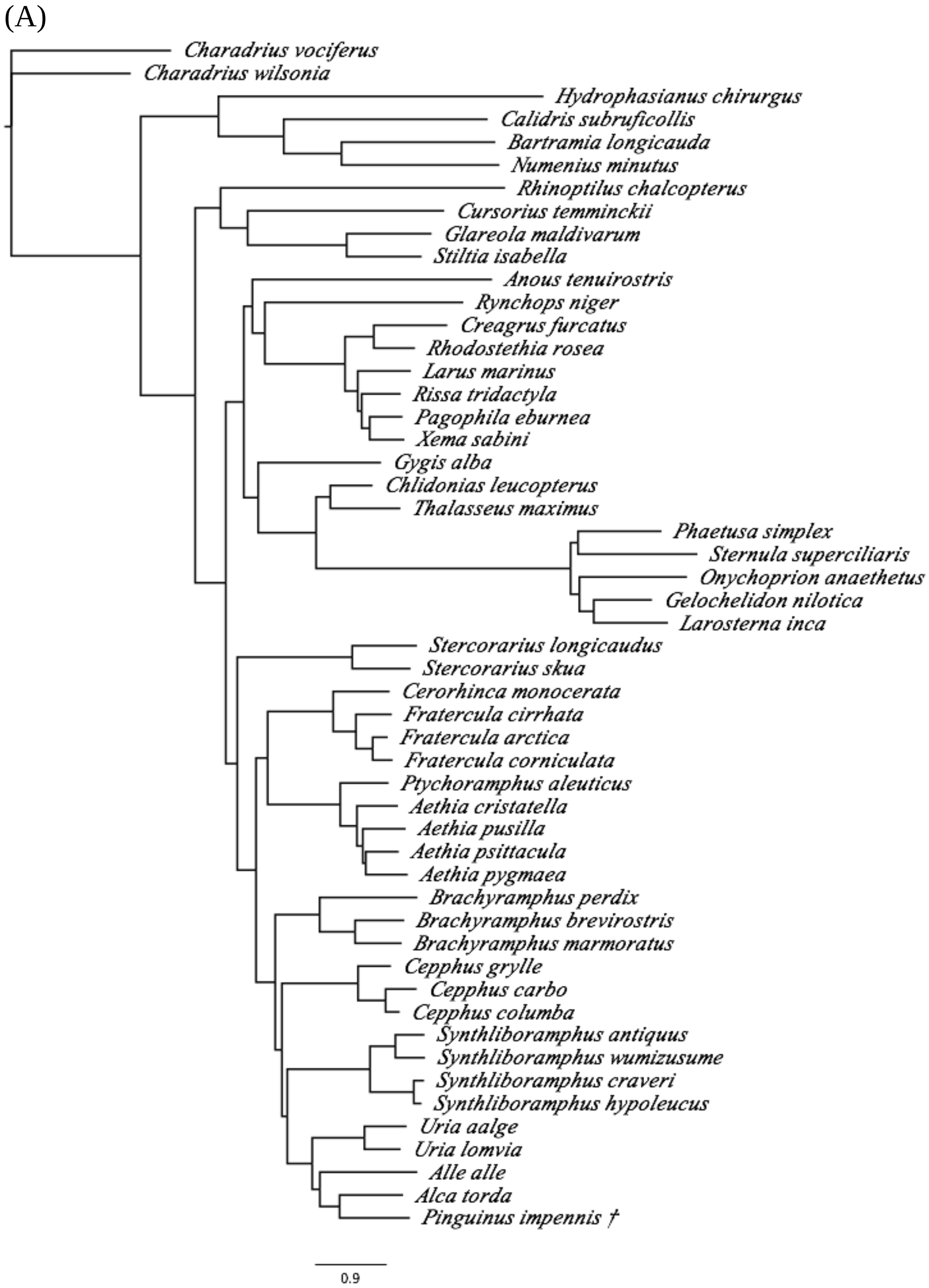


Figure 1. Relationships of extant Alcidae, *Pinguinus impennis*, and outgroup species inferred through a maximum likelihood analysis of molecular data in RaxML. **(A)** Phylogram of Alcidae and outgroup relationships. **(B)** Cladogram with bootstrap support values indicated at nodes.


(A)
Charadrius vociferus
Charadrius wilsonia
Hydrophasianus chirurgus
Calidris subruficollis
Bartramia longicauda
Numenius minutus
Rhinoptilus chalcopterus
Cursorius temminckii
Glareola maldivarum
Stiltia isabella
Anous tenuirostris
Rynchops niger
Creagrus furcatus
Rhodostethia rosea
Larus marinus
Rissa tridactyla
Pagophila eburnea
Xema sabini
Gygis alba
Chlidonias leucopterus
Thalasseus maximus
Phaetusa simplex
Sternula superciliaris
Onychoprion anaethetus
Gelochelidon nilotica
Larosterna inca
Stercorarius longicaudus
Stercorarius skua
Cerorhinca monocerata
Fratercula cirrhata
Fratercula arctica
Fratercula corniculata
Ptychoramphus aleuticus
Aethia cristatella
Aethia pusilla
Aethia psittacula
Aethia pygmaea
Brachyramphus perdix
Brachyramphus brevirostris
Brachyramphus marmoratus
Cepphus grylle
Cepphus carbo
Cepphus columba
Synthliboramphus antiquus
Synthliboramphus wumizusume
Synthliboramphus craveri
Synthliboramphus hypoleucus
Uria aalge
Uria lomvia
Alle alle
Alca torda
Pinguinus impennis †
0.9

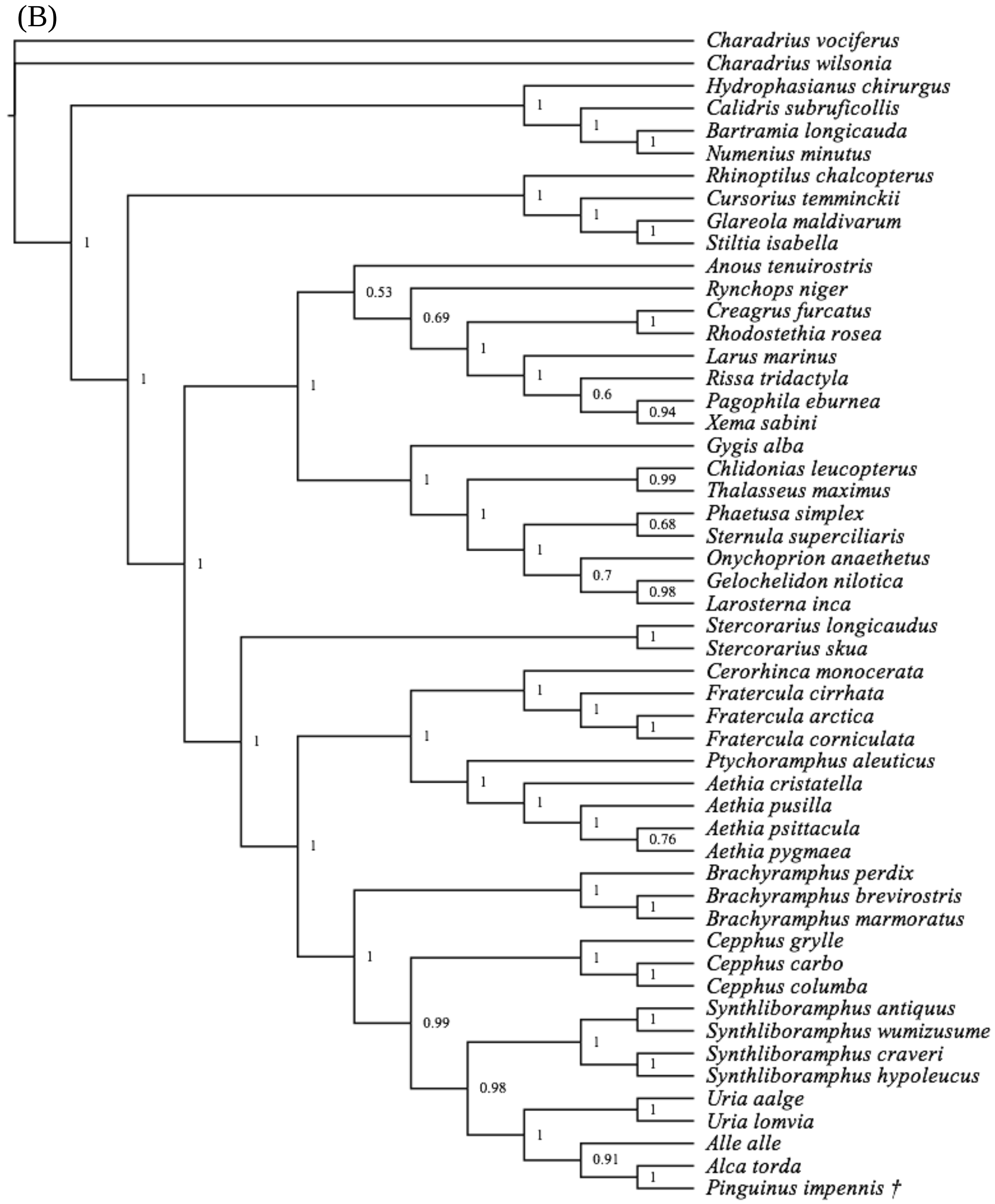
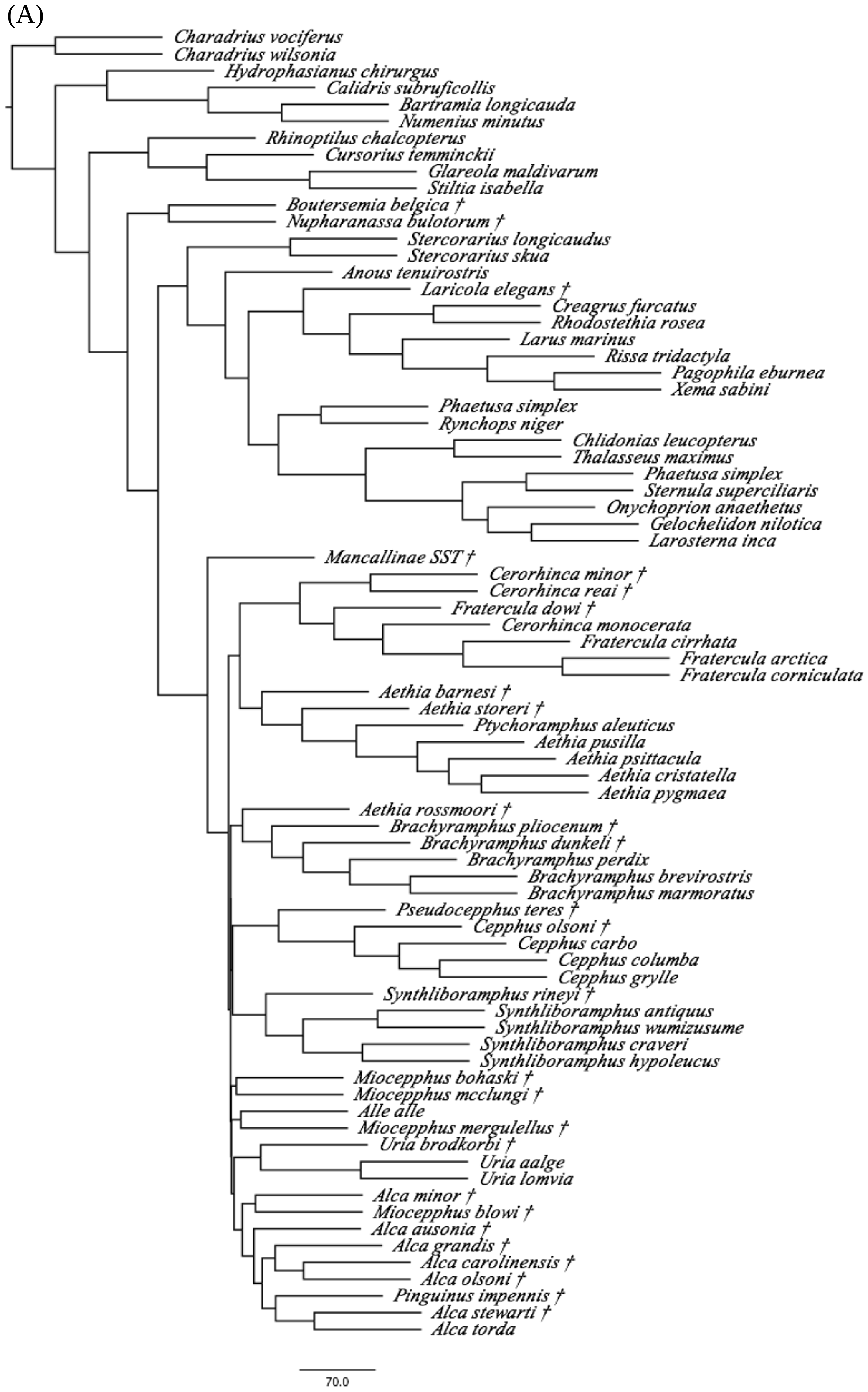


Figure 2. Relationships of extant Alcidae, *Pinguinus impennis*, and outgroup species inferred through a Bayesian analysis of molecular data using MrBayes. **(A)** Phylogram of Alcidae and outgroup relationships. **(B)** Cladogram with Bayesian posterior probability indicated at nodes.


(A)
Charadrius vociferus
Charadrius wilsonia
Hydrophasianus chirurgus
Calidris subruficollis
Bartramia longicauda
Numenius minutus
Rhinoptilus chalcopterus
Cursorius temminckii
Glareola maldivarum
Stiltia isabella
Boutersemia belgica †
Nupharanassa bulotorum †
Stercorarius longicaudus
Stercorarius skua
Anous tenuirostris
Laricola elegans †
Creagrus furcatus
Rhodostethia rosea
Larus marinus
Rissa tridactyla
Pagophila eburnea
Xema sabini
Phaetusa simplex
Rynchops niger
Chlidonias leucopterus
Thalasseus maximus
Phaetusa simplex
Sternula superciliaris
Onychoprion anaethetus
Gelochelidon nilotica
Larosterna inca
Mancallinae SST †
Cerorhinca minor †
Cerorhinca reai †
Fratercula dowi †
Cerorhinca monocerata
Fratercula cirrhata
Fratercula arctica
Fratercula corniculata
Aethia barnesi †
Aethia storeri †
Ptychoramphus aleuticus
Aethia pusilla
Aethia psittacula
Aethia cristatella
Aethia pygmaea
Aethia rossmoori †
Brachyramphus pliocenum †
Brachyramphus dunkeli †
Brachyramphus perdix
Brachyramphus brevirostris
Brachyramphus marmoratus
Pseudocepphus teres †
Cepphus olsoni †
Cepphus carbo
Cepphus columba
Cepphus grylle
Synthliboramphus rineyi †
Synthliboramphus antiquus
Synthliboramphus wumizusume
Synthliboramphus craveri
Synthliboramphus hypoleucus
Miocepphus bohaski †
Miocepphus mcclungi †
Alle alle
Miocepphus mergulellus †
Uria brodkorbi †
Uria aalge
Uria lomvia
Alca minor †
Miocepphus blowi †
Alca ausonia †
Alca grandis †
Alca carolinensis †
Alca olsoni †
Pinguinus impennis †
Alca stewarti †
Alca torda
70.0

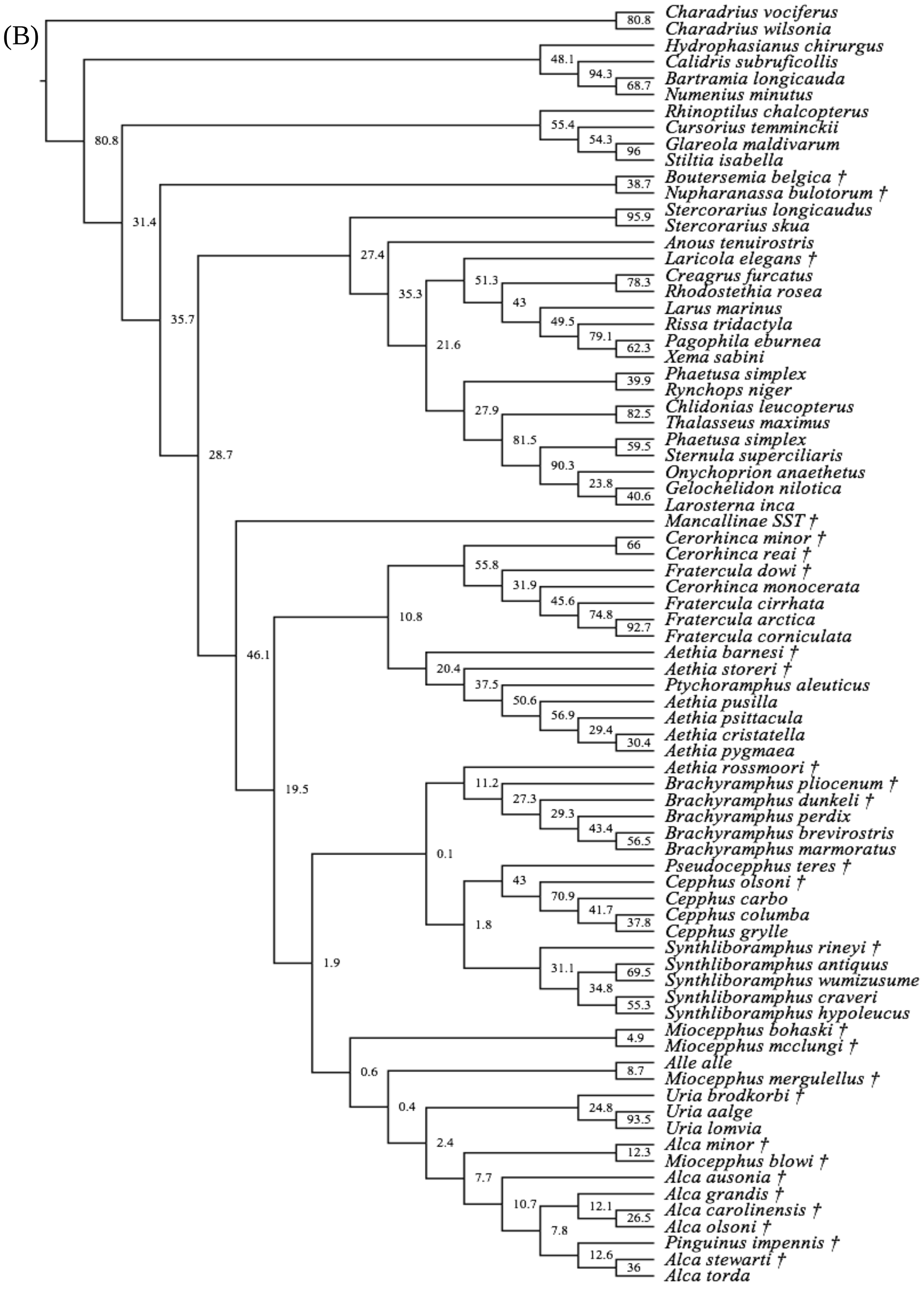
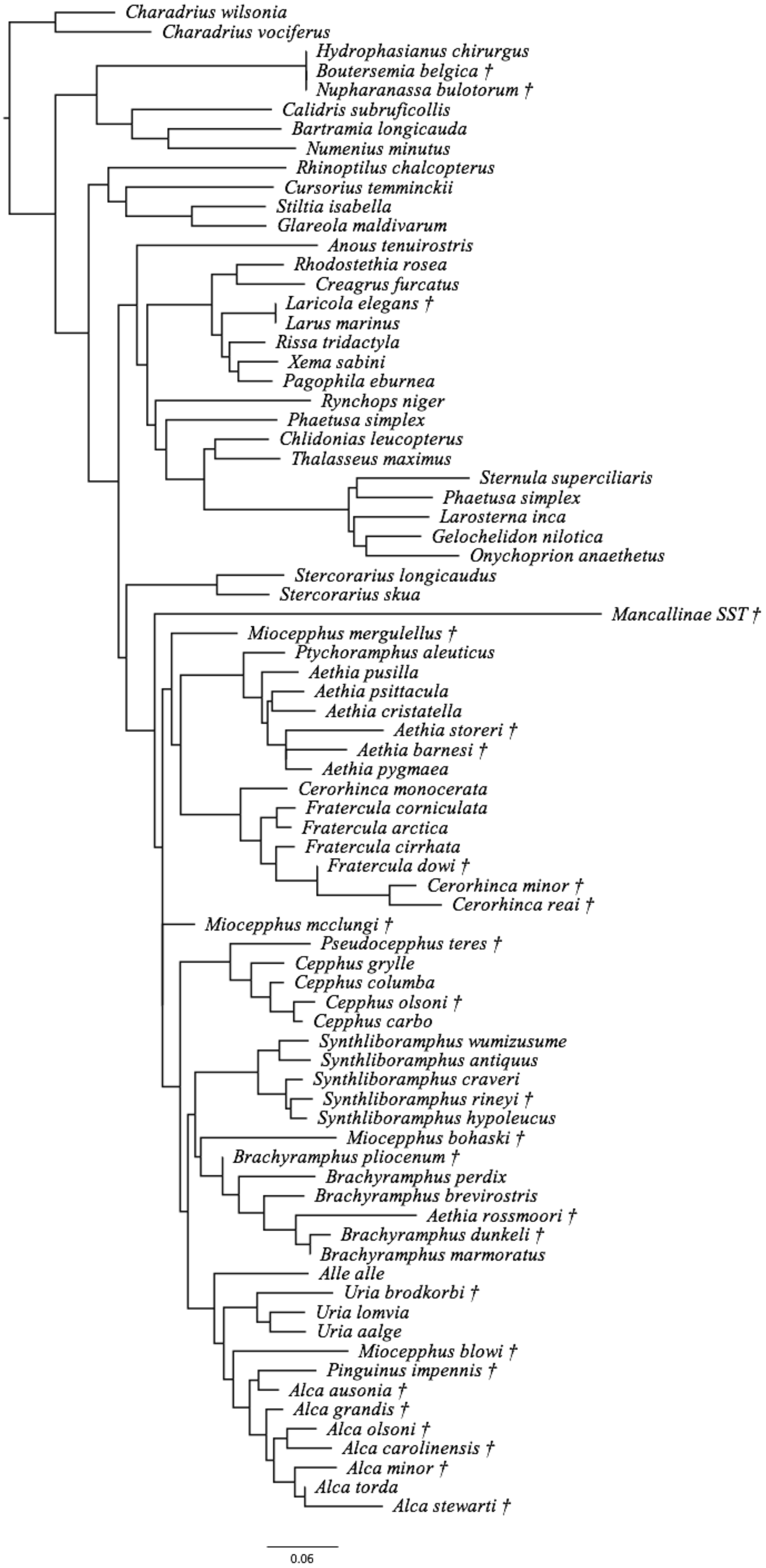


Figure 3. Relationships of Pan-Alcidae and outgroup species inferred through a parsimony analysis of morphological and molecular data. **(A)** Phylogram of Alcidae and outgroup relationships. **(B)** Cladogram with bootstrap support values indicated at nodes.

(A)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Charadrius vociferus
Hydrophasianus chirurgus
Boutersemia belgica †
Nupharanassa bulotorum †
Calidris subruficollis
Bartramia longicauda
Numenius minutus
Rhinoptilus chalcopterus
Cursorius temminckii
Stiltia isabella
Glareola maldivarum
Anous tenuirostris
Rhodostethia rosea
Creagrus furcatus
Laricola elegans †
Larus marinus
Rissa tridactyla
Xema sabini
Pagophila eburnea
Rynchops niger
Phaetusa simplex
Chlidonias leucopterus
Thalasseus maximus
Sternula superciliaris
Phaetusa simplex
Larosterna inca
Gelochelidon nilotica
Onychoprion anaethetus
Stercorarius longicaudus
Stercorarius skua
Mancallinae SST †
Miocepphus mergulellus †
Ptychoramphus aleuticus
Aethia pusilla
Aethia psittacula
Aethia cristatella
Aethia storeri †
Aethia barnesi †
Aethia pygmaea
Cerorhinca monocerata
Fratercula corniculata
Fratercula arctica
Fratercula cirrhata
Fratercula dowi †
Cerorhinca minor †
Cerorhinca reai †
Miocepphus mcclungi †
Pseudocepphus teres †
Cepphus grylle
Cepphus columba
Cepphus olsoni †
Cepphus carbo
Synthliboramphus wumizusume
Synthliboramphus antiquus
Synthliboramphus craveri
Synthliboramphus rineyi †
Synthliboramphus hypoleucus
Miocepphus bohaski †
Brachyramphus pliocenum †
Brachyramphus perdix
Brachyramphus brevirostris
Aethia rossmoori †
Brachyramphus dunkeli †
Brachyramphus marmoratus
Alle alle
Uria brodkorbi †
Uria lomvia
Uria aalge
Miocepphus blowi †
Pinguinus impennis †
Alca ausonia †
Alca grandis †
Alca olsoni †
Alca carolinensis †
Alca minor †
Alca torda
Alca stewarti †
0.06

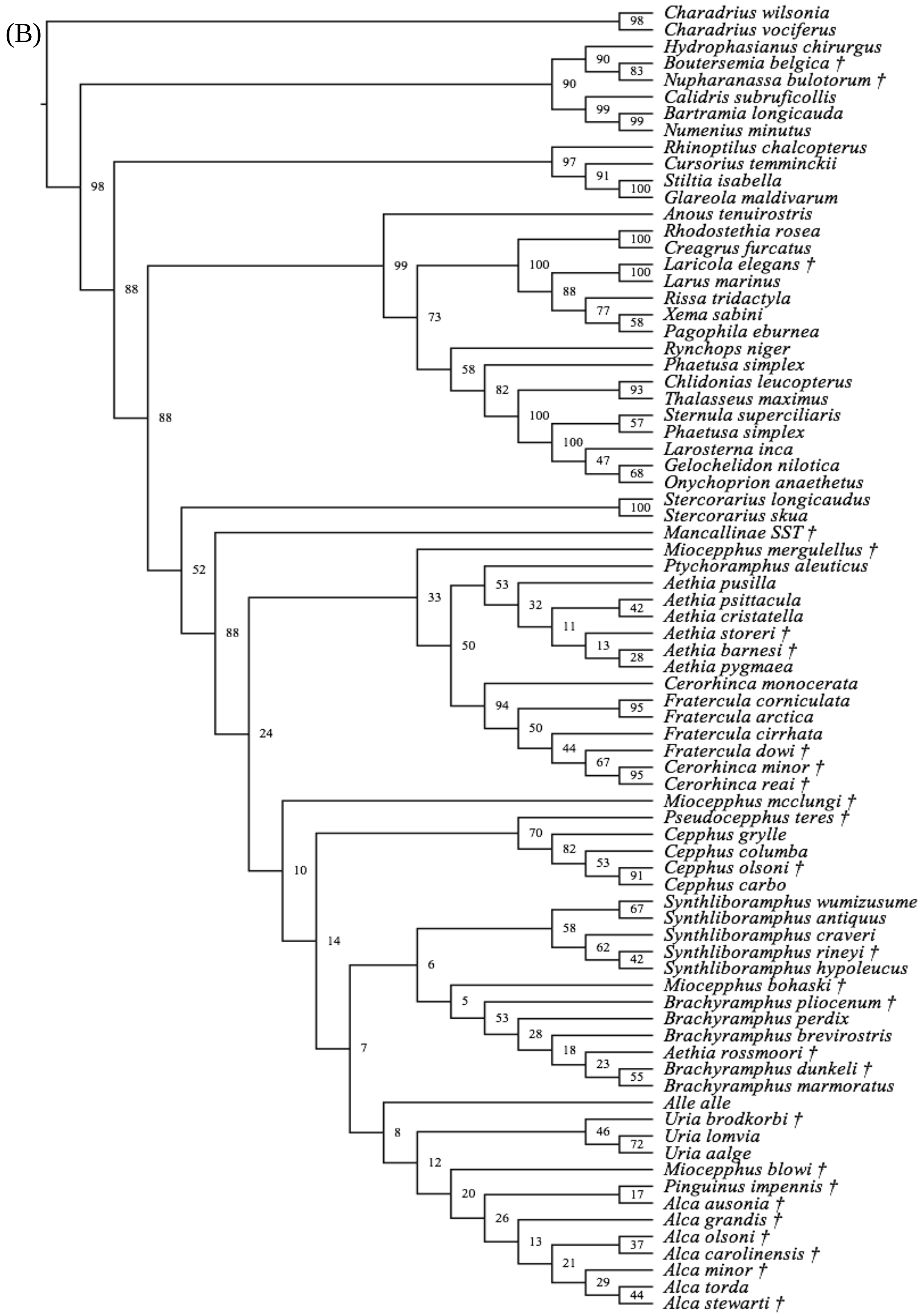
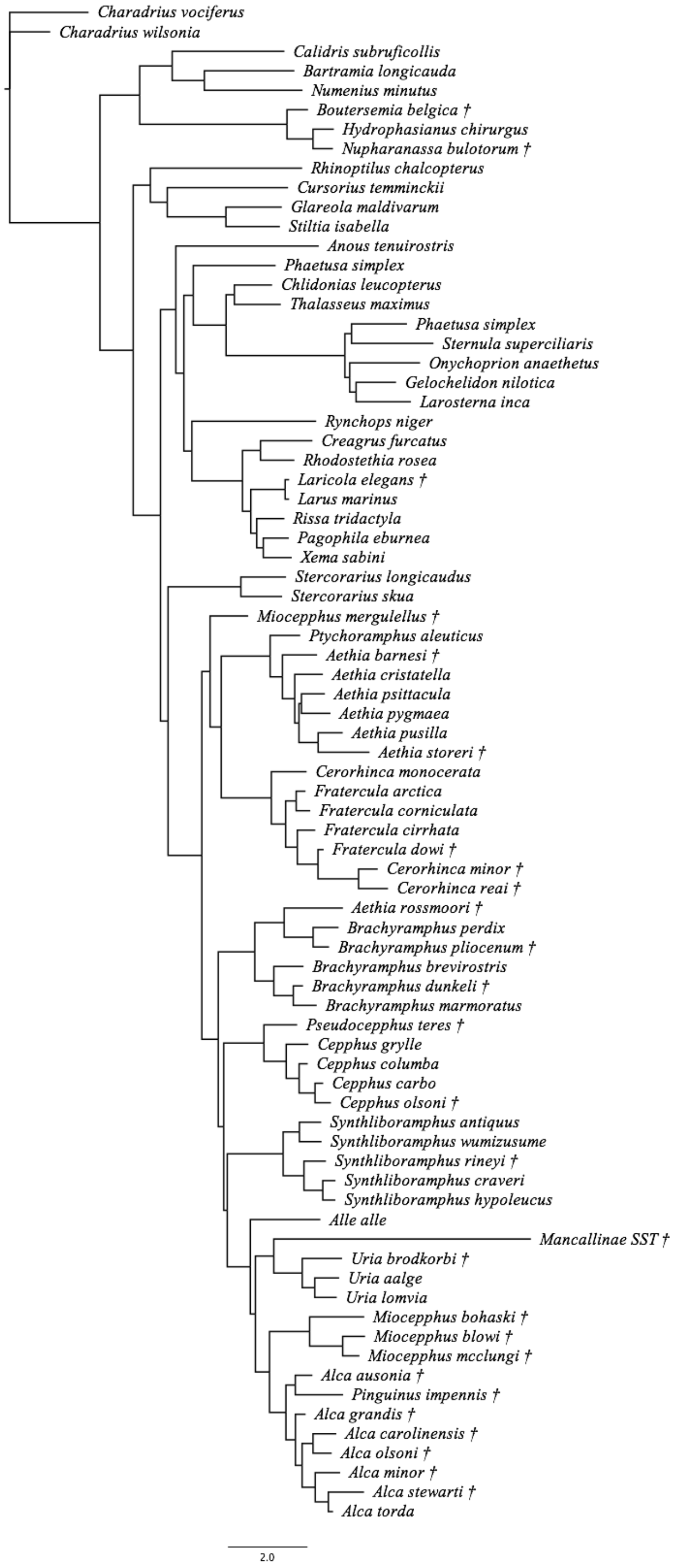


Figure 4. Relationships of Pan-Alcidae and outgroup species inferred through a combined maximum likelihood analysis of morphological and molecular data. **(A)** Phylogram of Alcidae and outgroup relationships. **(B)** Cladogram with bootstrap support values indicated at internal nodes.

(A)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Numenius minutus
Boutersemia belgica †
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Nupharanassa bulotorum †
Rhinoptilus chalcopterus
Cursorius temminckii
Glareola maldivarum
Stiltia isabella
Anous tenuirostris
Phaetusa simplex
Chlidonias leucopterus
Thalasseus maximus
Phaetusa simplex
Sternula superciliaris
Onychoprion anaethetus
Gelochelidon nilotica
Larosterna inca
Rynchops niger
Creagrus furcatus
Rhodostethia rosea
Laricola elegans †
Larus marinus
Rissa tridactyla
Pagophila eburnea
Xema sabini
Stercorarius longicaudus
Stercorarius skua
Miocepphus mergulellus †
Ptychoramphus aleuticus
Aethia barnesi †
Aethia cristatella
Aethia psittacula
Aethia pygmaea
Aethia pusilla
Aethia storeri †
Cerorhinca monocerata
Fratercula arctica
Fratercula corniculata
Fratercula cirrhata
Fratercula dowi †
Cerorhinca minor †
Cerorhinca reai †
Aethia rossmoori †
Brachyramphus perdix
Brachyramphus pliocenum †
Brachyramphus brevirostris
Brachyramphus dunkeli †
Brachyramphus marmoratus
Pseudocepphus teres †
Cepphus grylle
Cepphus columba
Cepphus carbo
Cepphus olsoni †
Synthliboramphus antiquus
Synthliboramphus wumizusume
Synthliboramphus rineyi †
Synthliboramphus craveri
Synthliboramphus hypoleucus
Alle alle
Mancallinae SST †
Uria brodkorbi †
Uria aalge
Uria lomvia
Miocepphus bohaski †
Miocepphus blowi †
Miocepphus mcclungi †
Alca ausonia †
Pinguinus impennis †
Alca grandis †
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Alca minor †
Alca stewarti †
Alca torda
2.0

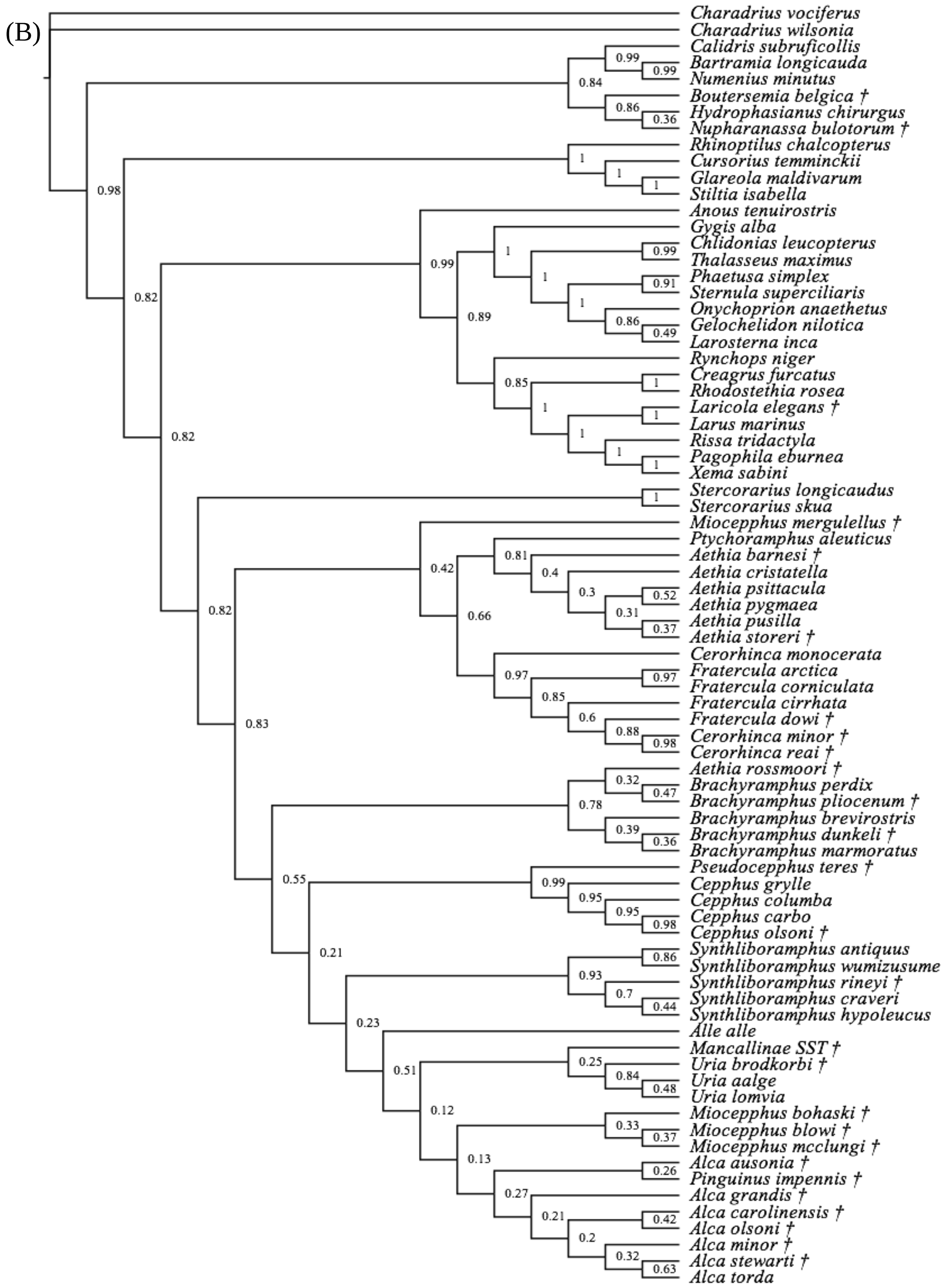


Figure 5. Relationships of Pan-Alcidae and outgroup species inferred through a combined Bayesian analysis of morphological and molecular data. **(A)** Phylogram of Alcidae and outgroup relationships. **(B)** Cladogram with Bayesian posterior probability indicated at nodes.

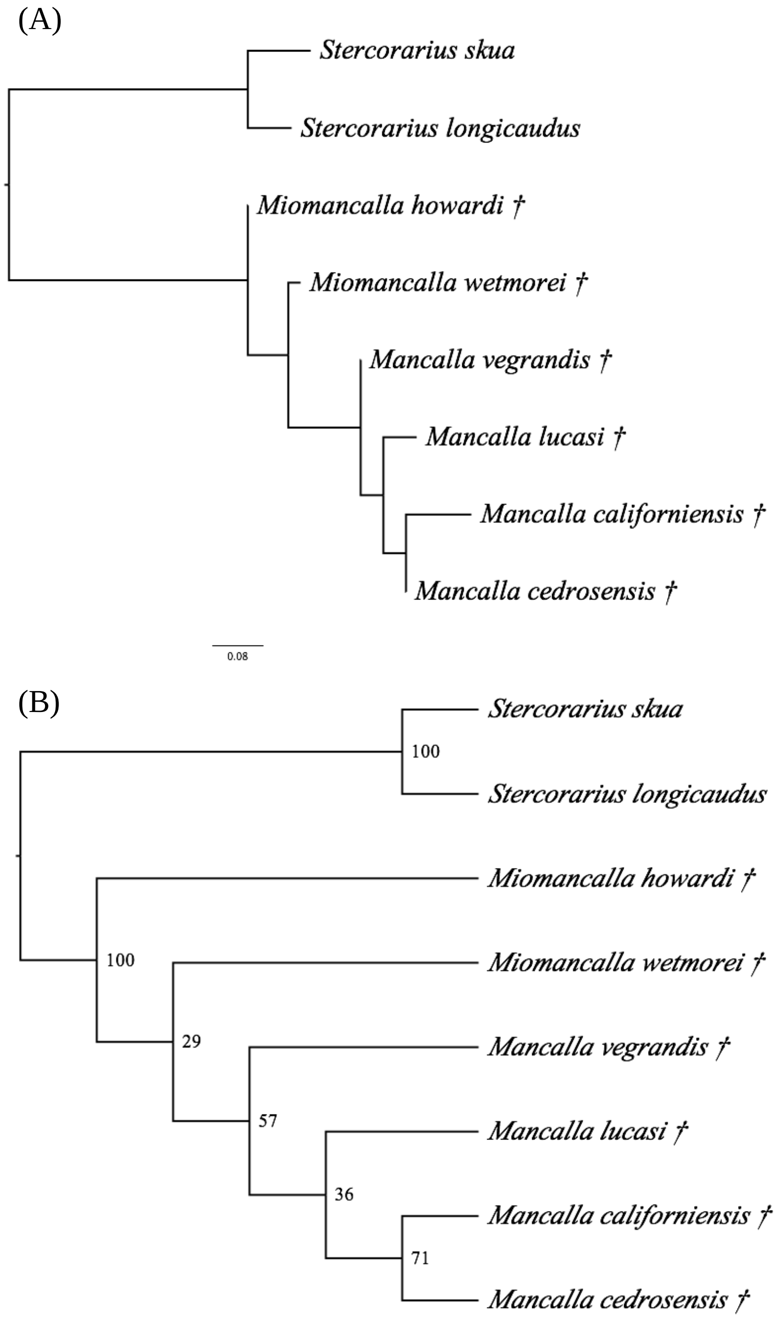
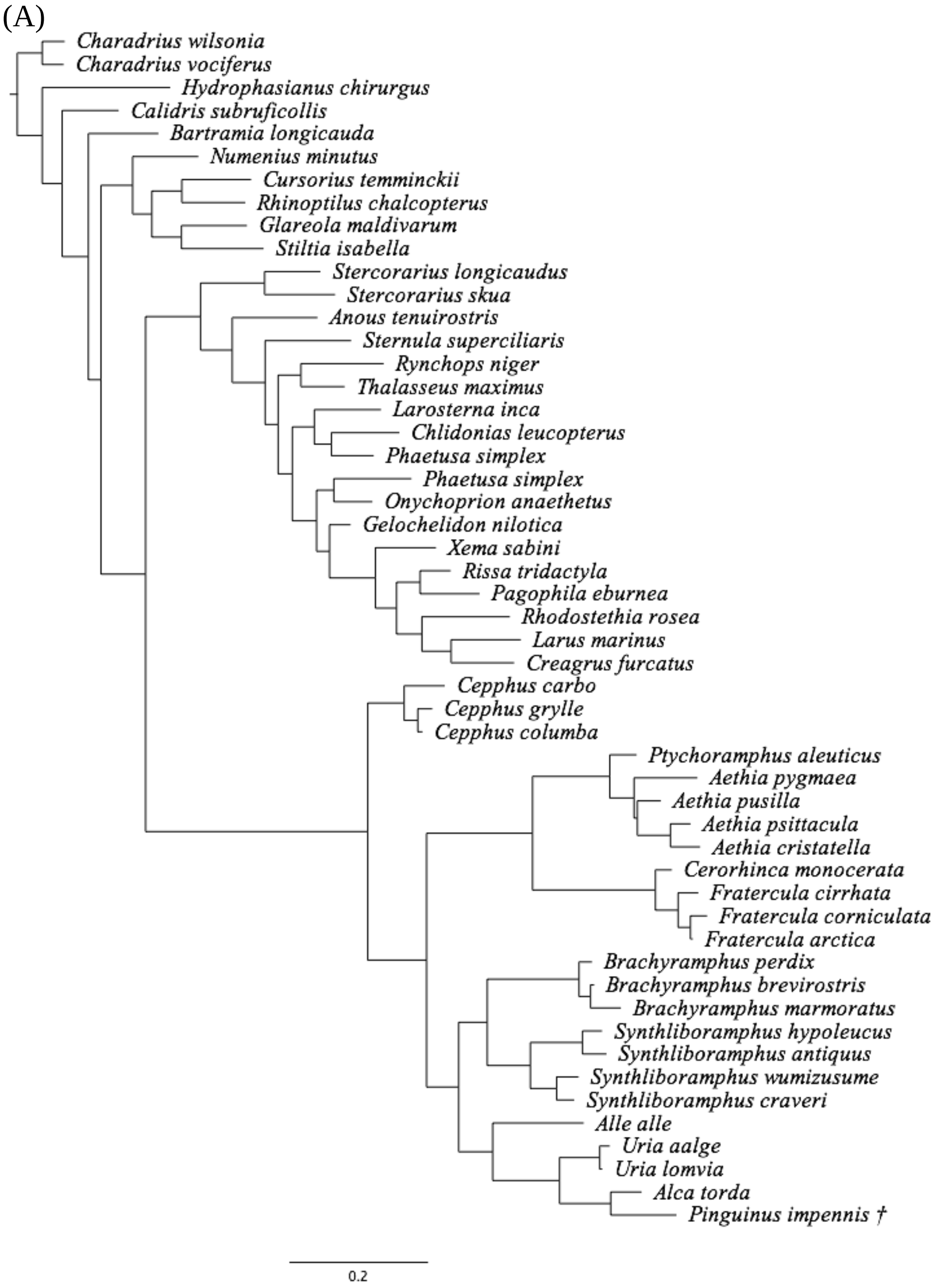


Figure 6. Relationships of the Mancllinae inferred through a maximum likelihood analysis of morphological data. **(A)** Phylogram of Mancallinae and outgroup relationships. **(B)** Cladogram with bootstrap support values indicated at internal nodes.


(A)
Charadrius wilsonia
Charadrius vociferus
Hydrophasianus chirurgus
Calidris subruficollis
Bartramia longicauda
Numenius minutus
Cursorius temminckii
Rhinoptilus chalcopterus
Glareola maldivarum
Stiltia isabella
Stercorarius longicaudus
Stercorarius skua
Anous tenuirostris
Sternula superciliaris
Rynchops niger
Thalasseus maximus
Larosterna inca
Chlidonias leucopterus
Phaetusa simplex
Phaetusa simplex
Onychoprion anaethetus
Gelochelidon nilotica
Xema sabini
Rissa tridactyla
Pagophila eburnea
Rhodostethia rosea
Larus marinus
Creagrus furcatus
Cepphus carbo
Cepphus grylle
Cepphus columba
Ptychoramphus aleuticus
Aethia pygmaea
Aethia pusilla
Aethia psittacula
Aethia cristatella
Cerorhinca monocerata
Fratercula cirrhata
Fratercula corniculata
Fratercula arctica
Brachyramphus perdix
Brachyramphus brevirostris
Brachyramphus marmoratus
Synthliboramphus hypoleucus
Synthliboramphus antiquus
Synthliboramphus wumizusume
Synthliboramphus craveri
Alle alle
Uria aalge
Uria lomvia
Alca torda
Pinguinus impennis †
0.2

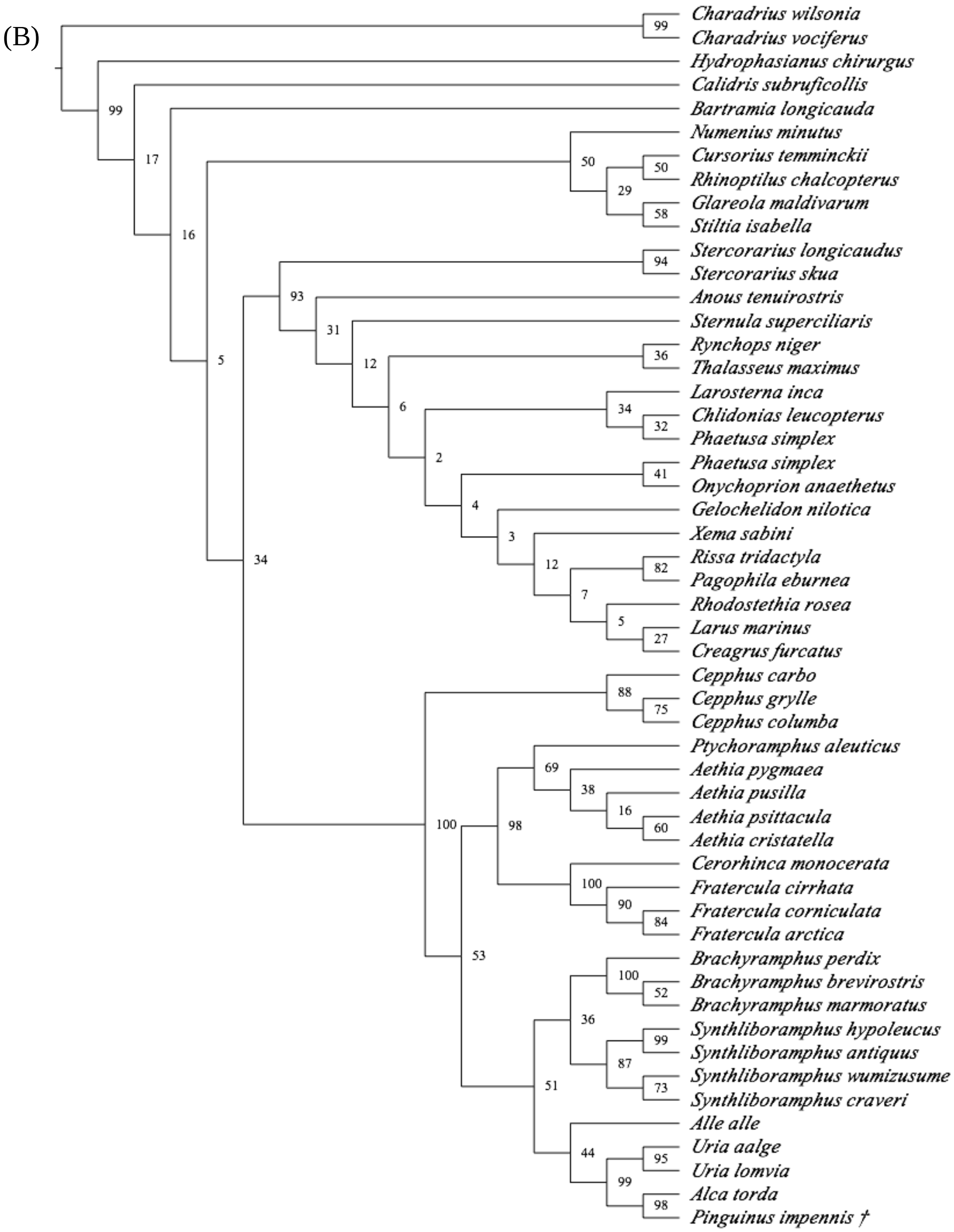
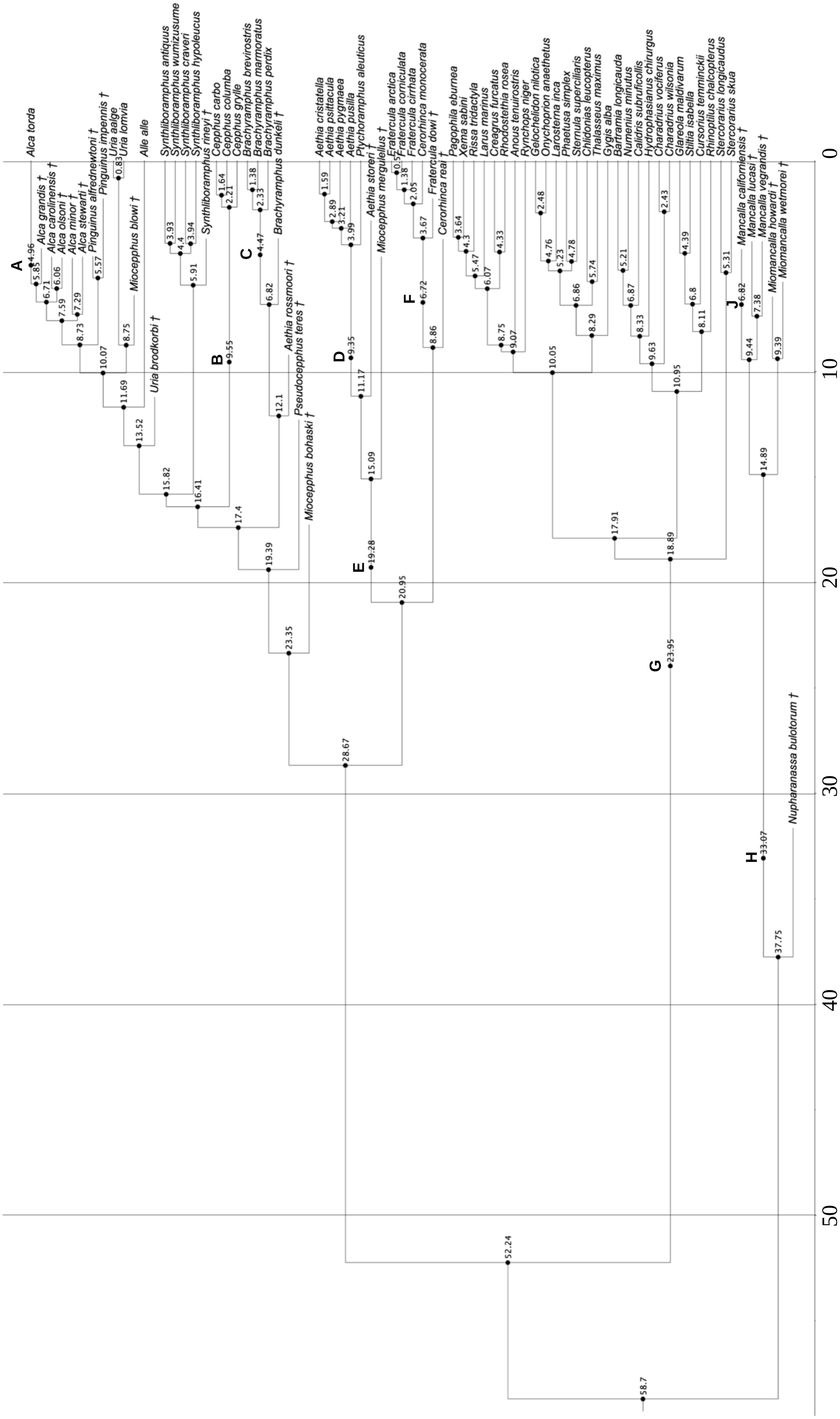


Figure 7. Relationships of extant Alcidae, *Pinguinus impennis*, and outgroup species inferred through a maximum likelihood analysis of morphology data using RaxML. **(A)** Phylogram of Alcidae and outgroup relationships. **(B)** Cladogram with bootstrap support values indicated at internal nodes.

(A)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Alca grandis †
Alca carolinensis †
Alca olsoni †
Alca minor †
Alca stewarti †
Pinguinus alfrednewtoni †
Pinguinus impennis †
Uria aalge
Uria lomvia
Miocepphus blowi †
Alle alle
Uria brodkorbi †
Synthliboramphus antiquus
Synthliboramphus wumizusume
Synthliboramphus craveri
Synthliboramphus hypoleucus
Synthliboramphus rineyi †
Cepphus carbo
Cepphus columba
Cepphus grylle
Brachyramphus brevirostris
Brachyramphus marmoratus
Brachyramphus perdix
Brachyramphus dunkeli †
Aethia rossmoori †
Pseudocepphus teres †
Miocepphus bohaski †
Aethia cristatella
Aethia psittacula
Aethia pygmaea
Aethia pusilla
Ptychoramphus aleuticus
Aethia storeri †
Miocepphus mergulellus †
Fratercula arctica
Fratercula corniculata
Fratercula cirrhata
Cerorhinca monocerata
Fratercula dowi †
Cerorhinca reai †
Pagophila eburnea
Xema sabini
Rissa tridactyla
Larus marinus
Creagrus furcatus
Rhodostethia rosea
Anous tenuirostris
Rynchops niger
Gelochelidon nilotica
Onychoprion anaethetus
Larosterna inca
Phaetusa simplex
Sternula superciliaris
Chlidonias leucopterus
Thalasseus maximus
Gygis alba
Bartramia longicauda
Numenius minutus
Calidris subruficollis
Hydrophasianus chirurgus
Charadrius vociferus
Charadrius wilsonia
Glareola maldivarum
Stiltia isabella
Cursorius temminckii
Rhinoptilus chalcopterus
Stercorarius longicaudus
Stercorarius skua
Mancalla californiensis †
Mancalla lucasi †
Mancalla vegrandis †
Miomancalla howardi †
Miomancalla wetmorei †
Nupharanassa bulotorum †
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4.96
5.85
6.06
6.71
7.59
7.29
8.73
5.57
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8.75
11.69
13.52
3.93
4.4
3.94
5.91
15.82
16.41
1.64
2.21
9.55
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2.33
4.47
6.82
12.1
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19.39
23.35
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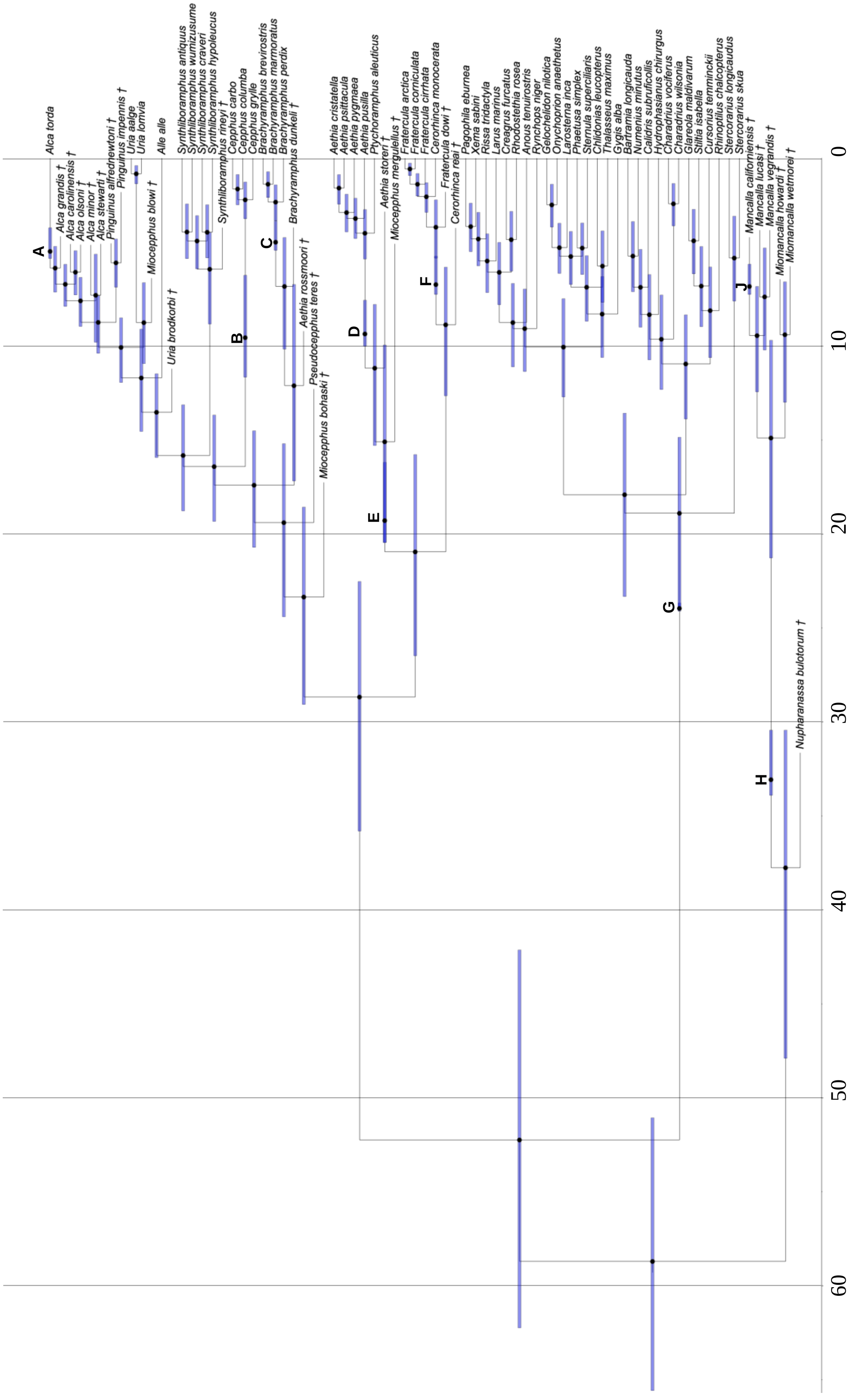
(B)



Alca torda
Alca grandis †
Alca carolinensis †
Alca olsoni †
Alca minor †
Alca stewarti †
Pinguinus alfrednewtoni †
Pinguinus impennis †
Uria aalge
Uria lomvia
Miocepphus blowi †
Alle alle
Uria brodkorbi †
Synthliboramphus antiquus
Synthliboramphus wumizusume
Synthliboramphus craveri
Synthliboramphus hypoleucus
Synthliboramphus rineyi †
Cepphus carbo
Cepphus columba
Cepphus grylle
Brachyramphus brevirostris
Brachyramphus marmoratus
Brachyramphus perdix
Brachyramphus dunkeli †
Aethia rossmoori †
Pseudocepphus teres †
Miocepphus bohaski †
Aethia cristatella
Aethia psittacula
Aethia pygmaea
Aethia pusilla
Ptychoramphus aleuticus
Aethia storeri †
Miocepphus mergulellus †
Fratercula arctica
Fratercula corniculata
Fratercula cirrhata
Cerorhinca monocerata
Fratercula dowi †
Cerorhinca reai †
Pagophila eburnea
Xema sabini
Rissa tridactyla
Larus marinus
Creagrus furcatus
Rhodostethia rosea
Anous tenuirostris
Rynchops niger
Gelochelidon nilotica
Onychoprion anaethetus
Larosterna inca
Phaetusa simplex
Sternula superciliaris
Chlidonias leucopterus
Thalasseus maximus
Gygis alba
Bartramia longicauda
Numenius minutus
Calidris subruficollis
Hydrophasianus chirurgus
Charadrius vociferus
Charadrius wilsonia
Glareola maldivarum
Stiltia isabella
Cursorius temminckii
Rhinoptilus chalcopterus
Stercorarius longicaudus
Stercorarius skua
Mancalla californiensis †
Mancalla lucasi †
Mancalla vegrandis †
Miomancalla howardi †
Miomancalla wetmorei †
Nupharanassa bulotorum †
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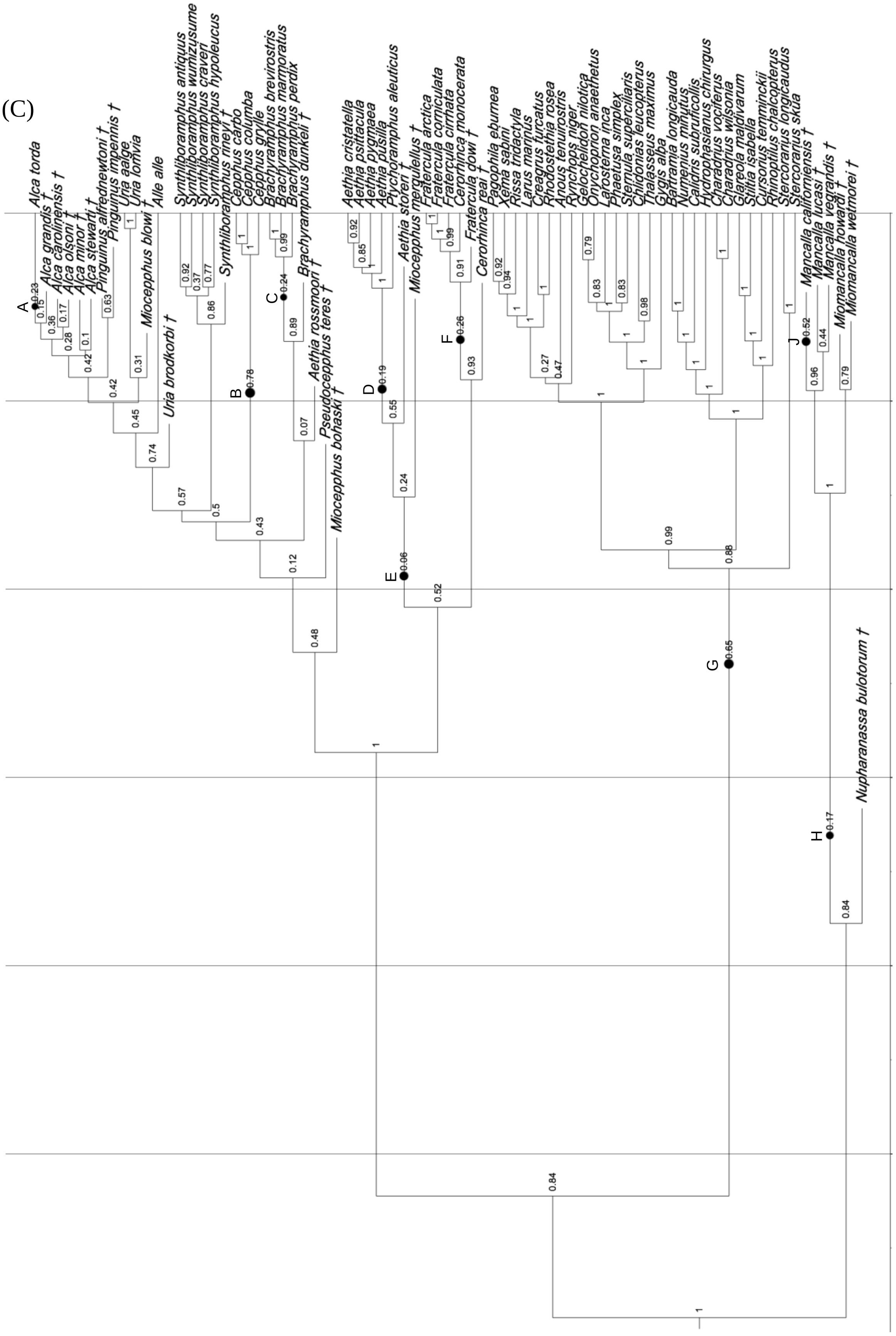
(C)
Alca torda
Alca grandis †
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Alca olsoni †
Alca minor †
Alca stewarti †
Pinguinus alfrednewtoni †
Pinguinus impennis †
Uria aalge
Uria lomvia
Miocepphus blowi †
Alle alle
Uria brodkorbi †
Synthliboramphus antiquus
Synthliboramphus wumizusume
Synthliboramphus craveri
Synthliboramphus hypoleucus
Synthliboramphus rineyi †
Cepphus carbo
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Cepphus grylle
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Brachyramphus marmoratus
Brachyramphus perdix
Brachyramphus dunkeli †
Brachyramphus †
Aethia rossmooni †
Pseudocepphus teres †
Miocepphus bohaski †
Aethia cristatella
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Aethia pygmaea
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Ptychoramphus aleuticus
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Fratercula arctica
Fratercula corniculata
Fratercula cirrhata
Cerorhinca monocerata
Fratercula dowi †
Cerorhinca reai †
Cerorhinca
Pagophila eburnea
Xema sabini
Rissa tridactyla
Larus marinus
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Larosterna inca
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Gygis alba
Bartramia longicauda
Numenius minutus
Calidris subruficollis
Hydrophasianus chirurgus
Charadrius vociferus
Charadrius wilsonia
Glareola maldivarum
Stiltia isabella
Cursorius temminckii
Rhinoptilus chalcopterus
Stercorarius longicaudus
Stercorarius skua
Stercorarius †
Mancalla californiensis †
Mancalla lucasi †
Mancalla vegrandis †
Miomancalla howardi †
Miomancalla wetmorei †
Nupharanassa bulotorum †
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0.23
0.15
0.36
0.17
0.28
0.1
0.42
0.63
0.42
1
0.31
0.45
0.74
0.57
0.92
0.37
0.77
0.86
0.5
1
1
0.78
1
0.99
0.24
0.89
0.07
0.43
0.12
0.48
0.92
0.85
1
1
0.19
0.55
0.24
0.06
1
1
0.99
0.91
0.26
0.93
0.52
1
0.92
0.94
1
1
1
0.27
0.47
0.79
0.83
1
0.83
1
0.98
1
1
1
1
1
1
1
1
1
1
1
0.99
0.88
0.65
1
0.52
0.96
0.44
0.79
1
0.17
0.84
0.84
1
0
10
20
30
40
50

Figure 8. Chronogram depicting relationships and divergence times of Pan-Alcidae and outgroup species inferred through a Bayesian total-evidence dating analysis. The bottom axis represents millions of years. Relationships of sampled ancestors are indicated at internal nodes by a circle marker and letter which corresponds to the following: A) *Alca ausonia* B) *Cepphus olsoni* C) *Brachyramphus pliocenum* D) *Aethia barnesi* E) *Miocepphus mcclungi* F) *Cerorhinca minor* G) *Laricola elegans* H) *Boutersemia belgica* J) *Mancalla cedrosensis*. **(A)** Chronogram with node ages indicated for all internal nodes. **(B)** Chronogram with 95% HPD intervals depicted as blue node bars. (**C)** Chronogram with Bayesian Posterior Probability indicated for all internal nodes.

Table 1: Missing Proportions of Morphology and Molecular Data

Percentages of missing morphology characters and molecular base pairs are indicated as well as the total percentage of missing data for all included taxa.

Taxa	**Combined Data**	**Morphology Data**	**Molecular Data**
Aethia barnesi †	99.8	93.8	100.0
Aethia cristatella	19.1	24.9	18.9
Aethia psittacula	18.4	12.2	18.7
Aethia pusilla	18.2	11.6	18.5
Aethia pygmaea	18.7	24.4	18.5
Aethia rossmoori †	99.8	94.9	100.0
Aethia storeri †	99.5	85.3	100.0
Alca ausonia †	99.5	84.1	100.0
Alca carolinensis †	98.7	62.9	100.0
Alca grandis †	99.0	70.5	100.0
Alca minor †	99.5	84.7	100.0
Alca olsoni †	99.0	71.4	100.0
Alca stewarti †	99.1	72.8	100.0
Alca torda	17.2	2.8	17.7
Alle alle	16.9	10.8	17.1
Anous tenuirostris	41.8	26.9	42.3
Bartramia longicauda	37.9	12.7	38.8
Boutersemia belgica †	99.9	98.3	100.0
Brachyramphus brevirostris	18.5	24.6	18.3
Brachyramphus dunkeli †	99.5	84.7	100.0
Brachyramphus marmoratus	18.0	5.1	18.5
Brachyramphus perdix	23.8	25.8	23.7
Brachyramphus pliocenum †	99.5	85.3	100.0
Calidris subruficollis	38.7	14.2	39.5
Cepphus carbo	23.9	24.9	23.8
Cepphus columba	19.6	3.1	20.2

Cepphus grylle	67.2	16.4	69.0
Cepphus olsoni †	99.5	84.7	100.0
Cerorhinca minor †	99.6	89.0	100.0
Cerorhinca monocerata	23.6	3.1	24.4
Cerorhinca reai †	99.5	85.0	100.0
Charadrius vociferous	5.5	11.3	5.3
Charadrius wilsonia	82.1	26.1	84.1
Chlidonias leucopterus	37.8	26.9	38.2
Creagrus furcatus	47.6	15.0	48.8
Cursorius temminckii	6.2	32.9	5.3
Fratercula arctica	0.1	3.1	0.0
Fratercula cirrhata	18.0	3.1	18.5
Fratercula corniculata	18.4	16.1	18.5
Fratercula dowi †	98.6	58.4	100.0
Gelochelidon nilotica	37.4	8.8	38.4
Glareola maldivarum	65.3	33.1	66.5
Gygis alba	38.2	17.0	38.9
Hydrophasianus chirurgus	42.0	28.0	42.5
Laricola elegans †	99.2	76.8	100.0
Larosterna inca	44.4	13.6	45.5
Larus marinus	37.4	23.8	37.9
Mancalla californiensis †	99.6	88.4	100.0
Mancalla cedrosensis †	98.8	64.6	100.0
Mancalla lucasi †	99.4	82.2	100.0
Mancalla vegrandis †	99.1	72.8	100.0
Mancallinae SST †	97.9	39.7	100.0
Miocepphus blowi †	98.9	67.1	100.0
Miocepphus bohaski †	99.4	81.3	100.0
Miocepphus mcclungi †	99.6	89.2	100.0
Miocepphus mergulellus †	99.5	85.3	100.0
Miomancalla howardi †	99.2	76.8	100.0
Miomancalla wetmorei †	99.5	85.8	100.0
Numenius minutus	39.4	32.3	39.6
Nupharanassa bulotorum †	99.9	98.0	100.0

Onychoprion anaethetus	64.6	26.6	65.9
Pagophila eburnea	39.1	15.6	39.9
Phaetusa simplex	37.6	16.4	38.4
Pinguinus alfrednewtoni †	98.9	68.0	100.0
Pinguinus impennis †	55.0	25.5	56.0
Pseudocepphus teres †	99.6	87.8	100.0
Ptychoramphus aleuticus	18.4	4.5	18.9
Ptychoramphus tenuis †	99.9	96.3	100.0
Rhinoptilus chalcopterus	45.9	19.0	46.9
Rhodostethia rosea	40.0	15.6	40.8
Rissa tridactyla	5.5	12.5	5.3
Rynchops niger	5.4	7.9	5.3
Stercorarius longicaudus	37.8	11.6	38.7
Stercorarius skua	5.3	7.6	5.3
Sternula superciliaris	41.5	30.9	41.9
Stiltia isabella	45.0	13.0	46.1
Synthliboramphus antiquus	0.7	4.0	0.6
Synthliboramphus craveri	23.9	24.4	23.9
Synthliboramphus hypoleucus	75.7	24.6	77.5
Synthliboramphus rineyi †	99.5	84.1	100.0
Synthliboramphus wumizusume	18.8	26.1	18.5
Thalasseus maximus	54.0	19.0	55.3
Uria aalge	16.8	4.0	17.3
Uria brodkorbi †	99.2	75.6	100.0
Uria lomvia	17.2	17.0	17.2
Xema sabini	38.1	15.3	38.9