Articles

Systematics and evolution of the Pan-Alcidae (Aves, Charadriiformes)

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Puffins, auks and their allies in the wing-propelled diving seabird clade Pan-Alcidae (Charadriiformes) have been proposed to be key pelagic indicators of faunal shifts in Northern Hemisphere oceans. However, most previous phylogenetic analyses of the clade have focused only on the 23 extant alcid species. Here we undertake a combined phylogenetic analysis of all previously published molecular sequence data (~ 12 kb) and morphological data (n = 353 characters) with dense species level sampling that also includes 28 extinct taxa. We present a new estimate of the patterns of diversification in the clade based on divergence time estimates that include a previously vetted set of twelve fossil calibrations. The resultant time trees are also used in the evaluation of previously hypothesized paleoclimatic drivers of pan-alcid evolution. Our divergence dating results estimate the split of Alcidae from its sister taxon Stercorariidae during the late Eocene (~ 35 Ma), an evolutionary hypothesis for clade origination that agrees with the fossil record and that does not require the inference of extensive ghost lineages. The extant dovekie *Alle alle* is identified as the sole extant member of a clade including four extinct Miocene species. Furthermore, whereas an *Uria + Alle* clade has been previously recovered from molecular analyses, the extinct diversity of closely related *Miocepphus* species yields morphological support for this clade. Our results suggest that extant alcid diversity is a function of Miocene diversification and differential extinction at the Pliocene–Pleistocene boundary. The relative timing of the Middle Miocene climatic optimum and the Pliocene–Pleistocene climatic transition and major diversification and extinction events in Pan-Alcidae, respectively, are consistent with a potential link between major paleoclimatic events and pan-alcid cladogenesis.

Collectively known as the Pan-Alcidae [crown clade Alcidae + stem lineage Mancallinae sensu Smith (2011a, b)], true auks (*Alca* and †*Pinguinus*), dovekies (*Alle* and †*Miocepphus*), murres (*Uria*), murrelets (*Brachyramphus* and *Synthliboramphus*), guillemots (*Cepphus*), auklets (*Aethia* and *Ptychoramphus*), puffins (*Fratercula* and *Cerorhinca*) and mancalline or Lucas auks (†*Miomancalla* and †*Mancalla*) are pelagic charadriiform seabirds characterized by wing-propelled pursuit diving and anatomical modifications associated with this derived method of foraging. Extant diversity within Alcidae includes 23 species of exclusively Holarctic distribution (del Hoyo et al. 1996) and likewise, fossil remains of Pan-Alcidae are also restricted to the Northern Hemisphere (Smith 2011a; our Fig. 1). The Neogene (i.e. pre-Pleistocene, > 2.58 Ma) pan-alcid fossil record is the richest among Charadriiformes, with approximately 17 000 documented specimens representing at least 31 species known from approximately 15 localities worldwide (Smith 2011a, 2013, Smith and Mayr 2013). In total, Pan-Alcidae fossil localities have an age distribution spanning more than 34 million yr from the Late Eocene through the Holocene (Olson 1985, Tyrberg 1998, Smith 2011a). Thus, extinct pan-alcid diversity spans the entire latter

half of the Cenozoic Era, outnumbers extant diversity and includes representatives of every extant genus. Surprisingly, this rich source of evolutionary data has been frequently excluded or, at times, misinterpreted. Exclusion of extinct taxa and misinterpretation of the pan-alcid fossil record has resulted in potentially biased estimates of clade origination area, phylogeny and divergence times, which have subsequently been used to generate hypotheses regarding evolutionary trends, morphological evolution and paleodiversity of Pan-Alcidae (Chandler 1990a, Pereira and Baker 2008, Weir and Mursleen 2013). The abundance of pan-alcid fossils makes them an important tool for studying the evolution of seabirds in general, and thus, a comprehensive re-evaluation of the clade has potential to influence interpretations regarding the response of avian pelagic taxa to climate change.

Only through phylogenetically evaluating the systematic positions of extinct pan-alcid taxa can we test previous hypotheses and generate new hypotheses regarding the evolution of the clade. Basic questions including systematic relationships, timing of cladogenetic events, area of origination, the evolution of wing-propelled diving, estimates of paleodiversity and potential responses to paleoclimatic
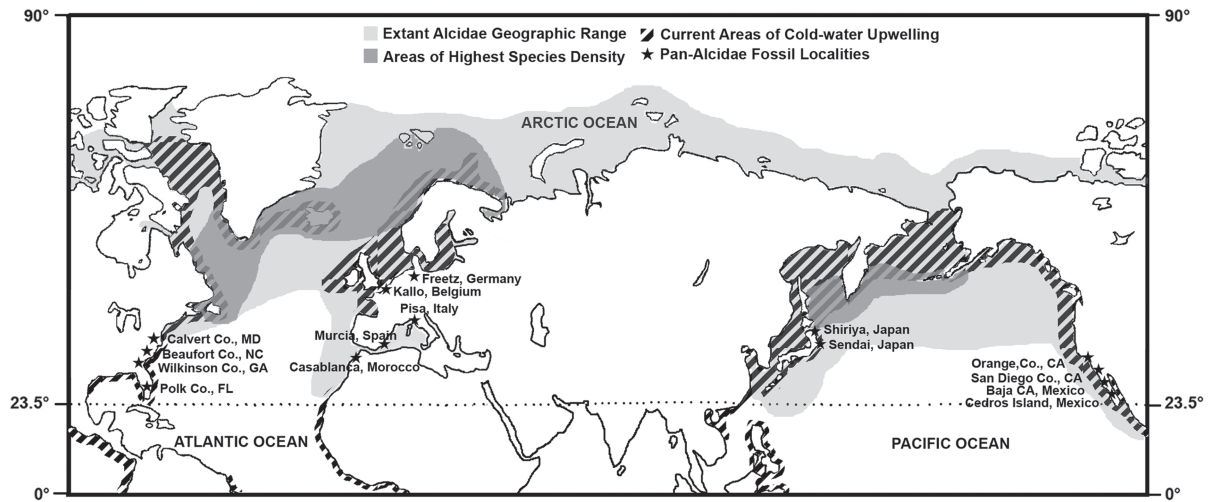
Figure 1. Geographic distribution of extant alcids (light grey) and including areas of highest extant species diversity (dark grey) compared with pan-alcid fossil localities (stars), and areas of modern cold-water upwelling (diagonal lines). Note that only 2 of the 15 fossil localities (Wilkinson County Georgia, Late Eocene Clinchfield Fm. and Polk County Florida, Early Pliocene Bone Valley Fm.) are outside the geographic range of extant Alcidae. Also note that although the range of extant alcids extends south of the Tropic of Cancer, no pan-alcid fossil localities are known south of that line of latitude (i.e. 23.5°N). Atlantic Ocean area of highest extant species density represents the area in which all 6 Atlantic endemic species ranges overlap. Pacific Ocean area of highest extant species density represents the area in which 14 of the 21 Pacific Ocean endemic species ranges overlap. The ranges of 5 additional Pacific endemic species partially overlap the shaded area of highest Pacific species density. The ranges of *Synthliboramphus hypoleucus* and *S. craveri* are outside the range of highest species density (i.e. southern California, USA and Baja California, Mexico). Ranges of extant alcids are based on del Hoyo et al. (1996) and upwelling intensities are based on NOAA (National Oceanic and Atmospheric Association 2011).

change remain unanswered or unexplored in a phylogenetic context. Evolutionary insights pertaining to extant and extinct pan-alcids have been advanced by recent studies of the endocranial anatomy, long-bone histology, and aerial and underwater flight mechanics and physiology (Watanuki and Burger 1999, Watanuki et al. 2003, 2006, Smith and Clarke 2012, 2014, Elliott et al. 2013). However, systematic evaluation of extinct taxa that would promote greater understanding of these life history parameters in deep time lagged behind until quite recently. Recent taxonomic revisions and description of new pan-alcid fossils has facilitated the systematic evaluation of extinct pan-alcids which had not been previously included in phylogenetic analyses (Wijnker and Olson 2009, Smith 2011a, b, 2013, 2014a, Smith and Clarke 2011, Smith and Mayr 2013).

Herein we expand on those recent studies and present combined phylogenetic analyses with dense taxonomic sampling of extinct and extant Pan-Alcidae and divergence time estimates for the clade constrained by previously vetted fossil calibrations. Based on the results of these new analyses and in the context of recent advances in knowledge of the pan-alcid fossil record, we present a new synthesis of data on Pan-Alcidae evolution. We discuss implications for the following five topics: 1) the effects of including extinct species on phylogenetic hypotheses for Pan-Alcidae; 2) the effects of using vetted fossil calibrations on node age estimates for Charadriiformes and specifically, for Pan-Alcidae; 3) the evolution of wing-propelled diving in Charadriiformes; 4) hypotheses of Pan-Alcidae origination area in light of recent fossil discoveries; 5) evaluation of previously hypothesized drivers of pan-alcid radiation and extinction.

Material and methods

Taxonomic, anatomical and geological conventions

Species-level taxonomy of extant North American Charadriiformes follows the 7th edition of the Checklist of North American Birds (American Ornithologists' Union 1998). With the exception of species binomials, all other taxonomic designations (e.g. Alcidae) are clade names as defined by the PhyloCode (Dayrat et al. 2008, Cantino and de Queiroz 2010), as detailed in Smith (2011a: Appendix 8), and are not intended to convey rank under the Linnaean system of nomenclature (Linnaeus 1758, ICZN 2000) regardless of use of italics or previous usage by other authors. Anatomical terminology are English equivalents of Baumel and Witmer (Baumel et al. 1993). Ages of geologic time intervals are based on the International Geologic Timescale (International Commission on Stratigraphy 2014).

Taxon and character sampling

The morphological matrix of Smith (2011a) was combined with a newly aligned molecular sequence matrix in the combined analyses (Appendix 3 in Smith 2011a for detailed morphological character descriptions). The morphological data matrix comprises 80 terminal taxa (Supplementary material Appendix 1, Table A1), scored for a maximum of 353 morphological characters (293 binary; 45 unordered multistate; 15 ordered multistate). Morphological character scorings were analyzed for all twenty-three extant alcids and 25 extinct pan-alcids. Twenty-nine extant charadriiforms and

3 extinct non-alcid charadriiforms complete the remainder of the taxa scored for analysis, and provide a dense outgroup taxon sample to test the monophyly of Pan-Alcidae with respect to other charadriiforms. The systematic relationships of the †Mancallinae were evaluated by Smith (Smith 2011b) and that taxon is represented by a supraspecific terminal in these analyses. Character variation was scored as polymorphism in the †Mancallinae supraspecific terminal; however, all other terminals represent species. Morphological character scorings range from 98.3% (†*Boutersemia belgica*) to 2.8% (e.g. *Alca torda*) incomplete, with an average morphological scoring completeness of 37.9% (see Supplementary material Appendix 1, Table A1 regarding details of missing data for all sampled taxa).

Morphological characters include osteological (n = 232), integumentary (n = 32), reproductive (n = 11), dietary (n = 2), myological (n = 24) and micro-feather (n = 52). One hundred and sixty-four characters were developed for this analysis. The other 189 characters were drawn from the work of Hudson et al. (1969; n = 24), Strauch (1978, 1985; n = 39), Chandler (1990a; n = 63), Chu (1998; n = 11), and Dove (2000; n = 52). Comparative material and detailed character descriptions are the same as those of Smith (2014a) and are available through Dryad (<http://dx.doi.org/10.5061/dryad.2637g>). Morphological character scorings for all taxa included in this analysis are the same as those of Smith (2011a).

Whenever possible, five or more specimens of each extant species including both sexes were evaluated to account for intraspecific character variation and potential sexual dimorphism respectively. Only adult specimens, assessed based upon degree of ossification (Chapman 1965), were evaluated and whenever possible, specimens from multiple locations within the geographic range of extant species (i.e. subspecies) were examined to account for intraspecies geographic variation. Reproductive, chick integument, dietary and some myological characters were scored from published sources (Stettenheim 1959, Del Hoyo et al. 1996, Baicich and Harrison 1997). With the exception of †*Laricola elegans*, which was scored from published sources and photos that were kindly provided by colleagues (Milne-Edwards 1868, De Pietri et al. 2011), all extinct taxa were coded from direct observation of holotype and referred specimens.

The cladistic matrix also includes aligned molecular sequences of 12 672 base pairs in length for sampled taxa (including gaps, 3.7–84.1% incomplete; average sequence completeness for sampled taxa = 38.6%; Supplementary material Appendix 1, Table A1). Molecular sequence data (mitochondrial: ND2, ND5, ND6, COI, cyt-*b*; ribosomal RNA: 12S, 16S; and nuclear: RAG1) from previously published sources (Moum et al. 1994, 2002, Friesen et al. 1996, Cohen et al. 1997, Groth and Barrowclough 1999, Whittingham et al. 2000, Paton et al. 2003, Hebert et al. 2004, Liebers et al. 2004, Bridge et al. 2005, Yamamoto et al. 2005, Paton and Baker 2006, Baker et al. 2007, Fain and Houde 2007, Kerr et al. 2007, Pereira and Baker 2008) were downloaded from GenBank (Supplementary material Appendix 1, Table A1–A2). Preliminary sequence alignments for each gene were obtained using Fast Sequence Alignment (Bradley et al. 2009) under a Tamura-Nei nucleotide substitution model with a gap factor = 1.0. Sequence alignments were concatenated using Sequence Matrix (Vaidya et al. 2011), exported in nexus format, and then manually adjusted using Se-Al (Rambaut 2002). The optimal partitioning scheme (5 partitions = nuclear; RNA; mitochondrial with codon model [1, 2, 3]) and nucleotide substitition model (GTR + I + G) were simultaneously identified using PartitionFinder (Lanfear et al. 2012). The general time reversible model with invariant sites and gamma distribution (GTR + I + G) was also independently estimated as the best nucleotide substitution model for each gene partition by MrModeltest (Nylander 2008).

Phylogeny estimation

A combined approach of phylogeny estimation was used to evaluate the systematic position of pan-alcid species. Parsimony and Bayesian phylogeny estimation approaches were explored because Bayesian methods allow incorporation of complex models of nucleotide substitution and partitioning schemes not present in parsimony methods (Huelsenbeck et al. 2001, 2002, Lewis 2001a, b, Holder and Lewis 2003, Nylander et al. 2004).

An analysis employing a maximum parsimony criterion of phylogenetic estimation was implemented in PAUP* (Swofford 2013). Parsimony tree search criteria are as follows: heuristic search strategy; 10 000 random taxon addition sequences; tree bisection–reconnection branch swapping; random starting trees; all characters equally weighted; minimum length branches = 0 collapsed; multistate (e.g. 0 & 1) scorings used only for polymorphism. Bootstrap values and descriptive tree statistics (i.e. CI, RI, RC) were calculated using PAUP* (Swofford 2013). Bootstrap value calculation parameters included 1000 heuristic search replicates with 100 random addition sequences per replicate. Bremer support values were calculated using a script generated in MacClade (Maddison and Maddison 2005) and analyzed with PAUP* (Swofford 2013). Based on the results of previous phylogenetic analyses of charadriiform relationships (Strauch 1978, Sibley and Ahlquist 1990, Chu 1995, Ericson et al. 2003, Paton et al. 2003, Thomas et al. 2004, Paton and Baker 2006, Baker et al. 2007), resultant trees were rooted with the clade Charadrii, herein represented by the species *Charadriius vociferous* and *Charadrius wilsonia*. Tree graphics were produced in Mesquite (Maddison and Maddison 2011). An additional analysis performed with all characters unordered did not result in topological differences, or an increase in the number of MPTs recovered.

Bayesian phylogenetic analyses of the combined data were performed using MrBayes (Ronquist et al. 2012). The Mk model (standard model; Lewis 2001a) was applied to morphological data and the general time reversible model with invariant sites and gamma distribution (GTR + I + G) was applied to the molecular sequence partitions. All trees were a priori rooted with *Charadrius vociferus* and *C. wilsonia*. Additional MrBayes parameters were as follows: two simultaneous independent runs with one cold and five heated chains each, starting trees random, Markov chain Monte Carlo (MCMC) samples taken every 1000 generations, six partitions in the combined analyses (1 morphological and 5 gene partitions), parameters unlinked across partitions, all fully resolved topologies considered equally likely, branch lengths

unconstrained (i.e. molecular clock not enforced): exponential (10.0), substitution rate flat Dirichlet (1, 1, 1, 1), state frequencies flat Dirichlet (1, 1, 1, 1), standard deviation of split frequencies < 0.01 considered evidence of convergence of MCMC chains, nodes with ≥ 0.90 posterior probability considered strongly supported. Log likelihoods and effective sample sizes (ESS) were evaluated to determine burn-in using Tracer (Rambaut and Drummond 2009), and the resulting consensus of retained trees was plotted using FigTree (Rambaut 2009). The MCMC chains in the Bayesian analysis of the combined charadriiform data were run for 50 million generations and the first 35 000 of the 50 001 retained trees were discarded as burn-in. Likely owing to the inclusion of multiple extinct taxa with high percentages of missing data, relationships in the subclade Alcinae were largely unresolved in the 50% consensus tree (i.e. contype = halfcompat; result not shown). Subsequently, a phylogenetic tree summarizing all compatible results (i.e. contype = allcompat) was produced using MrBayes (Ronquist et al. 2012).

Character optimization

Ancestral character states for adult diet and geographic distribution (i.e. origination area) were optimized on the parsimony based, strict consensus tree using parsimony (DELTRAN option, which minimizes reversals) in Mesquite (Maddison and Maddison 2011). Geographic distributions for extant taxa were taken from del Hoyo et al. (1996). Terrestrial species (e.g. *Cursorius*) were excluded from reconstruction of ancestral area (i.e. Pacific versus Atlantic). Two analyses of diet were conducted. The first involved only extant charadriiform species with known dietary preferences. In the second analysis, fossil taxa with unknown diet were assumed to have diets similar to their congeners.

Divergence time estimation

The age of cladogenetic events for Pan-Alcidae was estimated using a relaxed Bayesian molecular clock with uncorrelated lognormal rates model as implemented in BEAST (Drummond et al. 2012). The general time reversible model with invariant sites and gamma distribution (GTR + I + G) was applied as the nucleotide substitution model. The Birth–Death with incomplete sampling model of speciation was applied as a prior on the branching rates (Stadler 2009) and using a random starting tree. The analysis was run for 50 million MCMC generations and the MCMC chain was sampled every 1000 generations. Effective sample size and burn-in was assessed in Tracer (Rambaut and Drummond 2009) to determine if the MCMC chain was of sufficient length (effective sample size > 200 considered evidence of a sufficiently long run) and the retained sample of trees was summarized using TreeAnnotator (Drummond et al. 2012). Based on the resulting convergence statistics from the divergence time analysis (evaluated in Tracer; Rambaut and Drummond 2009), the first 10 000 of the 50 001 retained trees were discarded as burn-in. The resulting phylogenetic tree including node age estimates and associated error bars (95% highest posterior density interval) was plotted using FigTree (Rambaut 2009).

Twelve internal fossil calibrations were used to date the minimum divergence of charadriiform cladogenetic events (Supplementary material Appendix 1, Table A3). Consistent with the 'best practices' recommended by Parham et al. (2012), the age and systematic position of all fossil calibrations was evaluated prior to their use in this analysis (Smith 2014b). All calibrations were assigned a lognormal prior distribution (LogMean = 0.0; LogStdev = 1.0; offset = minimum fossil age). However, given the relatively poor fossil record of early charadriiforms and the ambiguity regarding the overall age of the clade, the LogMean of the calibration on the tree height (i.e. the calibration constraining the age of the basal divergence among crown Charadriiformes, see details regarding †*Jiliniornis huadianensis* in Supplementary material Appendix 1, Table A3 and details provided by Smith 2014b) was adjusted to a value of 1.0. This procedure provided a wider interval of confidence for the dating the root of the tree. Insufficient stratigraphic occurrence data is available to justify a priori alteration of the lognormal distribution (i.e. log standard deviation) or placement of a hard or soft minimum bound, such as that suggested by Warnock et al. (2012).

Prior to the divergence time analysis, a preliminary analysis was conducted using the 'empty alignment' function (i.e. without sequence data) in BEAST (Drummond et al. 2012). The topology, node ages and posterior probabilities differed from those of the final analysis, suggesting that the sequence data was sufficiently informative to overcome any potential biases introduced by the joint prior resulting from the interaction of the 12 fossil-based prior values (i.e. minimum age constraints and lognormal distribution of hyperpriors) assigned to calibrated nodes.

Paleodiversity estimation

Phylogenetically contextualized estimates of pan-alcid paleodiversity were assessed for each epoch of the Cenozoic using the time calibrated phylogenetic tree resulting from the combined analysis and based on the concept of ghost ranges (Norell 1992). Implied extinct diversity was compared to non-phylogenetic diversity counts based on the stratigraphic ranges of pan-alcid species reported in Supplementary material Appendix 1, Table A4. Pacific versus Atlantic Ocean basin diversity was also evaluated to investigate ocean-specific diversity trends.

Results

The parsimony-based analysis of the combined dataset resulted in 32 most parsimonious trees (L: 16 074; CI: 0.37; RI: 0.50; RC: 0.19; 3058 parsimony informative characters; Fig. 2–3). The strict consensus topology is well resolved with polytomies restricted to four clades (Jacanidae, *Larus*, Aethiini and the *Alca* + †*Pinguinus* clade) that, within Pan-Alcidae, have high relative proportions of fossil taxa with large percentages of missing data (Supplementary material Appendix 1, Table A1). Likewise, bootstrap and Bremer support values are highest for clades with low proportions of fossil taxa included (e.g. *Uria*). Stercorariidae was recovered as the sister taxon to Pan-Alcidae and Mancallinae was
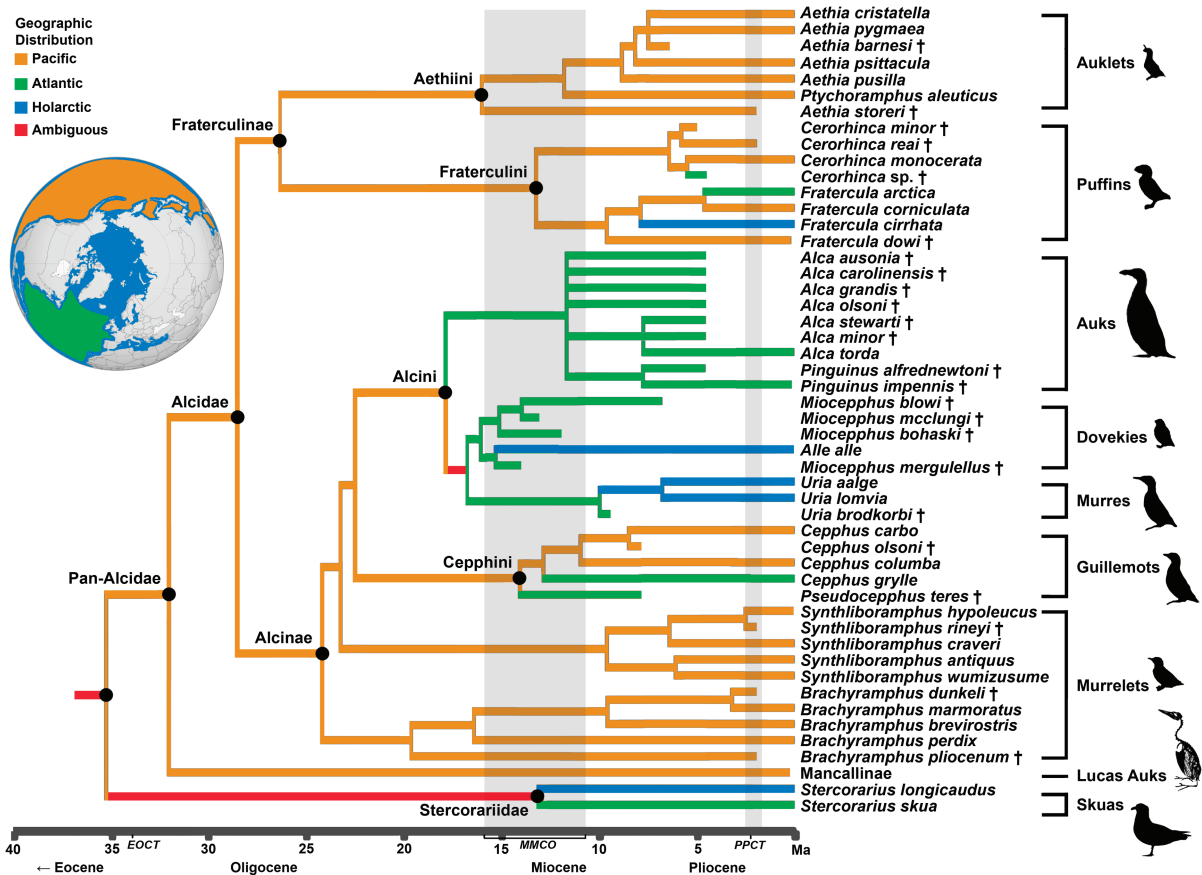
Figure 2. Phylogeny, divergence estimates, and ancestral area optimization of Pan-Alcidae (including 28 extinct species). This tree represents the relationships inferred using parsimony with branch lengths scaled to match the results of the Bayesian divergence time estimate (Supplementary material Appendix 1, Fig A2). Branches representing extinct taxa have been terminated at the age of their latest known stratigraphic occurrence (Supplementary material Appendix 1, Table A4). Estimated error associated with divergence times (i.e. 95% HPD) are depicted in Supplementary material Appendix 1, Fig. A2 and provided in Supplementary material Appendix 1, Table A5. Paleoclimatic event abbreviations: Eocene–Oligocene Climatic Transition, EOCT; Middle Miocene Climatic Optimum, MMCO; Pliocene–Pleistocene Climatic Transition, PPCT.

recovered as the sister taxon to a monophyletic alcid crown clade (i.e. Alcidae + †Mancallinae = Pan-Alcidae sensu Smith 2011b). Monophyly of major clades within Alcidae was also supported (i.e. Alcinae, Fraterculinae, Fraterculini, Aethiini, Alcini, and Cepphini sensu Smith 2011b). Because the monophyly of Pan-Alcidae and major pan-alcid subclades has been strongly supported in the results of previous analyses (Baker et al. 2007, Pereira and Baker 2008, Smith and Clarke 2011, Smith 2011a, b, 2014a), morphological character optimizations that support clades are not discussed herein; however, morphological apomorphies of recovered clades are discussed in detail by Smith (2011a).

Pan-Alcidae relationships resulting from the Bayesian combined analysis are largely in agreement with the parsimony-based results (Supplementary material Appendix 1, Fig. A1). As with the parsimony-based results, node support was consistently higher for clades with low proportions of incompletely scored extinct taxa. However, nodal support was relatively high with 28 of 52 nodes receiving a Bayesian posterior probability of 1.0 and an additional 7 nodes with values > 0.9. The monophyly of *Alca* with respect to †*Pinguinus* is supported and *Ptychoramphus* is placed as the sister taxon to the other extant auklets (i.e. *Aethia*). The only

major topological differences with respect to the parsimony analysis is that *Brachyramphus* is recovered as the sister taxon to Alcini rather than as the sister taxon to all other Alcinae. Other notable differences include the recovery of *Cerorhinca* paraphyly with respect to *Fratercula*; the Pliocene †*Cerorhinca* sp. (Smith et al. 2007) and extant *C. monocerata* were recovered at the base of Fraterculini. In contrast, a more traditional hypothesis is proposed based upon the parsimony analysis in which a *Cerorhinca* clade was recovered as the sister taxon to a monophyletic *Fratercula* (Fig. 2–3). Fossils referred to the three extinct species of *Cerorhinca* (†*C. reai*, †*C. minor*, †*C.* sp.) are restricted to humeri (contra Chandler 1990b; reviewed by Smith 2011a) and the lack of other data for these taxa may be responsible for the lack of phylogenetic resolution in the Bayesian analysis and the incongruence with the parsimony-based results. Also in contrast with the parsimony-based results, *Alle alle* was recovered as the sister taxon to a monophyletic *Uria*, with †*Miocepphus* species forming a paraphyletic assemblage along with *Uria* and *Alle*. Whereas a clade containing †*Miocepphus*, *Alle* and *Uria* is supported by the parsimony based results and is consistent with the results of Smith and Clarke (2011).
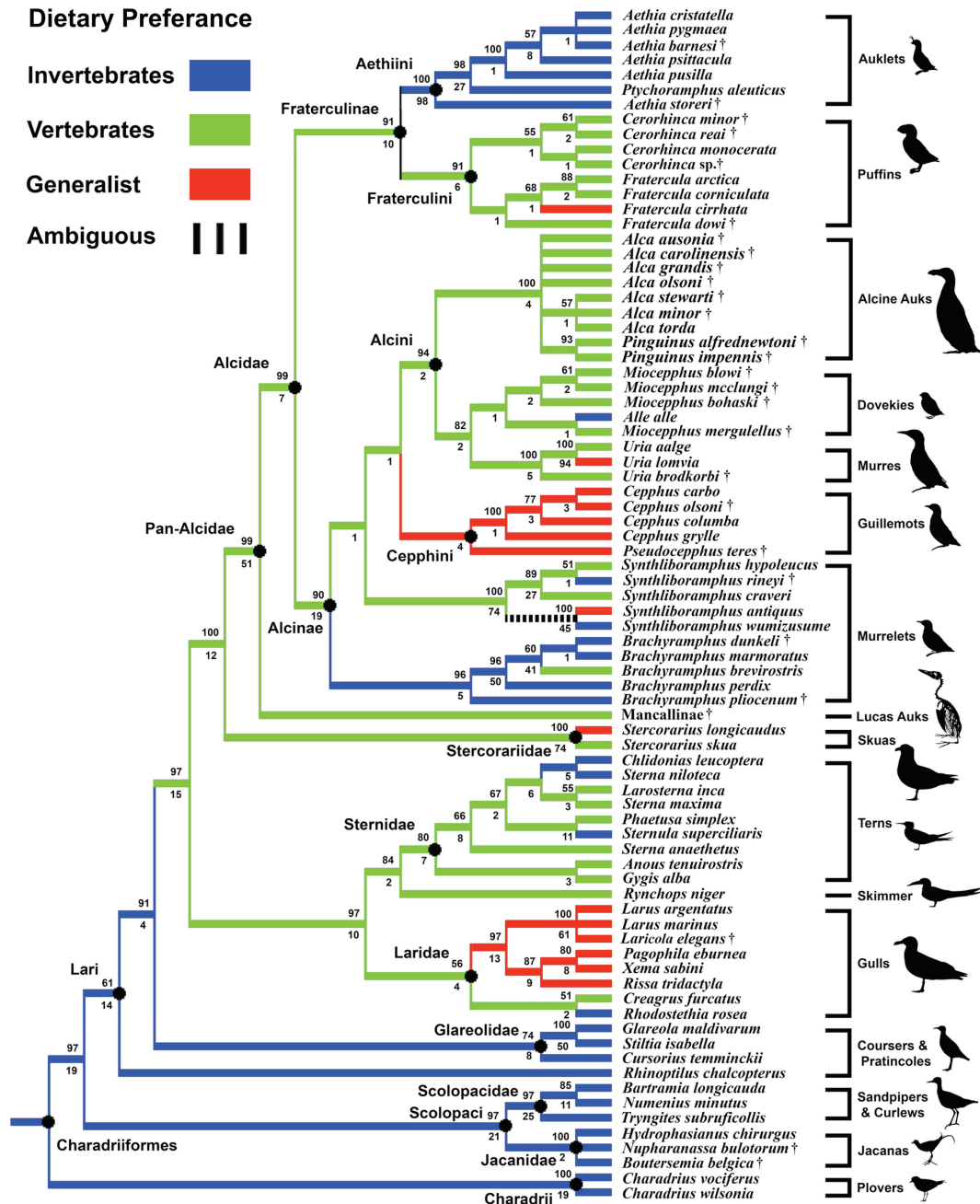
Figure 3. Optimization of pan-alcid diet on parsimony topology. Note that dietary preferences are scored for extinct taxa based on the diet of extant congeners, leading to a largely unambiguous reconstruction of ancestral diet for Pan-Alcidae. Reconstructions of ancestral diet were largely ambiguous when only extant taxa (and *P. impennis*) with known dietary preferences were scored (results not shown). Bootstrap values > 50% and Bremer support values appear above and below nodes respectively. Branch color key: forages primarily on vertebrates (green); forages primarily on invertebrates (blue); diet consists of large portions of both vertebrates and invertebrates (i.e. generalist; red).

Topological differences recovered among outgroup Charadriiformes include the placement of *Anous tenuirostris* as the sister to Laridae + Sternidae + *Rynchopidae* (represented by *R. niger*) in the Bayesian results (Supplementary material Appendix 1, Fig. A1); whereas *Anous* was placed as the sister to *Gygis alba* within Sternidae in the parsimony-based results (Fig. 3). Additionally, whereas *Rhinoptilus chalcopterus* was recovered as the sister to Glareolidae plus the rest of Charadriiformes in the parsimony-based results, that taxon was recovered as the sister taxon to other Glareolidae in the Bayesian analysis. As with the position recovered for *Anous*, this result also agrees with the placement of *Rhinoptilus* recovered in the Bayesian results of Baker et al. (2007) and appears to represent a systematic difference between phylogenetic hypotheses inferred using parsimony and Bayesian strategies.

The topology of the maximum clade credibility tree resulting from the divergence time analysis is largely congruent with previous analyses of extant charadriiform relationships and with the results of the parsimony-based and Bayesian

topologies recovered in the combined analyses (Supplementary material Appendix 1, Fig. A2). Nodal support was high with 38 of 52 nodes receiving a Bayesian posterior probability of 1.0 and an additional 8 nodes with values > 0.90 (Supplementary material Appendix 1, Fig. A2, Table A5).

The basal divergence of the charadriiform crown clade was estimated to have occurred in the Early Eocene (49.3 Ma, Ypresian; Supplementary material Appendix 1, Fig. A2). Our estimate dates the divergence between Pan-Alcidae and its sister taxon Stercorariidae to the Late Eocene (34.7 Ma; 95% HPD 34.2–35.5 Ma, Fig. 2, Supplementary material Appendix 1, Fig. A2, Table A5). The basal divergence among crown Alcidae (i.e. the split between Alcinae and Fraterculinae) was estimated at ~ 29 Ma (Early Oligocene, 95% HPD 25.7–31.4 Ma, Fig. 2, Supplementary material Appendix 1, Fig. A2, Table A5), a hypothesis that given fossil record of the clade, does not require the inference of extensive ghost lineages. Estimated ages for all recovered nodes and the error associated with each estimate are provided in Supplementary material Appendix 1, Fig. A2, Table A5. The estimated potential range of error for node ages (i.e. the 95% highest posterior density, HPD) is generally higher (i.e. a broader range of inferred dates) for more basal nodes (Supplementary material Appendix 1, Fig. A2, Table A5). For example, the HPD for the basal split among crown Charadriiformes (i.e. the split between Charadrii and the Scolopaci + Lari clade) spans 11.9 Ma from 55.5–43.6 Ma, whereas the HPD of divergence between sister taxa *Fratercula arctica* and *Fratercula corniculata* spans only 1.0 Ma from 5.2–4.2 Ma.

Phylogenetically contextualized estimates of pan-alcid species diversity were found to contrast markedly with estimates of diversity based on phylogenetically uncorrected stratigraphic occurrence data (Fig. 4). Raw counts of pan-alcid diversity were found to be underestimates for the Oligocene, Miocene, Pliocene, Pleistocene and Holocene. For example, whereas only 14 species of pan-alcid are known from Miocene fossils, a minimum of 33 species can be inferred to have been present. A trend of decreasing species diversity is inferred when phylogeny is considered; whereas a spurious trend of increasing species diversity was inferred when phylogeny was not considered.

The parsimony optimization of geographic distribution of extant and extinct species of Pan-Alcidae supports a Pacific Ocean ancestral area of origination for the clade (Fig. 2). With respect to Pan-Alcidae, ambiguous reconstructions are limited to the geographic origins of the *Uria* lineage and the common ancestral lineage shared by Stercorariidae and Pan-Alcidae. However, a Pacific Ocean area of origination conflicts to some degree with the fossil record of the clade and these results are likely biased by the paucity of Paleogene pan-alcid fossils (discussed below). Finally, parsimony optimization of diet suggests that early pan-alcids would have fed primarily on vertebrates, with specializations for feeding on invertebrates and more generalist foraging strategies evolving in more derived pan-alcid clades (Fig. 3).

Discussion

Phylogenetic relationships

The inclusion of extinct pan-alcids in the combined phylogenetic analyses provided support for using several extinct taxa as fossil calibrations in divergence dating analyses and also provided systematic hypotheses for species that had not been previously phylogenetically evaluated. In most cases, extinct species were recovered as the sister taxa to clades that are equivalent to extant genera. For example, †*Fratercula*
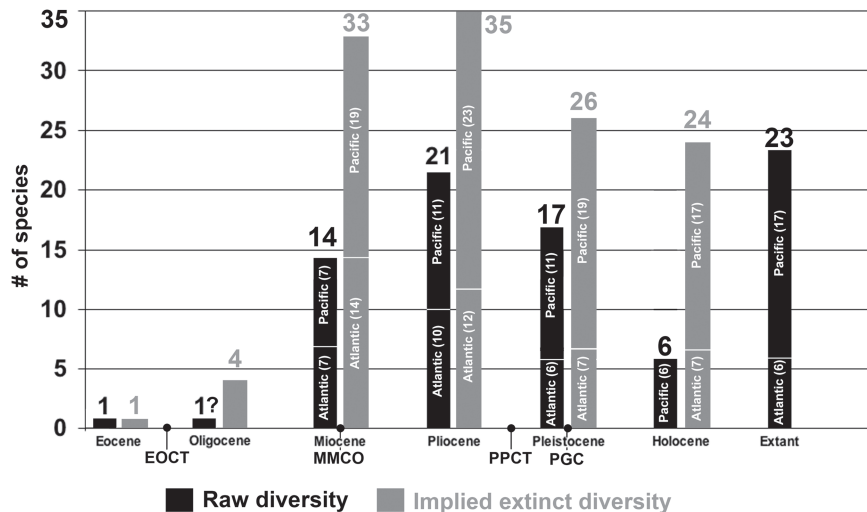

Figure 4. Contrasting trends in pan-alcid species diversity based on raw counts (raw diversity) versus taking into account ghost lineages (implied diversity). Stratigraphic ranges of species are based on Supplementary material Appendix 1, Table A4 (black) and numbers of species inferred based on stratigraphic occurrence of alcid fossils are based on Fig. 2 (grey). For raw diversity counts, species present in more than one epoch (e.g. †*Mancalla lucasi* remains known from Pliocene and Pleistocene deposits) are counted in each age bin. Note that diversity counts and estimates are further categorized by Atlantic and Pacific Ocean basin occurrences. Also note that the ranges of four of the six extant Atlantic Ocean endemic alcids extend into the Pacific Ocean basin also. Only a single pan-alcid fossil is known from the Eocene (Atlantic), and only a single potential occurrence of Pan-Alcidae is known from the Oligocene (Pacific). Abbreviations: EOCT, Eocene–Oligocene Climatic Transition; MMCO, Middle Miocene Climatic Optimum; PGC, Pleistocene Glacial Cycles; PPCT, Pliocene–Pleistocene Climatic Transition.

dowi, an extinct puffin from the Pleistocene of California, was placed at the base of a clade containing the three extant species of *Fratercula*. Additionally, †*Brachyramphus dunkeli* and †*Brachyramphus pliocenum* are grouped as a clade that is the sister to the extant species of *Brachyramphus* in the Bayesian results (Supplementary material Appendix 1, Fig. A1). As in previous analyses with similarly dense taxon sampling for Pan-Alcidae (e.g. Pereira and Baker 2008), *Ptychoramphus* is placed as the sister taxon to the other extant auklets (i.e. *Aethia*). However, as in the results of Smith (2014a), the placement of the extinct auklet †*Aethia storeri* in a position basal to *Ptychoramphus aleuticus* suggests that the taxonomic validity of the monotypic *Ptychoramphus* should be re-evaluated. Additionally, †*Pseudocepphus teres* was placed as the sister taxon to the four other species of *Cepphus* (including the extinct species †*C. olsoni*), a placement that conflicts with the original interpretation of that taxon as more closely related to *Alca* or †*Miocepphus* (Wijnker and Olson 2009). The placement of the flightless Mancallinae (*Miomancalla* + *Mancalla*) clade as the sister taxon to the crown clade (i.e. Alcidae + †Mancallinae = Pan-Alcidae) is congruent with the results of previous phylogenetic analyses (Chandler 1990a, Smith 2011a, b). Thus, the hypothesis that flightlessness evolved separately in the †*Pinguinus* and †Mancallinae lineages is strongly supported and the morphology shared by these taxa serves as a demonstrative example of convergence (Smith 2011b).

Some previous estimates of pan-alcid phylogeny did not include extinct taxa, had relatively limited morphological character sampling or used hypothetical outgroup taxa (Strauch 1985, Chandler 1990a, Thomas et al. 2004, Pereira and Baker 2008). However, despite the substantial increase in systematic knowledge gained through increased taxon and character sampling herein, persistent issues related to the systematic positions of the clades *Cepphus*, *Synthliboramphus*, and *Brachyramphus* were not fully resolved. A host of analyses, including those reported herein, using different character data (morphology, molecular sequence and combined data) and multiple tree estimation methods (parsimony, likelihood, Bayesian) have recovered these taxa in varying positions at, or near, the base of Alcinae outside a monophyletic Alcini clade including *Alca*, †*Pinguinus*, *Alle*, †*Miocepphus*, and *Uria* (Strauch 1985, Moum et al. 1994, Friesen et al. 1996, Thomas et al. 2004, Baker et al. 2007, Pereira and Baker 2008, Smith 2011a, b, 2014a). Support values (bootstrap, Bremer, posterior probabilities) are relatively low for basal nodes in Alcinae (Fig. 3). Branch lengths in that region of the tree are relatively short and are consistent with a relatively rapid radiation following the origination of Alcinae. Despite relative consensus that either *Brachyramphus* or *Synthliboramphus* occupies the basal-most position in Alcinae, resolution of these systematic issues may be further limited by the fact that the oldest fossils of those clades are Pliocene (≤ 3.6 Ma; Smith 2011a, 2014b). All of the more derived members of Alcinae (i.e. *Alca*, †*Pinguinus*, *Uria*, †*Miocepphus*, *Alle*, *Cepphus*) have older fossil records (Smith 2011a; Supplementary material Appendix 1, Table A4). Clearly the resolution of the relationships between these major alcid subclades is an area of alcid systematics that deserves further attention, perhaps through genomic analyses and recovery of additional fossils

of greater age that might preserve systematically informative character data.

The hypothesis that the little auk or dovekie *Alle alle*, is the sole survivor of a Miocene lineage of Alcini that was once much more diverse (i.e. an *Alle* + †*Miocepphus* clade) has some explanatory power with regards to the variety of placements of *A. alle* in the results of previous phylogenetic analyses (Strauch 1985, Chandler 1990a, Moum et al. 1994, Chu 1998, Moum et al. 2002, Thomas et al. 2004, Pereira and Baker 2008, Smith 2011b). Our phylogenetic hypothesis is consistent with relatively accelerated rate of cladogenesis linked with morphological divergence; that *A. alle* represents a long branch is supported in molecular analyses of extant taxa, regardless of the methods used (i.e. parsimony, likelihood, Bayesian) or its recovered phylogenetic position (Thomas et al. 2004, Baker et al. 2007, Pereira and Baker 2008, Smith and Clarke 2011). The inclusion of extinct taxa such as †*Miocepphus mergulellus* did not have an effect on the systematic position recovered for *A. alle* relative to other extant alcids (i.e. *A. alle* is still recovered in a clade that is the sister taxon to the murres: *Uria*). However, placement as part of a clade including species of †*Miocepphus* elucidates morphological and ecological evolution in this part of the alcid tree. The relatively small body mass (~ 170 g; Dunning 2008), planktivorous diet and morphology (osteological and integumentary; Smith 2011b) of *A. alle* contrast markedly with the larger body mass (~ 900 g), piscivorous diet and morphology of its extant sister taxon *Uria* (Fig. 3). With body sizes intermediate between the dovekie and murres and humeral morphologies similar to extant *Cepphus* guillemots (i.e. benthic foraging generalists with respect to other alcids; Wijnker and Olson 2009), these data indicate that these divergent ecologies may have evolved from a mid-sized generalist (Smith 2011a). †*Miocepphus* remains constrain the minimum divergence of these two lineages to at least 16 Ma and inform the characters optimized as ancestral to this clade (Wijnker and Olson 2009). Only given the antiquity of †*Miocepphus* remains (Miocene, ~ 16.0–6.5 Ma) does a close relationship between living species of *Uria* and *Alle* begin to make sense at the morphological and behavioral levels. Close relationship between *Alle* and *Uria* provides a good example of how consideration of data from the fossil record elucidated a seemingly counterintuitive systematic hypothesis (based on highly disparate morphology and behavior) that is nonetheless, strongly supported by molecular based inferences.

Divergence times

The estimated divergence of Pan-Alcidae from its sister taxon Stercorariidae at ~ 35 Ma is consistent with the oldest fossil record of the clade at ~ 34 Ma and similar to the ~ 36 Ma divergence estimate obtained by Weir and Mursleen (2013), which utilized the molecular sequence-based topologies inferred by Pereira and Baker (2008) and Hackett et al. (2008). The congruence between these estimates regarding the timing of divergences across Pan-Alcidae and the fossil record is striking. Our divergence estimates, like those of Weir and Mursleen (2013) do not support the previously inferred Paleocene origin of Pan-Alcidae (Pereira and Baker 2008). The basal divergence among crown Alcidae

(i.e. the split between Alcinae and Fraterculinae) is estimated at ~ 29 Ma (Early Oligocene), a date that does not conflict with the oldest crown Alcidae fossils from the Early Miocene (~ 12–16 Ma fossils of †*Miocepphus bohaski*; Wijnker and Olson 2009; our Fig. 2; Supplementary material Appendix 1, Fig. A2–A3). However, these divergence estimates suggest that despite the relative abundance of Neogene pan-alcid fossil remains (~ 17 000 specimens representing > 30 species; reviewed by Smith 2011a), many Paleogene taxa representing the stem lineage and early crown clade representatives of Pan-Alcidae remain to be discovered.

Comparison of cladogram fit to the age ranges of known fossil taxa provides a graphical means of making comparisons with molecular based divergence estimates and identifying the potential presence, distribution and magnitude of 'ghost lineages' (Norell 1992). The minimum-fit cladogram resulting from the combination of the parsimony based topology and the fossil record of Pan-Alcidae suggests a minimum of 20 Ma for the basal divergence of the Alcidae crown clade (Supplementary material Appendix 1, Fig. A3); whereas, the results of the divergence estimate indicate five divergences prior to the Oligocene-Miocene boundary at 23 Ma (Fig. 2, Supplementary material Appendix 1, Fig. A2). The Miocene (23–5 Ma) fossil record of Pan-Alcidae includes examples of every major lineage within the clade and demonstrates that divergences between these lineages must have occurred earlier (Smith 2011a). The only confirmed pre-Miocene (i.e. Paleogene) fossil record of Pan-Alcidae consists of an isolated distal humerus from the Late Eocene of the western Atlantic Ocean basin (~ 34 Ma; Chandler and Parmley 2002). However unlikely, the possibility that pan-alcid lineages diverged relatively quickly in the Early Miocene and that the results of the molecular-based analysis are an overestimation of divergence times cannot be excluded. Ultimately, recovery of Oligocene or older pan-alcid fossils would test these contrasting hypotheses.

The ~ 49 Ma (95% HPD 43.6–55.5 Ma, Supplementary material Appendix 1, Fig. A2, Table A5) estimate of basal divergence among crown Charadriiformes resulting from our analysis is congruent with the fossil record of the clade (Supplementary material Appendix 1, Fig. A2–A3). Because the oldest charadriiform fossil is ~ 47 Ma (Mayr 2000; reviewed by Smith 2014b), the hypothesis that basal crown charadriiform lineages diverged from one another between 77–93 Ma during the Late Cretaceous (Paton et al. 2002, 2003, Pereira and Baker 2006, Baker et al. 2007; reviewed by Smith 2011a, 2014b) requires the inference of a ghost lineage (Norell 1992) of at least 30 Ma. Such an early origin for crown Charadriiformes is unlikely, as it would indicate that the clade was not recorded in the fossil record during approximately the first third to first half of its existence. The earliest supported crown charadriiform fossil is ~ 40 Ma (Hou and Ericson 2002, Smith 2011a). Thus, a ghost lineage of only ~ 7 Ma is inferred based upon the hypothesis presented herein. Previous divergence time estimates for Pan-Alcidae and basal split among crown Charadriiformes have included incorrectly dated fossil calibrations, taxonomically misidentified fossils used as calibrations and use of secondary and external calibrations (Smith 2014b) and have consistently recovered older dates than the results reported here (Fig. 2, Supplementary material Appendix 1, Fig. A2). Contrary to previous divergence time estimates for cladogenetic events in crown Charadriiformes, no divergence dates or associated confidence intervals extend into the Cretaceous (i.e. no node ages ≥ 65.5 Ma). However, our results do not conflict with previous hypotheses (Baker et al. 2007) that recovered the divergence of Charadriiformes from its nearest outgroup in the Cretaceous. Our taxon sampling was not designed to test that hypothesis as there has been little consensus on the closest outgroups of Charadriiformes (Mayr and Clarke 2003, Ericson et al. 2006, Livezey and Zusi 2007, Hackett et al. 2008, McCormack et al. 2013) and the stem lineage of Charadriiformes remains poorly known (reviewed by Hope 2002, Mayr 2009).

Evolution of wing-propelled diving

Wing-propelled diving is a relatively rare form of locomotion among birds, restricted to approximately 50 of ~ 10 000 species of extant birds (i.e. a highly derived behavior). Among Charadriiformes, wing-propelled diving as a method of prey capture is restricted to Pan-Alcidae.

Hypotheses regarding the evolution of this locomotor behavior in Pan-Alcidae have changed along with revisions to the hypothesized systematic position of the clade within Charadriiformes. Morphologists of the 20th century largely regarded the characteristics of Pan-Alcidae as ancestral with Charadriiformes and early morphology based phylogenetic analyses that recovered Alcidae as the sister taxon to all other Charadriiformes supported this viewpoint (Strauch 1978, Chu 1995). That the underwater foraging strategy of alcids was developed from an escape strategy used by littoral-feeding charadriiforms, not from plunge-diving ancestors, was once considered consistent with the basal position of Pan-Alcidae in Charadriiformes (Stettenheim 1959; Fig. 5).

Recent analyses, including those reported here, consistently recover Pan-Alcidae nested in a derived position in the clade Lari (Fig. 3; gulls, terns, skimmers, and alcids;
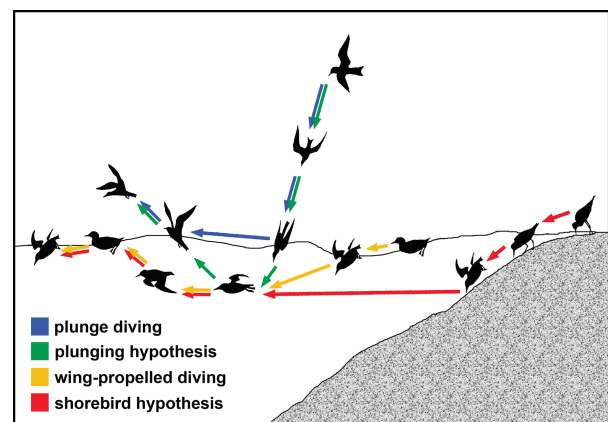

Figure 5. Hypotheses of the evolution of wing-propelled diving behavior: plunge diving as in extant terns in which the wings are not involved in underwater propulsion (blue); hypothetical intermediate stage in the evolution of wing-propelled diving from a plunge-diving ancestor (green); wing-propelled diving as in extant alcids, which involves diving from a sitting position on the waters' surface (yellow); hypothetical sequence involving the evolution of wing-propelled diving from a non-plunge diving shorebird (red).

Paton et al. 2002, 2003, Thomas et al. 2004, Paton and Baker 2006, Baker et al. 2007). These taxa share the webbed feet seen in Alcidae and used in paddling while floating on the surface of the water. Plunge diving is also a common behavior among many species of gulls and terns (del Hoyo et al. 1996) and the hypothesis that pan-alcids evolved from a plunge diving ancestor (Storer 1960), is congruent with the placement of Pan-Alcidae in Lari. However, extant alcids do not plunge into the water from the air like their close relatives (e.g. terns). Alcidae dive from a floating position on the surface of the water (Stettenheim 1959; our Fig. 5). Akin to the behavior characteristic of adult alcids, the chicks of at least six species (*Haematopus ostralegus*, *H. palliatus*, *H. bachmani*, *Recurvirostra americana*, *Himantopus mexicanus*, *Actitis macularia*) have also been observed to use the wings in underwater propulsion when threatened (Morgan 1994 and references therein). Records of adult shorebirds that use underwater wing strokes to avoid predation include the *A. macularia*, *Tringa totanus*, *T. melanoleuca* and *Numenius phaeopus*. Thus, representatives all three major clades of Charadriiformes (Lari, Charadrii and Scolopaci) are known to employ the wings in a form of aquatic locomotion at some stage of ontogeny. Wing-propelled diving has been reported in only 33 of ~ 350 extant charadriiform species; however, the distribution of this behavior across Charadriiformes has not been studied in detail (del Hoyo et al. 1996). Therefore, the evolution of the locomotor mode known as wing-propelled diving in pan-alcids should not be unambiguously assumed to be linked to aerial plunge-diving (i.e. plunge diving may represent the derived state). Foot-propelled surface paddling, and wing-propelled diving as an escape strategy appear likely plesiomorphic for more inclusive clades in Charadriiformes and would be thus retained in adult Alcidae. Within this conceptual framework, wing propelled diving is seen as one of a diverse set of locomotor and feeding ecologies to develop in the Lari, which include surface skimming, aerial foraging, as well as plunge and wing-propelled diving.

The oldest (~ 34 Ma) fossil pan-alcid is known from a humerus that displays the dorsoventral shaft compression that is characteristic of the clade and strongly associated with wing-propelled diving (Chandler and Parmley 2002). The derived morphology of that specimen suggests that pan-alcids evolved their characteristic humeral morphology relatively rapidly after divergence with Stercorariidae (skuas). However, basal divergence among the alcid crown clade is not estimated until ~ 6 Ma later (~ 28 Ma; Fig. 2) and does not support a rapid early diversification of basal crown lineages (i.e. an implied rate shift). Fossils representing †Mancallinae, the only known stem lineage representatives of Alcidae (though see Smith 2013 regarding the systematic position of †*Divisulcus demerei*), are no older than 10 Ma, are osteologically characteristic of wing-propelled divers (i.e. dorsoventral compression of forelimb bones), and therefore, are not informative regarding the transition from the putatively non-wing-propelled diving ancestor of Pan-Alcidae. The more rounded humeral shafts in taxa such as *Cepphus* (guillemots; not including species of *Uria*) and the Miocene (~ 14 Ma) species †*D. demerei* may indicate retention of ancestral morphologies (Fig. 3 in Smith 2013). Guillemots differ from other extant alcids in that they are primarily benthic foragers (del Hoyo et al. 1996). The more rounded

humeral shafts may be a functional correlate of decreased complexity of dive profile. Observations suggest that guillemots spend less time traversing distances underwater and primarily dive up and down through the water column. However, the dive profiles of *Cepphus* guillemots have not been studied in detail like those of murres (e.g. *Uria lomvia*; Watanuki et al. 2006). As with more rounded humeral morphology, benthic foraging strategy may represent the ancestral state for Pan-Alcidae. The reconstruction of ancestral diet in Pan-Alcidae suggests that early pan-alcids may have fed primarily on vertebrates (Fig. 3). However, the depth at which ancestral pan-alcids may have fed has not been evaluated. Perhaps littoral feeders transitioned to feeding in ever-deeper waters in search of prey until they eventually adapted to exploit benthic resources, and then only later began to free-swim in search of prey in the water column as do most extant alcids (e.g. *Alca torda*; Fig. 5).

Paleodiversity and origination area

A Pacific evolutionary area of origination for the Pan-Alcidae, based primarily on higher extant diversity in the Pacific Ocean is widely accepted (our Fig. 1–2; Storer 1960, Olson 1985, Konyukhov 2002, Pereira and Baker 2008). However, higher extant diversity in the Pacific is not necessarily evidence of origination area, but rather a reflection of the impact of environmental differences in past and present climate on alcid diversity. Extant alcid diversity and species densities are closely tied to cold-water upwelling that provides nutrient-rich feeding grounds, and based on geological interpretation of pan-alcid fossil bearing deposits, the same is likely true of extinct pan-alcids (Fig. 1). Indeed, molecular data for some Alcidae subclades (e.g. *Fratercula* and *Cepphus*; Friesen et al. 1996, Kidd and Friesen 1998) suggest that there may have been multiple periods of dispersal between Atlantic and Pacific Ocean lineages, rather than a simpler model of Miocene migration of species from the Pacific to the Atlantic basin. Furthermore, when extinct taxa are considered, known diversity of extinct Atlantic pan-alcids is now equal to or exceeds that of extinct Pacific pan-alcids (Fig. 1–2, 4).

Raw estimates of pan-alcid diversity are misleading, in that they indicate an overall increase in pan-alcid species diversity throughout the Cenozoic (Fig. 4). In direct contrast to those raw estimates, the phylogenetically contextualized estimate of pan-alcid diversity displays a general trend of decreasing species diversity throughout the Neogene. Whereas extant diversity of Alcidae includes 23 species, we estimate Pliocene pan-alcid diversity was at least 35 species and that Miocene pan-alcid diversity was at least 33 species. Weir and Mursleen (2013) also noted that known Pliocene pan-alcid diversity exceeds their estimated carrying capacity of ~ 29 species. Fifteen new pan-alcid taxa have been described since 2007 (Smith et al. 2007, Wijnker and Olson 2009, Smith 2011a, b, 2013, 2014a, Smith and Clarke 2011, Smith and Mayr 2013). Given the relative incompleteness of the fossil record in general and the poorly sampled stem lineage of Alcidae (i.e. Eocene and Oligocene taxa largely unknown), pan-alcid species diversity estimates for all geologic epochs are likely underestimates that will be revised as new fossils are discovered, further exaggerating the decreasing chronological trend in pan-alcid species diversity.

Based on the reconstruction of ancestral area for Pan-Alcidae and the exclusively Pacific occurrence of stem Alcidae (i.e. Mancallinae), the Pacific is favored as the area of origination (Fig. 2). However, the two oldest known pan-alcid fossils are both from Atlantic Ocean basin deposits (Chandler and Parmley 2002, Wijnker and Olson 2009). Given the ~ 15 Ma gap in the alcid fossil record (Late Eocene–Early Miocene) we would suggest there is currently not enough fossil data to inform whether pan-alcids originated in the Atlantic or Pacific Ocean basin. Although pan-alcids are present in the Eocene, Miocene and Pliocene of the northwestern Atlantic Ocean basin (Olson and Rasmussen 2001, Chandler and Parmley 2002), curiously, there are no records of pan-alcids from Oligocene deposits on the Atlantic coast of North America, including some that contain fossils of other seabirds (Olson 1985, Smith 2011a). Perhaps the range of Atlantic pan-alcids was further north during the Oligocene or there were other significant shifts in alcid distributions that are as yet uninformed by the fossil record.

Influence of Cenozoic paleoclimatic events

Because extant alcids are dependent on nutrient-rich, cold-water upwelling zones (del Hoyo et al. 1996; our Fig. 1), broad scale hypotheses of pan-alcid evolution have often focused on potential correlations with major climatic events that affected ocean circulation patterns (Warheit 1992, Emslie 1998, Pereira and Baker 2008). Four major paleoclimatic events that occurred during the evolution of Pan-Alcidae are the Eocene–Oligocene climatic transition (EOCT; ~ 34 Ma), the Middle Miocene climatic optimum (MMCO; ~ 16–11 Ma), the Pliocene–Pleistocene climatic transition (PPCT; ~ 3–2 Ma), and subsequent Pleistocene glacial events (2.5 Ma~12 ka; Fig. 2, 4).

Hypotheses regarding the Eocene–Oligocene climate transition (EOCT) suggest a ~ 4°C drop in average sea-surface temperatures relative to earlier Eocene seas, increased latitudinal thermal gradients, increased thermohaline circulation, and associated changes in sea chemistry (Miller et al. 2009). The hypothesized split between Pan-Alcidae and stem Stercorariidae at ~ 35 Ma suggests that the pan-alcid lineage may have initially diversified in response to this cooling climate regime (Fig. 2). However, temperatures during the EOCT were significantly warmer than today and the divergence estimates and the fossil record agree that alcids were present during this relatively warm episode of Earth history. Extant alcid species have shown varying degrees of interspecific tolerance to climate change (Kitaysky and Golubova 2000, Hyrenbach and Veit 2003, Gaston and Woo 2008, Morrison et al. 2011) and the more southerly distribution of extinct pan-alcids (Fig. 1) suggest that some extinct species could have had different or broader environmental tolerances than do extant alcids.

The MMCO was the warmest excursion in Earth's climatic history since the Early Eocene climatic optimum (~ 55 Ma) and the overall increase in Miocene ocean upwelling strength has been linked to the radiation of pan-alcids and other seabirds that are ecologically linked with cold-water upwelling systems (Warheit 1992, Flower and Kennett 1994). The minimum fit cladogram based on the fossil record of Pan-Alcidae (Supplementary material Appendix 1, Fig. A3) suggests that at least 13 divergences likely took place during this period. Similarly, with respect to the Bayesian divergence estimates among non-alcid charadriiforms, fifteen of the 27 divergences (considering the associated 95% HPD; Supplementary material Appendix 1, Table A5) occur in the Miocene, with 12 of those 15 divergences hypothesized among the Lari, close relatives of Alcidae including Stercorariidae, Laridae, and Sternidae. Furthermore, the first marine records of Laridae also occur in the Middle Miocene (~ 15 Ma; Warheit 1992, De Pietri et al. 2011). Many extant Lari prey on alcids (Ainley et al. 1990, Stempniewicz 1994) and although there is currently no evidence to suggest that this ecological interaction dates back to the Miocene, the colonization of the marine realm by Laridae may have played a role in post-Oligocene evolutionary interactions between these lineages.

In contrast to the significant Miocene pan-alcid diversification evident from the fossil record and supported by the divergence estimates, pan-alcid species diversity declines during the Pliocene and into the Pleistocene (Fig. 4). Only four extinct pan-alcid species are known to have crossed the Miocene–Pliocene boundary (~ 5.3 Ma; *A. stewarti*, *A. torda*, *M. californiensis*, *M. howardae*) and only five species are known to have crossed the Pliocene–Pleistocene boundary (~2.5 Ma; *F. arctica*, *F. cirrhata*; *A. torda*, *U. lomvia*, *M. lucasi*; Supplementary material Appendix 1, Table A4). Fossils representing at least 17 species of alcids are recorded from the Pleistocene, with 14 of those records representing extant species (Brodkorb 1967, Smith 2011a; Supplementary material Appendix 1, Table A4). Furthermore, estimates of diversity based on the fossil record suggest that the PPCT affected Pliocene pan-alcid diversity in different ways in the Atlantic and Pacific Ocean basins. Only a single species, *Alca torda*, representing the dominant Pliocene pan-alcid lineages of the Pacific and Atlantic (i.e. †Mancallinae and *Alca* respectively) survives today and extant Atlantic Ocean basin alcid species richness (n = 6, Fig. 4) pales in comparison to that of the Pacific Ocean basin (n = 17). To summarize, the divergence estimates suggest that extant alcid diversity is a function of radiation of modern lineages during the Miocene and differential survival among those lineages across the Pliocene–Pleistocene boundary. These findings are consistent with the decline of numerous marine vertebrates and invertebrates occurring at approximately the same time as faunal turnovers and exchange of terrestrial faunas between North America and South America during the Pliocene–Pleistocene climatic transition (Kameo and Sato 2000, Warheit 2002, Boessenecker and Smith 2011). Debate continues, however, regarding the relative contributions and interactions of the shallowing Central American Seaway, the onset Northern Hemisphere glaciation, and the reorganization of ocean circulation currents to this transition (Haug and Tiedemann 1998, Lunt et al. 2008, Molnar 2008). However, the correlations between pan-alcid radiation, extinction and rather drastic climatic changes such as the MMCO and PPCT are striking.

Orbitally-forced Pleistocene glacial cycles have been invoked, and subsequently refuted in speciation hypotheses for many terrestrial clades of birds (reviewed by Zink et al.

2004). Likewise, hypotheses of recent divergences among alcids owing to Pleistocene glacial and interglacial periods (Moum et al. 1994, Pereira and Baker 2008) are not indicated as major influences of extant alcid diversification by the results of our divergence time analysis (Fig. 2, Supplementary material Appendix 1, Fig. A2, Table A5). The only Pleistocene divergence hypothesized herein is that between extant gull species, *Larus marinus* and *L. argentatus* (~ 1 Ma). Furthermore, in some instances the fossil record of Pan-Alcidae records divergences between extant sister-species in the early Pliocene (~ 4.4 Ma, e.g. *Fratercula arctica* and *F. corniculata*, Olson and Rasmussen 2001, Smith et al. 2007). It may be expected, however, that the geographic distributions of extant species have been significantly impacted by glacial cycles (Moum et al. 1994, Zink et al. 2004, Pereira and Baker 2008).

The presence of numerous alcid species from the Miocene and Pliocene that are not known from Pleistocene and younger deposits agrees with the trends in faunal turnover that have been well documented in marine microfaunas and macrofaunas (Versteegh 1997, Kameo and Sato 2000). For example, walrus, squalodon, albatross, and pelagornithids (giant pseudotoothed birds) were present in the northern Atlantic Ocean during the Miocene and Pliocene but are absent there today (Ray 1987, Ray and Bohaska 2001, Ray et al. 2008). Likewise, Pacific Ocean diversity of other seabirds and marine mammals is also noted to decline from the Miocene to today (Repenning and Tedford 1977, Warheit 1992, Boessenecker 2011, Boessenecker and Smith 2011). Recent evaluation of hypotheses regarding competitive exclusion of flightless seabirds by marine mammals found support for significant interactions between marine mammals and Spheniscidae (penguins) in the Southern Hemisphere, and between the extinct flightless, wing-propelled †Plotopteridae of the Northern Pacific Ocean (Ando and Fordyce 2013). However, no significant diversity correlations were identified among marine mammals and flightless pan-alcids (†Mancallinae and †*Pinguinus*) and thus, pan-alcid evolutionary drivers may be more heavily influenced by physical factors such as paleoclimate (Ando and Fordyce 2013). Our results suggest that pan-alcids have diversified during periods of relative warmth (e.g. MMCO), and have experienced episodes of extinction concurrent with episodes of cooling (e.g. PPCT). This hypothesis is somewhat counterintuitive because alcids are ecologically linked with cold-water upwelling. Although the contemporary association of extant alcids with cold waters may lead to an expectation of increased diversity with global cooling since the late Miocene, the fossil record and divergence time estimates both support peak diversity during the relative warmth of the Miocene. The dynamics of how large-scale paleoclimate events affected interactions between sea surface temperature, ocean stratification and Miocene and Pliocene undersea topography is not well understood. These physical factors would likely have influenced the proximity and relative abundance of cold-water upwelling areas (i.e. foraging areas) available to Miocene and Pliocene pan-alcids. Alcids must deliver meals to their young in the nest and are, subsequently, dependent on upwelling areas in relatively close proximity to shore. Thus, changes in coastal topography (i.e. suitable breeding areas) and the locations of upwelling areas where pan-alcids feed are directly linked with shifts in sea level and ocean current organization (e.g. warming of the Atlantic in response to closure of the Panamanian Isthmus), and would likely have influenced pan-alcid species diversity through time.

The implications of this study regarding the sensitivity of seabird communities to environmental change may have bearing on the plight of seabirds in the face of current global warming and pressures from over-fishing and ocean pollution. If, as proposed, alcids are good candidates for environmental indicator species (Furness and Nettleship 1991, Montevecchi 1993), the increased understanding of extinct pan-alcid responses to environmental change may have unexplored conservation value. Extant seabird distributions, ecological interactions, and population dynamics that are changing rapidly in response to the current global warming trend (Kitaysky and Golubova 2000, Hyrenbach and Veit 2003, Gaston and Woo 2008, Morrison et al. 2011) are best contextualized with insights derived from knowledge of how past climate changes may have affected the mode and tempo of seabird evolution. This study provides the estimates of diversity, phylogenetic context, and estimates of divergence that will facilitate future comparisons between changes in extant alcid populations and factors that have influenced the diversity and distribution of seabird lineages such as the Pan-Alcidae.

Conclusions

The inclusion of 28 extinct species did not result in a significantly different hypothesis of phylogenetic relationships among extant taxa in the clade and the basal relationships in the subclade Alcinae remain poorly supported even with a larger morphological dataset and inclusion of extinct taxa. Short molecular and morphological branch lengths within this clade may be consistent with rapid diversification. Inclusion of extinct taxa did importantly inform inferred patterns of diversification and extinction as well as calibration choice for future divergence time estimation. Our results support a latest Paleogene origin of Pan-Alcidae followed by Miocene radiation and subsequent extinction close to the Pliocene–Pleistocene boundary. While support for potential linkages between diversification and the Middle Miocene climatic optimum and between extinction and the Pliocene–Pleistocene climatic transition is recovered, we did not recover any evidence that Pleistocene glacial cycles played a significant role in alcid speciation. Finer-scale sampling within the Pleistocene may be necessary to test proposed hypotheses of changing distributions related to these cycles. Divergence dating estimates for clade origination reveal the distribution and magnitude of estimated ghost lineages (Supplementary material Appendix 1, Fig. A3) and provide direction for ongoing efforts to recover fossils of stem lineage pan-alcids and basal representatives of the alcid crown. Additional fossils of early pan-alcids are needed to further resolve debates related to the origination area of the clade and the evolution of wing-propelled diving. However, the distribution of wing-propelled diving as an escape behavior in Charadriiformes is greater than previously realized and plunge diving can no longer be assumed as the ancestral state in Pan-Alcidae. Selective pressure driving a shift in feeding ecology could lead to cooption of a behavior retained within

a plesiomorphic behavioral repertoire – and its persistence in adults. Exaptation of escape diving as related to the evolution of wing-propelled diving in Charadriiformes should be considered in phylogenetic context as more data pertaining to its distribution among extant taxa become available and as additional insights are gleaned from the fossil record of the Pan-Alcidae.

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Supplementary material (Appendix JAV-00487 at <www.avianbiology.org/readers/appendix>). Appendix 1.