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The fossil record and phylogeny of the auklets (Pan-Alcidae, Aethiini)

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The auklets *Aethia* and *Ptychoramphus* comprise the smallest known Alcidae (Aves, Charadriiformes) and have a fossil record that extends into the Miocene. The evolution of auklets is poorly understood because systematic hypotheses of relationships among extant auklets are largely incongruent, the morphology of auklet fossils has not been evaluated in detail, and extinct species of auklets have not been previously included in a phylogenetic analysis. Previously described auklet fossil remains are reviewed and two new species of auklet, *Aethia barnesi* sp. nov. and *Aethia storeri* sp. nov., are described from the Miocene and Pliocene of southern California, USA. Previously described auklet fossil remains, the two newly described extinct species of auklet, and extant species of auklets and other alcids are included in combined phylogenetic analyses of morphological and molecular sequence data. Based on the results of the phylogenetic analyses, the taxonomy of fossils referred to Aethiini is revised and the evolution of the clade is evaluated in a phylogenetic context. The osteological morphology of extinct auklets appears to be little changed from their extant relatives, suggesting that the ecological attributes of these small wing-propelled divers may also be relatively unchanged since the Miocene.

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Keywords: *Aethia*; Charadriiformes; fossil seabirds; palaeodiversity; wing-propelled diving; *Ptychoramphus*

Introduction

Pan-Alcidae Smith, 2011 (i.e. stem lineage Mancallinae plus crown clade Alcidae *sensu* Smith 2011a) are pelagic, wing-propelled, pursuit-diving charadriiforms with an exclusively Holarctic range (del Hoyo *et al.* 1996). Auklets are among the smallest of pan-alcids, and ecologically, tend to be specialized for planktivory more so than many species in the clade (Bédard 1985; del Hoyo *et al.* 1996). There are five extant species of auklets: Cassin's Auklet *Ptychoramphus aleuticus* (Pallas, 1811), Least Auklet *Aethia pusilla* (Pallas, 1811), Parakeet Auklet *Aethia psittacula* (Pallas, 1769), Whiskered Auklet *Aethia pygmaea* (Gmelin, 1789), and Crested Auklet *Aethia cristatella* (Pallas, 1769). The Least Auklet is the smallest species of extant alcid, whereas other auklets are similar in size to the murrelets (i.e. *Brachyramphus* Brandt, 1837 and *Synthliboramphus* Brandt, 1837). As in their sister taxon the Fraterculini Storer 1960 (i.e. puffins: *Cerorhinca* Bonaparte, 1831 and *Fratercula* Brisson, 1760), many Aethiini Storer, 1960 (i.e. auklets: *Ptychoramphus* Brandt, 1837 and *Aethia* Merrem, 1788) are characterized by crests and tufts of feathers adorning their heads, and the bills of primarily planktivorous auklets (e.g. *Aethia psittacula*) are relatively shorter and broader than the more terete bills of primarily piscivorous alcids such as *Uria* Pontoppidan, 1763.

The monophyly of extant Aethiini has been supported in phylogenetic analyses of morphological, molecular sequence and combined data (Strauch 1985; Watada *et al.* 1987; Chandler 1990a; Moum *et al.* 1994; Friesen *et al.* 1996; Thomas *et al.* 2004; Baker *et al.* 2007; Pereira & Baker 2008; Smith 2011a, b). The morphology-based compatibility analysis of Strauch (1985) placed Fraterculini as the sister group to all other alcids, with Aethiini in a more derived position as the sister taxon to the remainder of Alcidae. All subsequent phylogenetic analyses have recovered Aethiini as the sister taxon to Fraterculini (Watada *et al.* 1987; Chandler 1990a; Moum *et al.* 1994; Friesen *et al.* 1996; Thomas *et al.* 2004; Baker *et al.* 2007; Pereira & Baker 2008; Smith 2011a, b). Within Aethiini, *Ptychoramphus aleuticus* has been consistently recovered as the sister taxon to the four species of *Aethia* (Strauch 1985; Watada *et al.* 1987; Chandler 1990a; Moum *et al.* 1994; Friesen *et al.* 1996; Thomas *et al.* 2004; Baker *et al.* 2007; Pereira & Baker 2008; Smith 2011a, b). However, relationships within *Aethia* are more contentious, with the relative positions of *Aethia* species variable or unresolved in the results of previous analyses (Moum *et al.* 1994; Friesen *et al.* 1996; Thomas *et al.* 2004; Baker *et al.* 2007; Pereira & Baker 2008; Smith 2011a, b). It has been suggested that ancestral DNA polymorphism or incomplete lineage sorting may be responsible for

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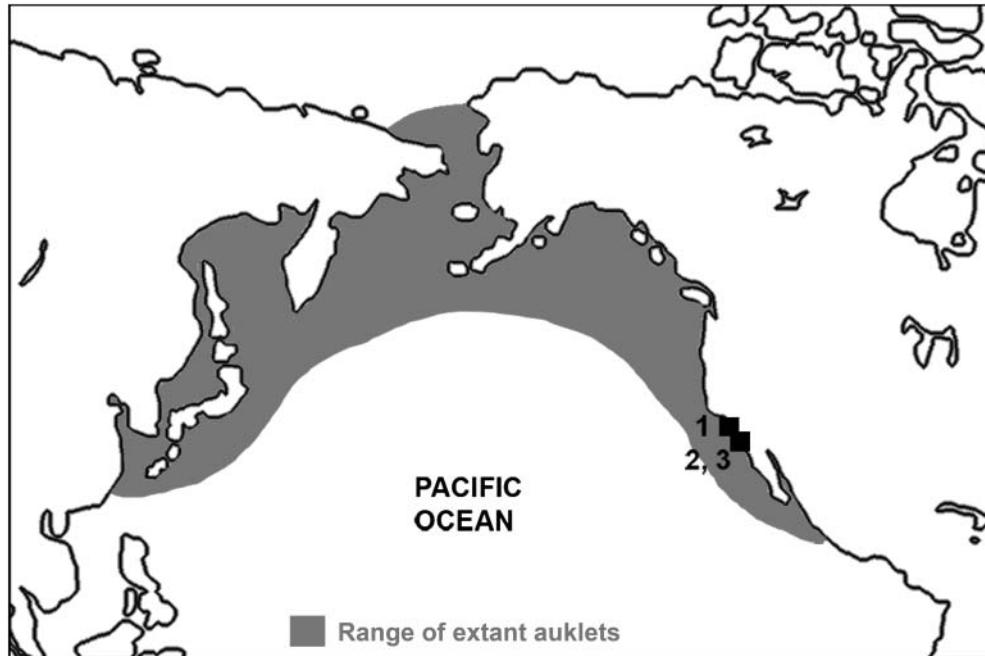


Figure 1. Map depicting the geographic restriction of auklet fossil localities and the broad geographical distribution of extant auklets (altered from del Hoyo *et al.* 1996). 1, Laguna Niguel, California (Howard 1978); 2, Laguna Hills, California (Howard 1968); 3, San Diego, California (Howard 1949; Miller & Bowman 1958; Howard 1982; Chandler 1990b).

the variable placements recovered for *Aethia* species in previous phylogenetic analyses (Walsh & Friesen 2003; Walsh *et al.* 2005).

Congruent with the distribution of extant auklets, all fossil records of Aethiini are restricted to the Pacific Ocean basin (Olson 1985; Fig. 1). Although extinct species of *Ptychoramphus* and *Aethia* have not been previously included in a phylogenetic analysis, systematic positions for *Ptychoramphus tenuis* Miller & Bowman 1958 and *Aethia rossmoori* Howard 1968 were proposed in the form of a cladogram by Chandler (1990a). However, scorings for these taxa were not included in the cladistic matrix, and thus, the placement of extinct taxa in the cladograms presented by Chandler (1990a) seems to stem from the optimization of selected characters (i.e. character mapping). Herein, an apomorphy-based approach was applied to evaluate the systematic position of previously described Aethiini fossils. Apomorphies shared between extant species of Aethiini and fossils referred to this clade will allow the referral of additional fossils to the species level. Two newly described species of extinct auklet and previously described auklet fossil remains are included in combined phylogenetic analyses that help elucidate the poorly understood relationships and evolutionary history of this clade. Based on the results of the phylogenetic analyses, a taxonomic revision of previously described auklet fossil remains is provided.

The fossil record of auklets

Unlike the abundant remains referred to some other panalcid taxa (e.g. ~4000 specimens referred to Mancallinae; Smith 2011a), the fossil record of auklets is limited to ~13 specimens from three localities in southern California (Miller & Bowman 1958; Howard, 1968, 1978, 1982; Chandler 1990b; Fig. 1). A right tarsometatarsus (UCMP 45662; Fig. 2) from the Pliocene San Diego Formation of San Diego, California was initially referred, albeit tentatively, to *Brachyramphus pliocenium* Howard, 1949 by Miller (1956). However, the resemblance of this specimen to *Aethia* and *Ptychoramphus*, and notable differences from *Brachyramphus*, were cited by Miller (1956). Subsequently, UCMP 45662 was formally, yet tentatively referred to *Ptychoramphus* and designated as the holotype specimen of *Ptychoramphus tenuis* by Miller & Bowman (1958; Table 1). Curiously, the holotype specimen of *Ptychoramphus tenuis* and three additional specimens (left distal humerus, SDSNH 24937; proximal left carpometacarpus, SDSNH 22884; left proximal scapula, SDSNH 25276) from the San Diego Formation referred to this taxon by Chandler (1990b) are the only previously published Pliocene records of Aethiini. Additional records are all from the Miocene (Howard 1968, 1978, 1982). Because the holotype specimen of *Ptychoramphus tenuis* is a tarsometatarsus, and because there are no known

Table 1. Previously published auklet fossil remains.

Taxon	Material	Provenance	Age	Reference
<i>Ptychoramphus tenuis</i>	Tarsometatarsus	California	Pliocene	Miller & Bowman 1958
<i>Aethia rossmoori</i>	Ulna	California	Late Miocene	Howard 1968
<i>Aethia</i> sp.	Distal humerus	California	Late Miocene	Howard 1978
<i>Aethia</i> sp.	Humerus	California	Late Miocene	Howard 1982

associated specimens referable to that species, there was no basis for referral of additional elements (humerus, carpometacarpus, scapula) to *Ptychoramphus tenuis* by Chandler (1990b) from San Diego Formation localities that have also produced remains of *Brachyramphus*, *Synthliboramphus*, *Cerorhinca* and *Mancalla* (Chandler 1990b; Smith 2011a). Herein, further references to *Ptychoramphus tenuis* refer only to the holotype specimen of this taxon (UCMP 45662).

Aethia rossmoori was described by Howard (1968) based upon a right ulna (LACM 18948; Fig. 3) from Late Miocene deposits in Laguna Hills, California (Table 1). Presumably based on its small size, *Aethia rossmoori* was originally diagnosed relative only to the diminutive extant species *Aethia pusilla*. Because the holotype specimen of *Aethia rossmoori* is an ulna, and because there are no known associated specimens of *Aethia rossmoori*, there was no basis for referral of additional elements (left humerus, LACM 18949; proximal radius, LACM 18953; distal carpometacarpus, LACM 18951; partial coracoids, LACM 18952, LACM 18954) by Howard (1968) from a locality that also contains remains of other species of alcids (*Alcodes*, *Cerorhinca*, Mancallinae). Furthermore, because the holotype ulna of *Aethia rossmoori* does not possess any apomorphies relative to other species of Pan-Alcidae, there was also no basis for referral of a distal ulna (LACM 18960) by Howard (1968; i.e. morphological similarity is not sufficient evidence of species identity).

A distal humerus (LACM 37686) from the Late Miocene Monterey Formation at Laguna Niguel, California was referred by Howard (1978) to *Aethia* (Table 1). LACM 37686 was not figured in Howard's publication and its whereabouts is uncertain. An empty specimen box with a temporary loan tag labelled 'Hildegard Howard study cabinet' was found during a search of the LACM collections by the author in 2007. Because LACM 37686 could not be located, and because there are no published photographs from which characters could be scored, this specimen is not considered further herein.

A distal right humerus (LACM 107031; mistakenly listed as a left humerus by Howard 1982) from the Late Miocene San Mateo Formation (San Luis Rey River Local Fauna) of San Diego, California, was referred by Howard (1982) to *Aethia* (Table 1; Fig. 4). Although there are no apomor-

phies that allow differentiation between *Ptychoramphus* and *Aethia* humeri, the ventral projection of the entepicondyle, lack of proximal extension of the dorsal supracondylar process, and the abrupt transition of the deltopectoral crest



Figure 2. Right tarsometatarsi of *Ptychoramphus* in anterior view. A, holotype specimen of *Ptychoramphus tenuis*, UCMP 45562; B, *Ptychoramphus aleuticus*, NCSM 18088.



Figure 3. Holotype right ulna of *Aethia rossmoori* in anterodorsal view, LACM 18948.

to the humeral shaft, support the previous referral of this specimen to Aethiini (i.e. the clade composed of *Aethia* + *Ptychoramphus*).

Material and methods

Previously described auklet remains, extant species of auklets, other species of extant alcids, and charadriiform outgroup taxa were evaluated through combined phylogenetic analyses to assess the systematic positions of

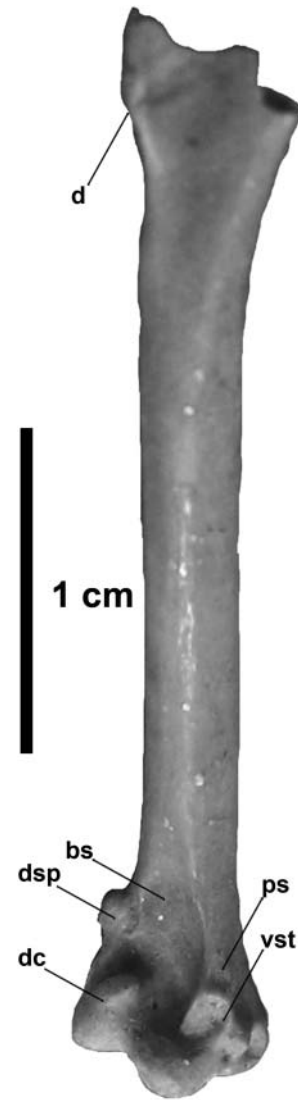


Figure 4. *Aethia barnesi* sp. nov. partial right humerus in anterior view, LACM 107031. Anatomical abbreviations: bs: m. brachialis scar; d: deltopectoral crest; dc: dorsal condyle; dsp: dorsal supracondylar process; ps: m. pronator sublimis scar; vst: ventral supracondylar tubercle.

these taxa. Taxonomic revisions are provided based on the results of the phylogenetic analyses and implications for the evolution of these taxa are discussed in the context of revised estimates of species richness and the results of the phylogenetic analyses.

In the anatomical descriptions, the English equivalents of the Latin osteological nomenclature summarized by Baumel & Witmer (1993) are primarily used. The terminology of Howard (1929) is followed for features not treated by Baumel & Witmer (1993). With the exception of the terms anterior and posterior substituted for cranial and caudal, respectively, the terms used for the anatomical orientation of a bird are those used by Clark (1993). Measurements follow those of von den Driesch (1976). All measurements

were taken using digital calipers and rounded to the nearest 10th of a millimetre. Ages of geological time intervals are based on the International Geologic Timescale (Gradstein *et al.* 2004; Ogg *et al.* 2008). Species-level taxonomy of extant North American charadriiforms follows the seventh edition of the *Checklist of North American Birds* (American Ornithologists' Union 1998). With the exception of species binomials, all taxonomic designations (e.g. *Aethia*) are clade names as defined by the PhyloCode v. 4c (Dayrat *et al.* 2008; Cantino & de Queiroz 2010) and are not intended to convey rank under the Linnaean system of nomenclature, regardless of use of italics or previous usage by other authors. The term alcid is used to refer to the crown clade Alcidae, and the term pan-alcid is used to refer to the clade that includes Alcidae + Mancallinae (Smith 2011a).

Sampled taxa included all 23 extant alcids, the recently extinct Great Auk *Pinguinus impennis*, the extinct taxa *Aethia rossmoori* and *Ptychoramphus tenuis*, and five fossils previously referred to Aethiini or referred to Aethiini herein (SDSNH 63195, SDSNH 24937, SDSNH 59027, SDSNH 59028, LACM 107031). A gull (*Larus marinus*) and a skua (*Stercorarius skua*) were included as charadriiform outgroup taxa.

A list of comparative osteological material, measurement data from extant specimens, illustrated morphological character descriptions, GenBank accession numbers and sequence authorship information, and the phylogenetic matrix can be found in the Online Supplementary Material and have also been deposited in the Dryad Repository (<http://dx.doi.org/10.5061/dryad.2637g>). Sampled morphological characters include osteological ($n = 232$), integumentary ($n = 32$), reproductive ($n = 11$), dietary ($n = 2$), myological ($n = 24$) and micro-feather ($n = 52$). Whenever possible, five or more specimens of each extant species and both sexes were evaluated to account for intraspecific character variation and potential sexual dimorphism, respectively. Only adult specimens, assessed based on degree of ossification (Chapman 1965), were evaluated, and whenever possible specimens from multiple locations within the geographical ranges of extant species (i.e. subspecies) were examined to account for geographical variation. Osteological characters for all fossil specimens were coded from direct observations. Characters for *Aethia storeri* were scored from the hypodigm representing this species (i.e. the holotype and three additional specimens referred herein).

Previously published molecular sequence data (mitochondrial: ND2, ND5, ND6, CO1, CYTB; ribosomal RNA: 12S, 16S; and nuclear: RAG1) were downloaded from GenBank (<http://www.ncbi.nlm.nih.gov/genbank>). Preliminary sequence alignments were obtained using ClustalX v2.0.6 (Thompson *et al.* 1997) and then manually adjusted using Se-Al v2.0A11 (Rambaut 2002). Alignment and concatenation of sequence data resulted in a final molecular matrix of 11,601 base pairs. Molecular sequence data

were combined with morphological characters for a matrix of 11,954 characters. Molecular sequence coverage ranged from ~22% to 94% complete for sampled taxa (average sequence completeness = 66%). Morphological scorings were > 98% complete for all extant taxa; however, scorings for extinct auklets were ~97% incomplete.

A combined approach of phylogeny estimation was used to evaluate the systematic position of auklet species. Phylogenetic analyses employed parsimony as implemented in PAUP* v4.0b10 (Swofford 2002). Parsimony tree search criteria were as follows: heuristic search strategy; 10 000 random taxon addition sequences; tree bisection–reconnection branch swapping; random starting trees; all morphological and molecular characters equally weighted; 15 ordered multistate morphological characters (see character descriptions); minimum length branches = 0 collapsed; multistate (e.g. 0 & 1) scorings used only for polymorphism. Bootstrap values and descriptive tree statistics (e.g. consistency index (CI), retention index (RI) and rescaled consistency index (RC)) were calculated using PAUP* v4.0b10 (Swofford 2002). Bootstrap value calculation parameters included 1000 heuristic replicates with 100 random addition sequences per replicate. Bremer support values were calculated using a script generated in MacClade v4.08 (Maddison & Maddison 2005) and analysed with PAUP* v4.0b10 (Swofford 2002). Resultant trees were rooted with *Larus marinus* based on the results of previous phylogenetic analyses of charadriiform relationships (Strauch 1978; Sibley & Ahlquist 1990; Chu 1995; Ericson *et al.* 2003; Paton *et al.* 2003; Thomas *et al.* 2004; Baker *et al.* 2007; Smith 2011a, b).

Because the common English name Rhinoceros Auklet that is currently applied to *Cerorhinca monocerata* by the American Ornithologists' Union (1998) is a misnomer, the term auklet is used only to refer to species of *Aethia* and *Ptychoramphus* herein. Frequently encountered references to other common names applied to *Cerorhinca monocerata*, including Rhinoceros Puffin, Horn-billed Puffin and Unicorn Puffin (Coues 1868; Storer 1945; Thoresen 1985; De Santo & Nelson 1995; del Hoyo *et al.* 1996), are all more accurate characterizations of this taxon. *Cerorhinca monocerata* has been consistently recovered as the sister taxon to *Fratercula* in phylogenetic analyses of morphological data (Strauch 1985; Chandler 1990a), molecular sequence data (Friesen *et al.* 1996; Baker *et al.* 2007; Pereira & Baker 2008), and combined data (Smith 2011a, b). *Cerorhinca monocerata* was presumably allied with the auklets based upon its size, which is smaller than other Pacific Ocean endemic puffins. However, size alone is not an appropriate criterion for classification and the size of *Cerorhinca monocerata* is larger than that of the Atlantic Puffin *Fratercula arctica* (del Hoyo *et al.* 1996). A recent proposal to change the English name of *Cerorhinca monocerata* was rejected primarily on the basis of maintaining nomenclatural stability (American Ornithologists' Union

Table 2. Measurements of auklet humeri and tarsometatarsi* (in mm). Extant specimen numbers and measurement data available as Supplementary material and through Dryad (doi:10.5061/dryad.2637g).

Taxon	Specimen	Bd	Bp	Dd	Dip	Gl	Sc
<i>Ptych. aleuticus</i>	Average ($n = 5$)	7.0	9.4	5.0	9.3	45.1	3.4
<i>Ptych. aleuticus*</i>	Average ($n = 5$)	4.0	4.5	—	—	22.1	2.0
<i>Ptych. tenuis*</i>	UCMP 45662	4.1	4.8	—	—	25.2	2.1
<i>Aethia cristatella</i>	Average ($n = 5$)	8.4	11.5	5.9	11.4	52.3	4.1
<i>Aethia psittacula</i>	Average ($n = 7$)	8.7	11.9	6.3	11.3	54.3	4.3
<i>Aethia pusilla</i>	Average ($n = 6$)	5.5	7.7	4.0	7.3	34.9	2.5
<i>Aethia pygmaea</i>	Average ($n = 4$)	5.9	8.1	4.3	7.8	37.9	2.8
<i>Aethia barnesi</i>	LACM 107031	5.0	—	3.4	—	—	2.7
<i>Aethia storeri</i>	SDSNH 63195	6.2	9.0	5.3	8.1	41.0	2.7
<i>Aethia storeri</i>	SDSNH 24937	6.2	—	5.0	—	—	2.8
<i>Aethia storeri</i>	SDSNH 59027	—	9.0	—	8.4	—	3.1
<i>Aethia storeri</i>	SDSNH 59028	—	9.2	—	8.4	—	—

Abbreviations: Bd, breadth of the distal end; Bp, breadth of proximal end; Dd, distal diagonal; Dip, diagonal of proximal end; Gl, greatest length; Ptych., *Ptychoramphus*; Sc, smallest dorsoventral breadth of corpus (shaft).

2008). *Cerorhinca monocerata* is not an auklet and emendation of the common name of this species to reflect its affinities with other puffins should be reconsidered by the American Ornithologists' Union.

Institutional abbreviations

LACM: Natural History Museum of Los Angeles County, Los Angeles, CA, USA; **NCSM:** North Carolina Museum of Natural Sciences, Raleigh, NC, USA; **SDSNH:** San Diego Natural History Museum, San Diego, CA, USA; **UCMP:** University of California Museum of Paleontology, Berkeley, CA, USA; **UMMZ:** University of Michigan Museum of Zoology, Ann Arbor, MI, USA.

Phylogenetic results

A preliminary analysis including all four extinct auklet taxa of interest, *Pinguinus impennis* and 25 extant taxa resulted in a tree with relationships completely unresolved at the base of Alcidae (results not shown). Given that a previous analysis of these data that was restricted to extant taxa resulted in a fully resolved hypothesis of relationships among auklets and their sister taxon Fraterculini (Smith 2011b, fig. 1.25), it is apparent that the inclusion of fossils with large percentages of missing morphological data (*Ptychoramphus tenuis* 96% incomplete; *Aethia rossmoori* 95% incomplete) is responsible for the lack of resolution in the consensus topology resulting from the initial analysis. Two additional analyses, which are described below, were performed to investigate further the effect of these potential 'wildcard taxa' (Nixon & Wheeler 1992; Kearney 2002).

Inclusion of *Ptychoramphus tenuis* in a phylogenetic analysis with all 23 extant alcids, *Pinguinus impennis*

and two outgroup charadriiforms (*Stercorarius skua*, *Larus marinus*) resulted in a single most parsimonious tree (MPT) (L: 7673; CI: 0.49; RI: 0.54; RC: 0.27; Fig. 5). Not surprisingly, *Ptychoramphus tenuis* is recovered as the sister taxon to the extant species *Ptychoramphus aleuticus*. *Ptychoramphus tenuis* could be scored for only 14 of 353 morphological characters. Because *P. tenuis* is an operational equivalent of *P. aleuticus* it was not included in subsequent analyses. Furthermore, the size difference between *P. tenuis* and *P. aleuticus* (Table 2) is within the statistically supported range of size variation for extant alcids estimated by Smith & Clarke (2011). Additionally, the age of the San Diego Fm. has been estimated between 3.6 and 1.8 Ma, and it is, therefore, quite plausible that *P. tenuis* represents the extant species *P. aleuticus*. *Ptychoramphus tenuis* cannot be differentiated from *P. aleuticus* on the basis of morphological characters or measurement data and it is, therefore, considered a junior synonym of *P. aleuticus*.

Inclusion of *Aethia rossmoori* in a phylogenetic analysis with all 23 extant alcids, *Pinguinus impennis* and two outgroup charadriiforms resulted in two MPTs (L: 7674; CI: 0.51; RI: 0.56; RC: 0.29). *Aethia rossmoori* was placed in a polytomy at the base of a monophyletic Alcidae (Fig. 6). The two MPTs placed *A. rossmoori* as the sister taxon to all other Alcidae, or as the sister taxon to *Brachyramphus marmoratus*. Because *A. rossmoori* was not recovered in Aethiini (i.e. the taxon of interest herein), and because the inclusion of this taxon significantly reduced phylogenetic resolution, it was not included in subsequent analyses. Based on these phylogenetic results *A. rossmoori* should be considered Alcidae *incertae sedis*.

Taxon sampling for the final combined phylogenetic analysis included all 23 extant alcids, the recently extinct taxon *Pinguinus impennis*, two outgroup charadriiforms and scorings for two additional auklet fossils (LACM 107031, SDSNH 63195). Although this analysis resulted

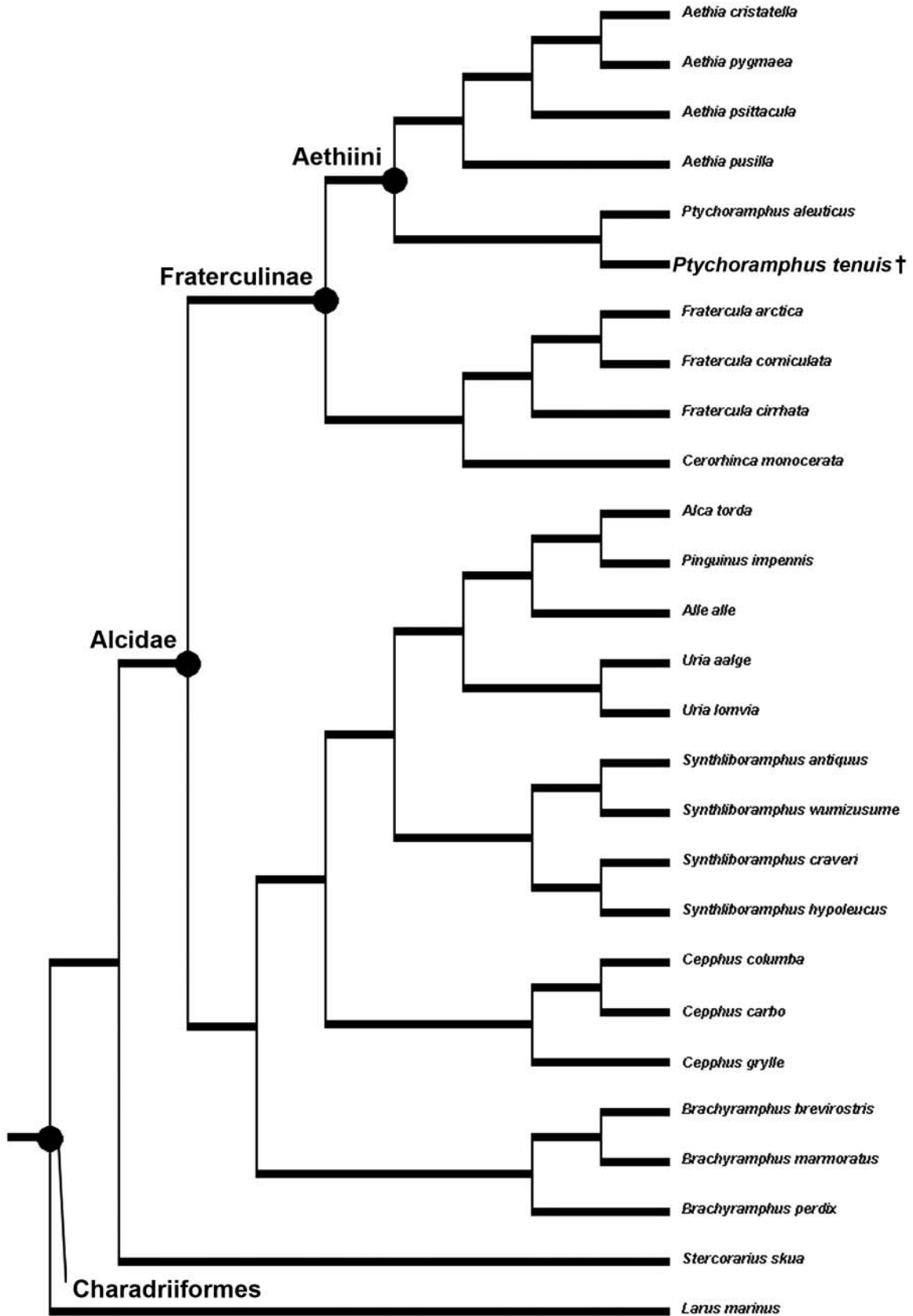


Figure 5. Single MPT indicating the sister-taxon relationship between *Ptychoramphus tenuis* and *P. aleuticus*.

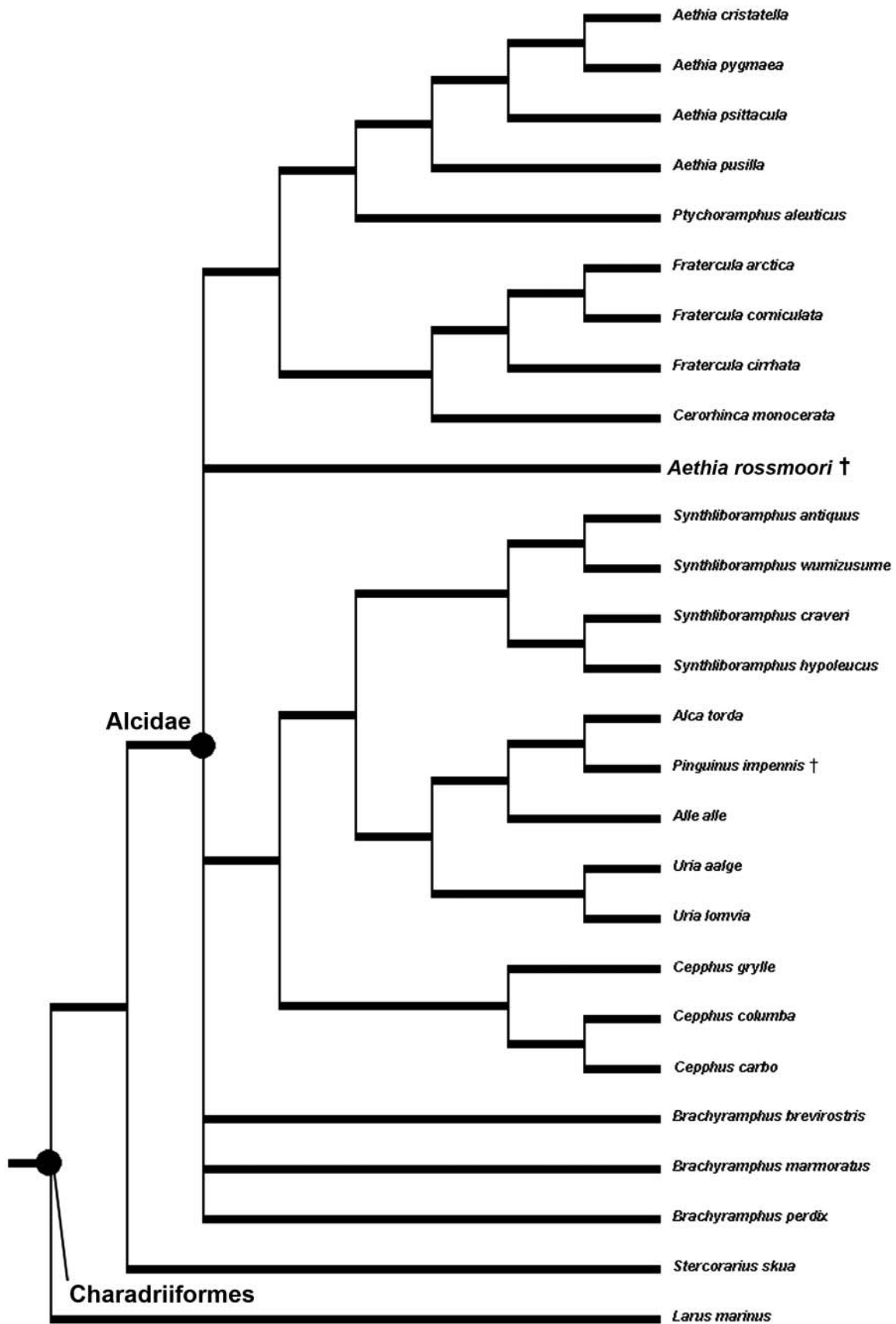


Figure 6. Strict consensus cladogram of two MPTs indicating the unresolved phylogenetic position of *Aethia rossmoori* in Alcidae.

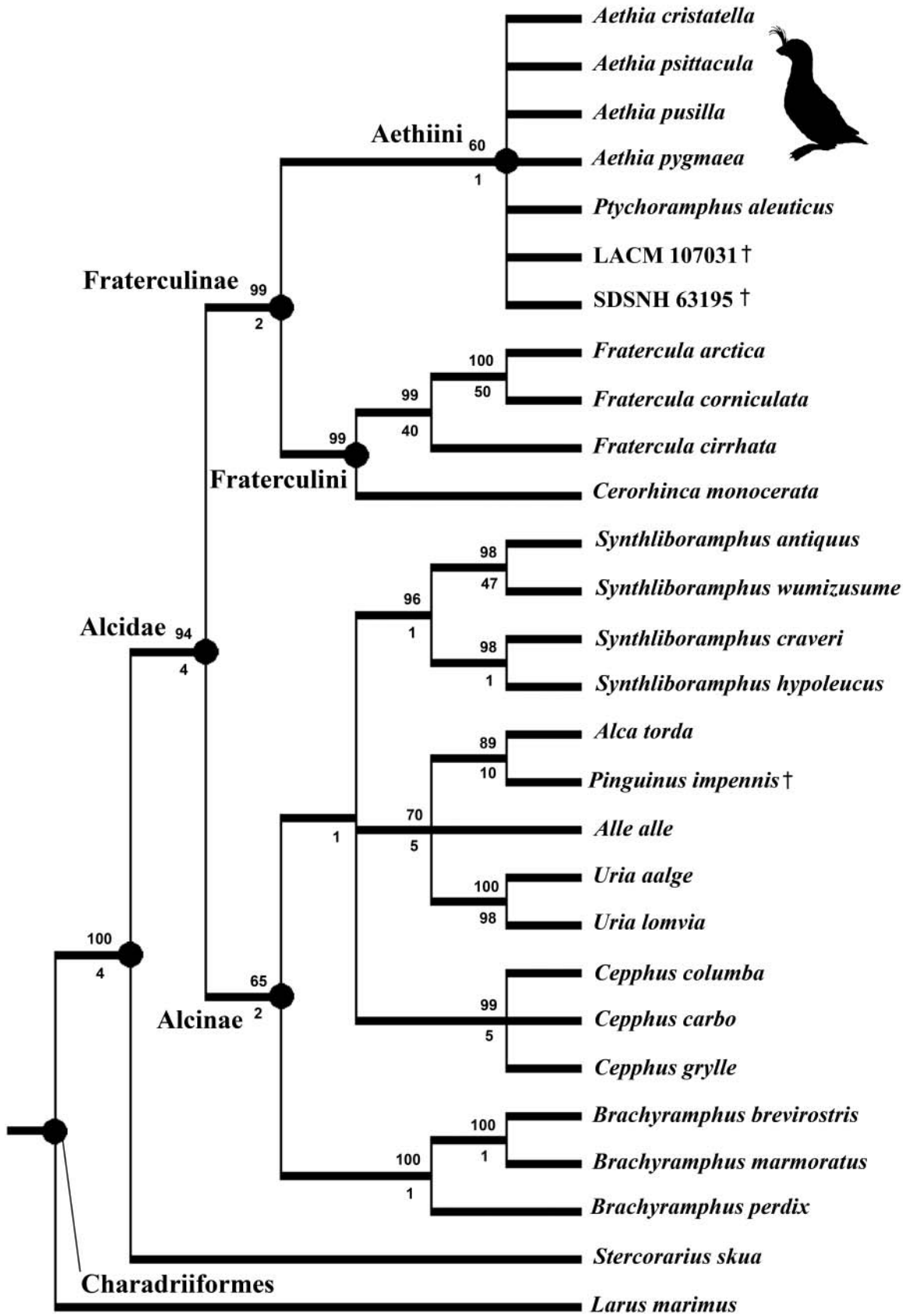


Figure 7. Strict consensus cladogram of 12 MPTs showing the unresolved systematic relationships in Aethiini.

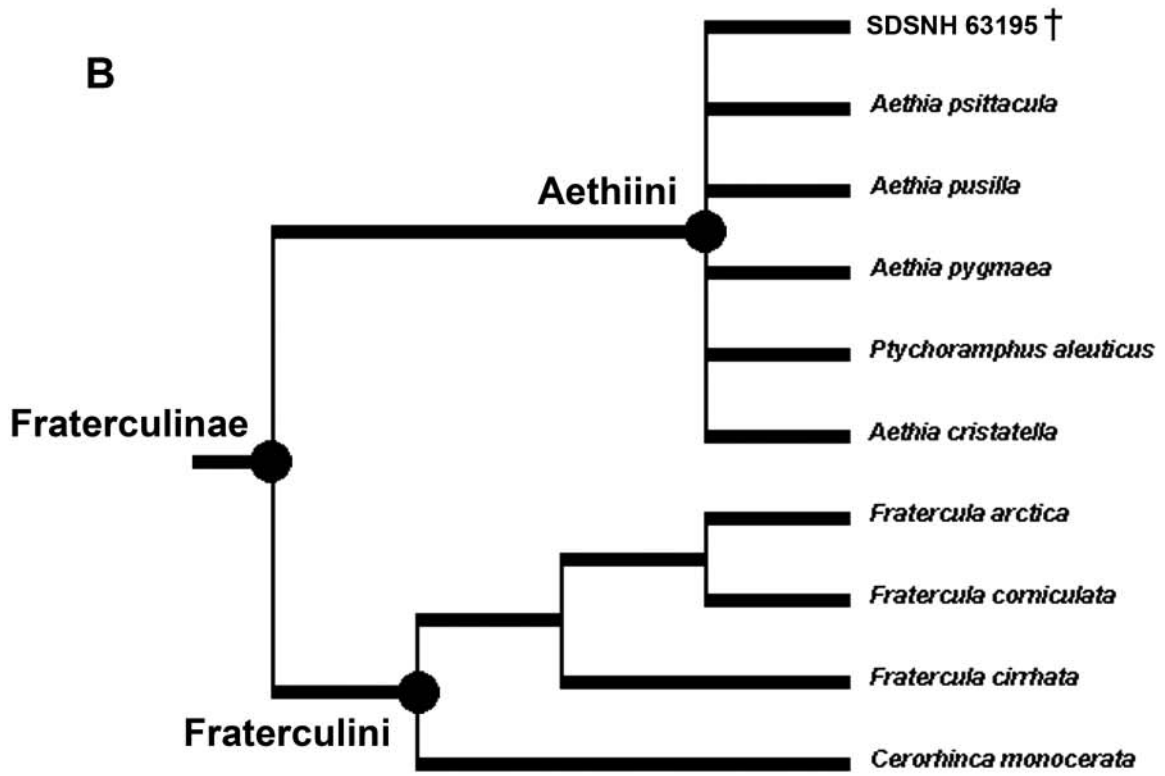
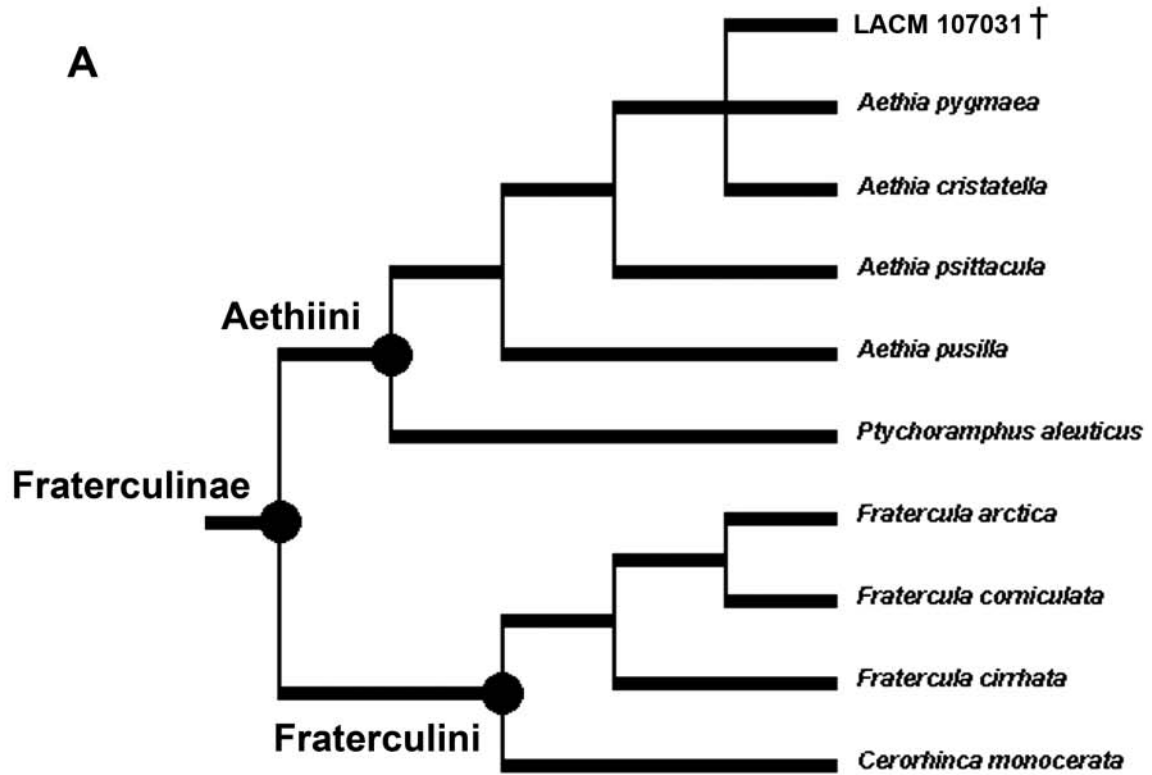


Figure 8. Strict consensus cladograms showing the phylogenetic positions recovered for **A**, LACM 107031 and **B**, SDSNH 63195.

Table 3. Unambiguously optimized apomorphies with a CI = 1.0 supporting clades in the resultant phylogenetic trees. Character numbers from Online Supplementary Material are followed by character state symbols (e.g. 23:0 = character number 23, state 0). Characters followed by ‘*’ are locally optimized apomorphies with a CI < 1.0. Optimizations for Aethiini and *Ptychoramphus* are based on the topology depicted in Fig. 5. Optimizations for *Aethia* are based on the topology depicted in Fig. 8A.

Clade	Character numbers and states that support monophyly
Aethiini	8:1; 11:1; 89:0; 207:1
<i>Aethia</i>	66:1*; 196:0*; 205:0*; 266:1*
<i>Ptychoramphus</i>	224:0*

in a well-resolved strict consensus tree, Aethiini (contents include *Aethia* + *Ptychoramphus*) is unresolved in the strict consensus topology (12 MPTs; L: 7678, CI: 0.52, RI: 0.59, RC: 0.31; Fig. 7). Because previous analyses of extant auklets have resulted in fully resolved topologies (e.g. Smith 2011a, figure 1.25), the two extinct auklet species were iteratively swapped in subsequent analyses to explore the effects of the inclusion or exclusion of each fossil individually. Removal of SDSNH 63195 (newly referred humerus; see below) in a subsequent analysis resulted in the placement of LACM 107031 (distal humerus; Fig. 5) in a polytomy with *Aethia cristatella* and *A. pygmaea*, with *A. psittacula*, *A. pusilla* and *Ptychoramphus aleuticus* placed in successively more basal positions in Aethiini (Fig. 8A; six MPTs; L: 7677; CI: 0.52; RI: 0.59; RC: 0.31). Removal of LACM 107031 in a subsequent analysis resulted in the placement of SDSNH 63195 in an unresolved position in Aethiini (Fig. 8B; three MPTs; L: 7674; CI: 0.50; RI: 0.56; RC: 0.28). Morphological apomorphies that support the monophyly of recovered clades are summarized in Table 3.

Systematic palaeontology

Aves Linnaeus 1758

Charadriiformes Huxley 1867

Pan-Alcidae Smith 2011

Alcidae Leach 1820

Fraterculinae *sensu* Smith 2011

Aethiini Storer 1960

Diagnosis. Aethiini, the clade composed of *Aethia* Merrem 1788 and *Ptychoramphus* von Brandt 1837, is diagnosed based upon the following four apomorphies: maxillopalatine process of the maxilla dorsoventrally flattened rather than concave in ventral view (8:1); ventral margin of the ventral palatine crest extends ventral to the lateral margin of the palatine (11:1); brachial tuberosity of coracoid rounded rather than elongated (89:0); posterior end of dorsal iliac spine blunt rather than pointed (207:1). These characters

could not be evaluated in the extinct taxa described below, which are all known exclusively from humeri. However, the humeri of Aethiini can be differentiated from those of other alcids by the following combination of characters: the distal margin of the humeral head in posterior view is pointed (105:1) in all Aethiini except *Aethia storeri*, rather than more rounded as in many other alcids (e.g. *Cerorhinca minor*); the deltopectoral crest transitions to the humeral shaft abruptly (108:1) rather than smoothly as in many other alcids (e.g. *Brachyramphus*); the m. supracoracoideus scar is shallowly excavated (115:1); the m. supracoracoideus scar does not broaden proximally as in Fraterculini; the secondary pneumotricipital fossa is shallow (130:0) rather than moderately excavated as in Fraterculini; in anterior view the capital groove appears rounded as in *Cerorhinca monocerata* (140:0) rather than a notch or a deep groove as in all other alcids; the dorsal supracondylar process is a small dorsally pointing projection (147:1) as in *Brachyramphus*; the ventral margin of the ventral epicondyle is flared ventrally (rather than straight) as in all Fraterculinae.

Aethia Merrem, 1788

Diagnosis. *Aethia* is differentiated from *Ptychoramphus* based upon the following four locally optimized apomorphies: possession of a lateral sternal fenestra rather than an unenclosed lateral sternal notch (66:1); distal extent of articulation facet for manual digit II:1 level with articulation facet for manual digit III:1 (196:0); post-acetabular dorsal iliac crest broadens (205:0), rather than narrows; nest site a natural crevice rather than a bare rock (266:1). As with the diagnostic characters of Aethiini, these characters could not be evaluated in the extinct taxa described below, which are known only from humeri. There are no autapomorphies of the humerus of *Ptychoramphus aleuticus* that differentiate the humeri of that species from the humeri of *Aethia* species. *Ptychoramphus tenuis* is known only from an isolated tarsometatarsus.

Aethia barnesi sp. nov.
(Figs 4, 9)

Etymology. This species is named after the collector of the holotype specimen and in recognition of the many contributions to the study of the vertebrate palaeontology of California by Lawrence G. Barnes.

Holotype. LACM 107031 is a partial right humerus missing the proximal end. The specimen was collected by L. G. Barnes on 19 March 1975.

Locality and horizon. The holotype specimen was collected from the Late Miocene San Mateo Formation (San Luis Rey River Local Fauna) of Lawrence Canyon, Oceanside, San Diego County, California. The vertebrate assemblages of the San Mateo Formation were discussed by Barnes *et al.* (1981) who designated the lower assemblage

as the San Luis Rey River Local Fauna (SLRRLF), and the upper assemblage as the Lawrence Canyon Local Fauna (LCLF). Alcid fossils, including the holotype humerus (LACM 107031) and those of the flightless alcid taxon Mancallinae, were recovered from the older SLRRLF. Age estimates for the SLRRLF based upon terrestrial mammal and marine bird fossils range from approximately 6.7 to 10.0 Ma (i.e. Late Miocene or Tortonian equivalent; Barnes *et al.* 1981; Domning & Deméré 1984).

Diagnosis. *Aethia barnesi* is differentiated from all other species of Aethiini by the greater width of the scapulotricipital sulcus (151:2) as compared to the humerotricipital sulcus of the distal humerus (Howard 1982). In all other species of Aethiini, the humerotricipital sulcus is wider than the scapulotricipital sulcus. *Aethia barnesi* differs from extant species of *Aethia* in the following characteristics noted by Howard (1982): cross-section of humerus at mid-shaft slightly more rounded; brachial impression with more distinct dorsal and ventral margins than in extant species of auklets; ventral supracondylar tubercle positioned more dorsally. *Aethia barnesi* is also smaller than all other species of Aethiini for which the humerus is known (Table 2).

Description. There are no apomorphies that allow differentiation between *Ptychoramphus* and *Aethia* humeri. However, the ventral projection of the ventral entepicondyle relative to the humeral shaft (150:0), the less proximally extended dorsal supracondylar process (148:0), and the abrupt transition of the deltopectoral crest to the humeral shaft (108:1) support the referral of this specimen to Aethiini (i.e. the clade composed of *Aethia* + *Ptychoramphus*; Fig. 8A). Like *Ptychoramphus aleuticus*, *Aethia psittacula* and *A. pygmaea*, there is a small scar that contacts the ventral supracondylar tubercle (163:1). This scar marks the attachment point of m. pronator sublimis and in *A. barnesi* it is located at the proximal point of the ventral supracondylar tubercle as in *A. pygmaea* (164:0).

Remarks. This specimen (Table 1; Figs 4, 9) was previously referred to *Aethia* by Howard (1982). The placement of LACM 107031 in a polytomy with *A. cristatella* and *A. pygmaea* (Fig. 8A) is supported by the proximal position of the m. pronator sublimis scar adjacent to the ventral supracondylar tubercle of the distal humerus. However, the possibility that this specimen is referable to *A. rossmoori* cannot be ruled out because the humerus of that taxon is not known. A survey of Alcidae ulnae, including the holotype specimen of *Aethia rossmoori*, did not identify any apomorphies that allow isolated ulnae of *Aethia*, *Ptychoramphus*, *Synthliboramphus*, *Brachyramphus* or *Alle* to be differentiated from one another. It is, therefore, unlikely that the true affinities of *Aethia rossmoori* in Alcidae will ever be known, unless a specimen is discovered with multiple asso-



Figure 9. Holotype specimen of *Aethia barnesi* sp. nov. in posterior view, LACM 107031. Anatomical abbreviations: dc: deltopectoral crest; dsp: dorsal supracondylar process; hs: humerotricipital sulcus; ss: scapulotricipital sulcus.

ciated elements, including an ulna that is comparable to the holotype ulna of *Aethia rossmoori*.

Aethia storeri sp. nov.
(Fig. 10)

Etymology. The species epithet *storeri* is in recognition of the many contributions made to ornithology by the late Robert W. Storer (1914–2008).

Holotype. SDSNH 63195 is a complete left humerus collected by R. A. Cerutti on 11 December 1994.

Referred specimens. Distal left humerus (SDSNH 24937; previously referred to *Ptychoramphus tenuis* by Chandler 1990b; Table 3; Fig. 11); proximal right humerus (SDSNH 59027; Table 3; Fig. 11); proximal left humerus (SDSNH 59028; Table 3; Fig. 11). All referred specimens were collected from the Pliocene San Diego Formation in

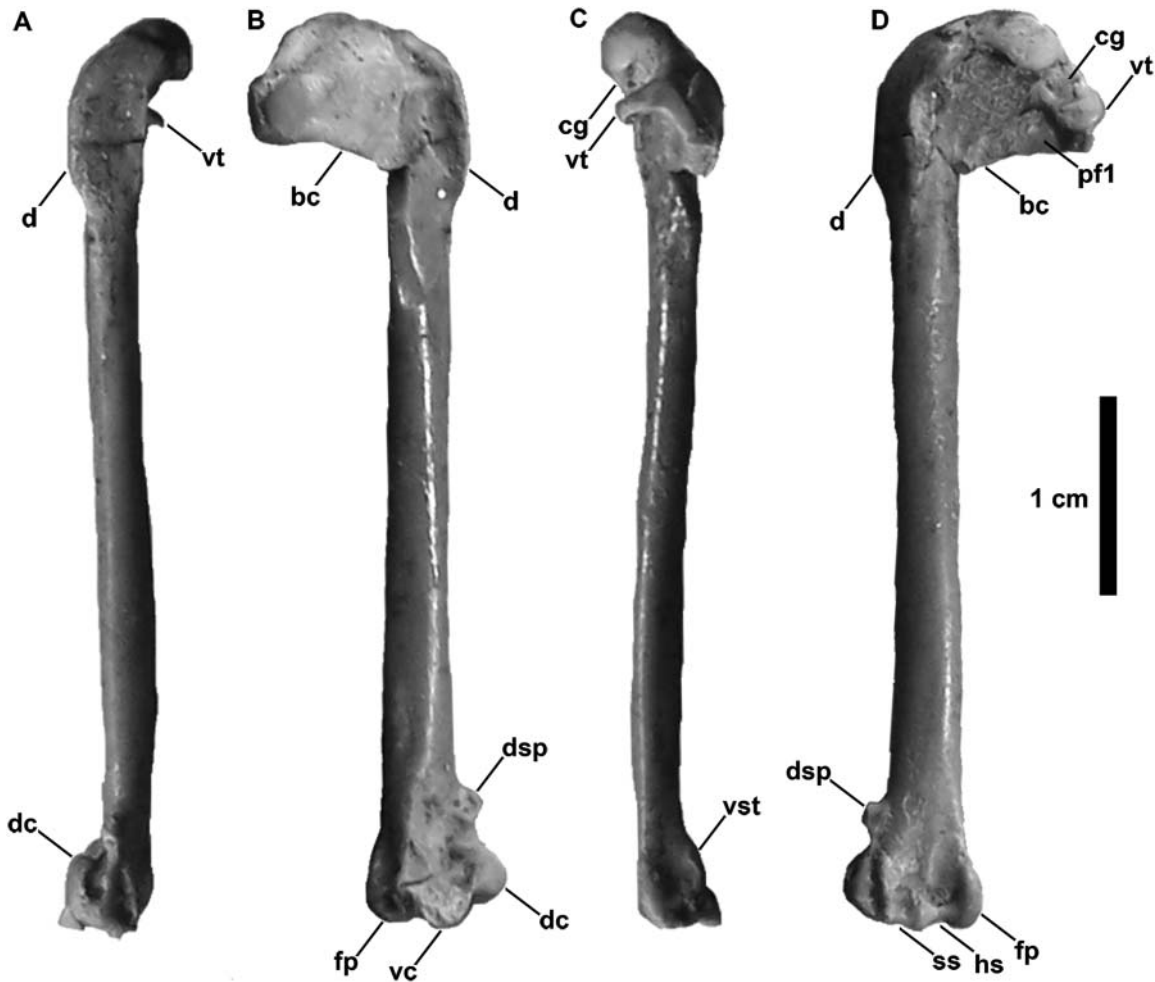


Figure 10. Holotype left humerus of *Aethia storeri* sp. nov. (SDSNH 63195) in **A**, dorsal; **B**, anterior; **C**, ventral; and **D**, posterior views. Anatomical abbreviations: bc: bicipital crest; cg: capital groove; d: deltopectoral crest; dc: dorsal condyle; dsp: dorsal supracondylar process; fp: flexor process; hs: humerotricipital sulcus; pf1: primary pneumotricipital fossa; ss: scapulotricipital sulcus; vc: ventral condyle; vst: ventral supracondylar tubercle; vt: ventral tubercle.

San Diego County, California, USA. There was no basis for referral of SDSNH 24937 to *Ptychoramphus tenuis* by Chandler (1990b) because the holotype specimen of *P. tenuis* (UCMP 45562) is a tarsometatarsus and there are no known associated specimens of *P. tenuis* that would allow for referral of humeri to that species. These referred specimens are operational equivalents of the holotype specimen of *Aethia storeri* (SDSNH 63195).

Locality and horizon. The holotype specimen was collected from Member 4 (*sensu* Wagner *et al.* 2001) of the Pliocene San Diego Formation, San Diego County, California, USA. Latitude, longitude and elevation data are on file at SDSNH (locality 3982). The San Diego Formation predominantly consists of Pliocene and Pleistocene marine sandstones with minor amounts of conglomerates and claystones, which are interpreted as shore-face and

shallow-depth shelf facies deposits (Deméré, 1982 1983; Wagner *et al.* 2001). Based upon microfaunal analysis and correlation with mammalian and molluscan assemblages of known age, the San Diego Formation is estimated to range from 3.6 to 1.8 Ma (i.e. Middle Pliocene to Pleistocene; Piacenzian–Early Calabrian; Wagner *et al.* 2001).

Diagnosis. *Aethia storeri* is differentiated from all other Aethiini by the convexly rounded (rather than pointed) and posteriorly overturned humeral head (105:0). Also, the secondary (i.e. dorsal) pneumotricipital fossa is not divided by a crest beneath the posteriorly overturned humeral head (132:0), and the ventral supracondylar tubercle is triangular (162:0) rather than rounded.

Description. The holotype specimen of *Aethia storeri* (SDSNH 63195) is complete except for a small fragment

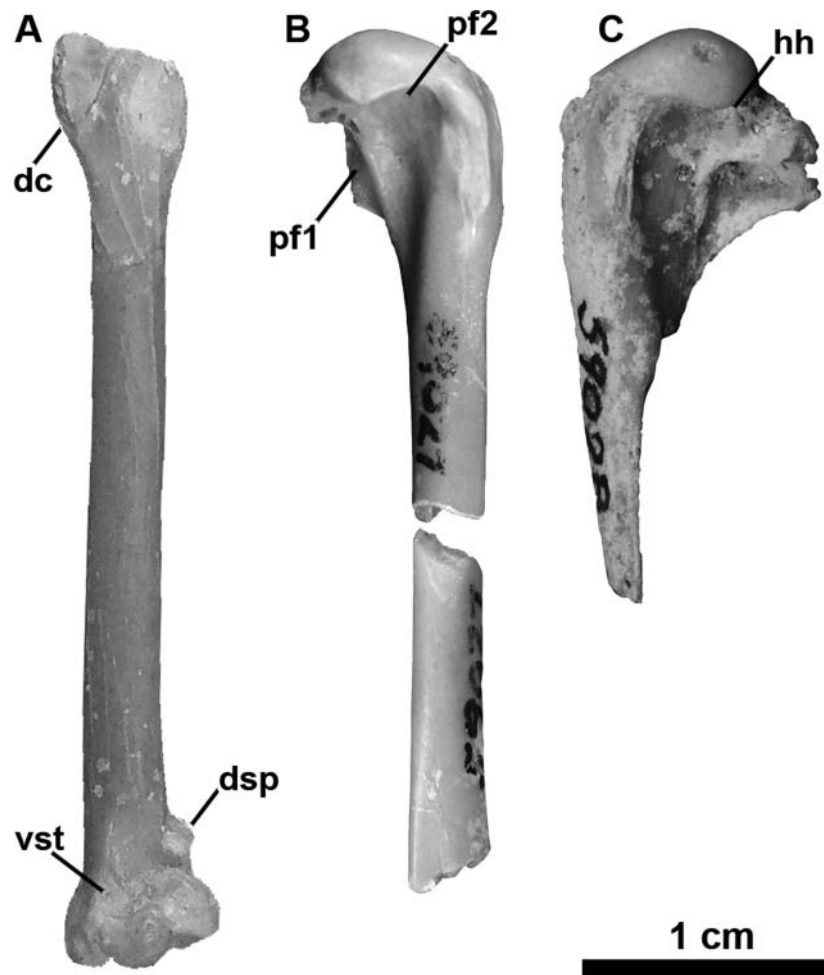


Figure 11. *Aethia storeri* sp. nov. referred humeri. **A**, SDSNH 24937 in anterior view; **B**, SDSNH 59027 in posterior view; **C**, SDSNH 59028 in posterior view. Anatomical abbreviations: (dc) deltopectoral crest; (dsp) dorsal supracondylar process; (hh) humeral head; (pf1) primary pneumotricipital fossa; (pf2) secondary pneumotricipital fossa; (vst) ventral supracondylar tubercle.

of bone missing at the junction of the bicipital crest and the humeral shaft (Fig. 10). As in the extant species *Aethia pusilla*, *A. pygmaea* and *Ptychoramphus aleuticus*, the distal edge of the bicipital crest is nearly perpendicular to the humeral shaft (111:1; Fig. 12). As in *A. pygmaea* the dorsal margin of the primary pneumotricipital fossa (i.e. crus dorsale fossae, Baumel & Witmer 1993) does not extend to the junction of the bicipital crest and the humeral shaft (118:0). The m. subcoracoideus scar is positioned more ventrally along the posteroventral margin of the primary pneumotricipital fossa than in other Aethiini (127:1). Character numbers 132 and 105 (see Diagnosis above) could not be evaluated in the holotype specimen of *Aethia barnesi* because it is missing the proximal end. Within Aethiini only *A. pusilla* and *A. barnesi* are smaller in size (Table 2).

Discussion

The relatively slender proportions of the shaft and the trochlea of the holotype tarsometatarsus of *Ptychoram-*

phus tenuis (UCMP 45662) and all morphological characters scored for UCMP 45662 are consistent with that of the extant species *Ptychoramphus aleuticus*. Based on the phylogenetic results, which place UCMP 45662 as the sister taxon to *P. aleuticus* (Fig. 5), and the lack of significant differences in size between these taxa (Table 2), *P. tenuis* is best considered a *nomen dubium* (Table 4).

A survey of alcid ulnae did not identify any apomorphies that allow isolated ulnae of *Alle*, *Aethia*, *Ptychoramphus*, *Synthliboramphus* or *Brachyramphus* to be differentiated from one another. Because the phylogenetic results place *Aethia rossmoori* in an unresolved position at the base of Alcidae (Fig. 6), this species is best considered as Alcidae *incertae sedis* (Table 4).

Although the systematic positions of *Aethia barnesi* and *A. storeri* are unresolved in the strict consensus topology (Fig. 7), their inclusion in a monophyletic Aethiini does provide definitive evidence that auklets were a part of the Miocene and Pliocene avifauna of the eastern Pacific Ocean basin. Additionally, *A. barnesi* is the earliest fossil record



Figure 12. Comparison of extant auklet left humeri in posterior (A, C, D, E) and anterior (B) views. A, *Aethia pusilla*, NCSM 17734; B, *A. pygmaea*, UMMZ 224883 (specimen mislabelled 224483 in photograph); C, *Ptychoramphus aleuticus*, NCSM 18088; D, *A. cristatella* (NCSM 17746); E, *A. psittacula*, NCSM 14804.

of Fraterculinae (6.7–10.0 Ma; Late Miocene or Tortonian equivalent; Barnes *et al.* 1981; Domning & Deméré 1984) and provides a calibration point (i.e. a minimum age of 6.7 Ma) for the divergence between Aethiini and Fraterculini. The divergence estimates of Baker *et al.* (2007) and Pereira & Baker (2008) dated the divergence between puffins and auklets at >45 Ma (i.e. Eocene or older). However, the results of those analyses have been criticized because of the choice of fossil calibrations and the ages applied to those calibrations (Wijnker & Olson 2009; Mayr

2011). Additionally, Eocene divergence of the puffin and auklet lineages would require the inference of an ~35 Ma long ghost range (Norell 1992) for these taxa based on the fossil record.

Detailed examination of pan-alcid fossils continues to reveal previously undocumented diversity among Miocene and Pliocene remains, with 13 new species recognized since 2007 (Smith *et al.* 2007; Wijnker & Olson 2009; Smith 2011a; Smith & Clarke 2011). *Aethia barnesi* and *A. storeri* are the only extinct auklet species known from the Miocene

Table 4. Summary of taxonomic revision of Aethiini.

Original taxonomic assignment	Reference	Specimen	Revised taxonomic assignment
<i>Ptychoramphus tenuis</i>	Miller & Bowman 1958	UCMP 45562	<i>nomen dubium</i>
<i>Aethia rossmoori</i>	Howard 1968	LACM 18948	Alcidae <i>incertae sedis</i>
<i>Aethia</i> sp.	Howard 1978	LACM 37686	Location uncertain
<i>Aethia</i> sp.	Howard 1982	LACM 107031	<i>Aethia barnesi</i>

and the Pliocene. However, sparse and often fragmentary remains of auklets reported in the last century (Table 1), along with the auklet fossils described herein, suggest that independent lineages of small alcids have been a part of the Pacific Ocean avifauna since at least the Late Miocene.

Considered in combination, the small size of extant auklets and the basal position hypothesized for small Alcinae taxa *Brachyramphus* and *Synthliboramphus* (Thomas *et al.* 2004; Pereira & Baker 2008; Smith 2011a, b) suggests that small body size may be plesiomorphic for Pan-Alcidae. However, the earliest known pan-alcid fossil is comparable in size to extant specimens of *Alca torda*, one of the largest extant alcids (Chandler & Parmley 2002), and the stem alcid lineage Mancallinae displays a range of sizes from quite small (e.g. *Mancalla vegrandis*) to quite large (e.g. *Miomancalla howardae*; Smith 2011a).

Regardless of the ambiguous optimization of ancestral body size for Pan-Alcidae, body size in extant alcids has been correlated with dive depth and feeding ecology (Piat & Nettleship 1985; Prince & Harris 1988; Watanuki & Burger 1999), and smaller body size in extant alcids is primarily associated with planktivory (Bradstreet & Brown 1985). Although planktivory is optimized as plesiomorphic for Aethiini based on the ecology of extant auklets, it would be premature to ascribe ecological attributes such as planktivory to these extinct species of auklets in the absence of associated skeletal remains that preserve characteristics associated with particular feeding strategies (i.e. bill shape; Bédard 1969). However, the co-occurrence of multiple species of small alcids with multiple species of larger alcids such as the flightless Mancallinae suggests that niche partitioning by size among alcids (Ainley 1990) may have been in place since the Miocene.

Although the Early to Middle Miocene was a time of relative warmth, little or no glacial activity, and relatively unstratified oceans, it was immediately followed by a cooling trend that led to the cooler temperatures, prevalent Northern Hemisphere glaciation, and temperature stratified oceans of today (Schoell *et al.* 1994; Westerhold *et al.* 2005; You *et al.* 2009). The Middle Miocene Climatic Optimum (MMCO) and the cooling trend that followed have been documented using a variety of methods including oxygen and carbon isotope stratigraphy, palynology and magnetostratigraphy (Schoell *et al.* 1994; Krijgsman *et al.* 1994; Westerhold *et al.* 2005; You *et al.* 2009). The age range of fossils described here (~10–3 Ma) coincides with the transition from the warmer climate of the Late Miocene to the cooler climate at the end of the Pliocene. This cooling trend was punctuated by several episodes of potentially intense Northern Hemisphere glaciation that would have dramatically lowered sea level. One such episode at 13.8–10.4 Ma would have resulted in an ~40 m drop in global sea level (Westerhold *et al.* 2005). The severity of such an event with respect to the reproductive success and ultimately the survival of pelagic birds such as auklets may have been

significant given the tendency of extant auklets for nest site fidelity (Ainley 1990). However, the sparseness of the auklet fossil record prevents detailed evaluation of these factors on auklet palaeodiversity.

Sea surface temperatures for the MMCO (~17–11 Ma) are estimated at ~3°C higher than today, near the levels predicted to result from global warming in the next century (You *et al.* 2009). Because sea surface temperature has been correlated with reproductive success in alcids, with warmer temperatures leading to decreased reproduction in planktivorous alcids (Kitaysky & Golubova 2000), the post-MMCO cooling trend may offer an explanation for the faunal turnover among Miocene and Pliocene pan-alcids. The fossil record provides evidence that pan-alcids were successful, potentially dominant seabirds throughout the Late Miocene and Early Pliocene (Wijnker & Olson 2009; Smith 2011a; Smith & Clarke 2011). However, there are very few examples of individual pan-alcid species that span this time period (i.e. extinct species that occur in both Miocene and Pliocene deposits). Thus, it would appear that the Miocene–Pliocene boundary represents a faunal turnover for pan-alcids similar to the one documented for the Pliocene–Pleistocene climatic transition (Smith 2011b).

The two new species of *Aethia* described herein add to our knowledge of Miocene and Pliocene auklet diversity. These new discoveries, along with the phylogenetic evaluation of previously referred potential fossil auklets, give a more detailed picture of the evolution of these clades and also provide a phylogenetically analysed calibration point for molecular-based divergence time estimation. Given the small quantity of morphological characters that separate *Aethia* and *Ptychoramphus* and the dubious status of the only fossil referred to *Ptychoramphus* (i.e. *P. tenuis*), the monotypic taxon *Ptychoramphus* should be considered for synonymy with *Aethia* by the American Ornithologists' Union. Furthermore, because *P. tenuis* is an operational equivalent of *P. aleuticus*, the possibility that *P. tenuis* represents a Pliocene occurrence of this extant taxon should be considered.

There are few differences in range of size (Table 2) or morphological characteristics between the newly described extinct auklets *Aethia barnesi* and *A. storeri* and extant auklets, and known auklet fossil localities are within the geographical range of extant auklets (Fig. 1). These data suggest that the ecology of auklets may have changed little since the Late Miocene and that the auklet avifauna of the past 10 Ma may have resembled that of their extant congeners. One unanswered question is why this clade has not colonized the Atlantic Ocean basin, where only a single small planktivorous alcid, *Alle alle*, is endemic today. However, the feeding ecology of other small extinct Atlantic Ocean Alcini (e.g. *Miocepphus mergulellus* and *Alca minor*) are not known. Regardless of the feeding ecology of those other small Atlantic Ocean alcids, current data suggest that the small, primarily planktivorous, Atlantic

Ocean alcid niche has been occupied solely by *Alle alle* since at least the late Pliocene.

The restriction of auklets to the Pacific Ocean basin and the relatively low degree of morphological and size changes in auklets through time might be viewed as evidence of ecological stability and may be a reflection of a relatively limited set of environmental tolerances in this clade. Although not considered endangered by the International Union for Conservation of Nature (IUCN) because of the relatively large geographical ranges and relatively large populations of mature individuals, population sizes of extant auklets are decreasing (IUCN 2010). Links between large-scale climatic factors that affect auklet prey species (i.e. primary marine productivity), adult auklet survival, and reproductive rates have been documented (Springer *et al.* 1993; Jones *et al.* 2002). Although most records involve short-term trends (e.g. responses to decadal cycles of the California Current System; Yen *et al.* 2004), population-level changes associated with large-scale and more long-lasting environmental events have also been documented. For example, the colonization of the Farallon Islands by *Ptychoramphus aleuticus* between 1870 and 1900 was proposed to be directly related to the end of a prolonged episode of tropical warm water intrusion into the North Pacific (Springer *et al.* 1993), and today *Ptychoramphus aleuticus* is one of the most abundant species breeding on the Farallon Islands (Ainley 1990). It is not known if the scale of population decline experienced by other alcids in response to climatic changes is similar to that of auklets. However, given the ability of *Ptychoramphus* to track suitable prey and environmental conditions, it is even more surprising that fossil records of Aethiini are relatively rare and restricted to the eastern Pacific Ocean basin. Furthermore, based on the limited fossil data currently available, it is unclear how the distribution of auklets may have changed through time and when auklets may have achieved the widespread Pacific distribution of extant auklets.

Conclusions

Although Miocene pan-alcid diversity was once considered insignificant (Brodkorb 1967; Olson 1985) in comparison with much better known Pliocene pan-alcid faunas (Olson & Rasmussen 2001; Chandler 1990b), a more complete picture of Miocene pan-alcid diversity is emerging from recent re-examination of pan-alcid fossil remains (Wijnker & Olson 2009; Smith 2011a, b). The new auklet species described herein provide additional evidence that the diversity of Miocene and Pliocene Pan-Alcidae were both greater than previously thought. The morphological similarity of extinct and extant auklets suggests that Miocene and Pliocene pan-alcid faunas were composed of many species that would appear familiar today (e.g. small auklets and larger auks) and species that have no

extant correlates (e.g. flightless Mancallinae). This study confirmed that all three of the major pan-alcid clades (i.e. Mancallinae, Fraterculinae and Alcinae) were present in the Miocene. However, even though the Neogene pan-alcid fossil record is by far the most extensive among Charadriiformes, previous divergence estimates (Baker *et al.* 2007; Pereira & Baker 2008) and a single Eocene fossil record (Chandler & Parmley 2002) suggest that the early (i.e. Palaeogene) fossil record of Pan-Alcidae is still significantly incomplete. Eocene and Oligocene pan-alcid fossils are needed to further our understanding of the diversity represented by Neogene Pan-Alcidae.

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Supplementary material

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References

- Ainley, D. G. 1990. Farallon seabirds: patterns at the community level. Pp. 349–380 in D. G. Ainley & R. J. Boekelheide (eds) *Seabirds of the Farallon Islands: ecology, dynamics, and structure of an upwelling-system community*. Stanford University Press, Stanford.
- American Ornithologists' Union. 1998. *Check-list of North American Birds: the species of birds of North America from the Arctic through Panama, including the West Indies and Hawaiian Islands*. 7th edition. American Ornithologists' Union, Washington, 829 pp.
- American Ornithologists' Union. 2008. North American check-list committee proposals 2008-A-06. Adopt a new English name for *Cerorhinca monocerata* (Charadriiformes, Alcidae). [updated at http://www.aou.org/committees/nacc/proposals/2008_A_votes_web.php#2008-A-6]; Last accessed 10/31/2012.

- Baker, A. J., Pereira, S. L. & Paton, T. A.** 2007. Phylogenetic relationships and divergence times of Charadriiformes genera: multigene evidence for the Cretaceous origin of 14 clades of shorebirds. *Biology Letters*, **3**, 205–209.
- Barnes, L. G., Howard, H., Hutchison, J. H. & Welton, B. J.** 1981. The vertebrate fossils of the marine Cenozoic San Mateo Formation at Oceanside, California. Pp. 53–70 in P. L. Abbott & S. O'Dunn (eds) *Geologic Investigations of the Coastal Plain*. San Diego Association of Geologists, San Diego County.
- Baumel, J. & Witmer, L.** 1993. Osteologica. Pp. 45–132 in J. J. Baumel, A. S. King, J. E. Breazile, H. E. Evans & J. C. Vanden Berge (eds) *Handbook of Avian Anatomy, nomina anatomica avium*. 2nd edition. Publications of the Nuttall Ornithology Club, **23**.
- Bédard, J.** 1969. Adaptive radiation in the Alcidae. *Ibis*, **111**, 189–198.
- Bédard, J.** 1985. Evolution and characteristics of the Atlantic Alcidae. Pp. 1–50 in D. N. Nettleship & T. R. Birkhead (eds) *The Atlantic Alcidae: the evolution, distribution, and biology of the auks inhabiting the Atlantic Ocean and adjacent water areas*. Academic Press, London.
- Bonaparte, C. L.** 1831. *Saggio di una distribuzione metodica degli animali vertebrati*. Presso Antonio Boulzaler, Rome, 144 pp.
- Bradstreet, M. S. W. & Brown, R. G. B.** 1985. Feeding ecology of the Atlantic Alcidae. Pp. 263–318 in D. N. Nettleship & T. R. Birkhead (eds) *The Atlantic Alcidae: the evolution, distribution, and biology of the auks inhabiting the Atlantic Ocean and adjacent water areas*. Academic Press, London.
- Brandt, J. F., von.** 1837. Rapport sur une monographie de la famille des Alcades. *Bulletin Scientifique, l'Académie Impériale des Sciences de Saint Pétersbourg*, **2**, 344–349.
- Brisson, M. J.** 1760. *Ornithologie ou méthode contenant la division des oiseaux en ordres, sections, genres, espèces & leurs variétés*. Volume I. Jean-Baptiste Bauche, Paris, 256 pp.
- Brodkorb, P.** 1967. Catalogue of fossil birds, Part 3 (Ralliformes, Ichthyornithiformes, Charadriiformes). *Bulletin of the Florida State Museum, Biological Sciences*, **11**, 99–220.
- Cantino, P. D. & de Queiroz, K.** 2010. *International Code of Phylogenetic Nomenclature*. v4c. [updated at <http://www.ohio.edu/phylocode/>]; Last accessed 10/31/2012.
- Chandler, R. M.** 1990a. *Phylogenetic analysis of the alcids*. Unpublished PhD thesis, University of Kansas, Lawrence, 133 pp.
- Chandler, R. M.** 1990b. Fossil birds of the San Diego Formation, Late Pliocene, Blencoe, San Diego County California. *Ornithological Monographs*, **44**, 73–161.
- Chandler, R. M. & Parmley, D.** 2002. The earliest North American record of an auk (Aves, Alcidae) from the Late Eocene of central Georgia. *Oriole*, **68**, 7–9.
- Chapman, W. L.** 1965. Appearance of ossification centers and epiphyseal closures as determined by radiographic techniques. *Journal of the American Veterinary Medical Association*, **147**, 138–141.
- Chu, P. C.** 1995. Phylogenetic reanalysis of Strauch's data set for the Charadriiformes. *Condor*, **97**, 174–196.
- Chu, P. C.** 1998. A phylogeny of the gulls (Aves: Larinae) inferred from osteological and integumentary characters. *Cladistics*, **14**, 1–53.
- Clark, G. A. Jr** 1993. Termini situm et directionum partium corporis indicantes. Pp. 1–5 in J. J. Baumel, A. S. King, J. E. Breazile, H. E. Evans & J. C. Vanden Berge (eds) *Handbook of Avian Anatomy: nomina anatomica avium*. 2nd edition. Publications of the Nuttall Ornithological Club, **23**.
- Clarke, J. A., Tambussi, C. P., Noriega, J. I., Erickson, G. M. & Ketchum, R.** 2005. Definitive fossil evidence for the extant avian radiation in the Cretaceous. *Nature*, **433**, 305–308.
- Coues, E.** 1868. A monograph of the Alcidae. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **13**, 215–257.
- Dayrat, B., Cantino, P. D., Clarke, J. A. & de Queiroz, K.** 2008. Species names in the *Phylocode*: the approach adopted by the International Society for Phylogenetic Nomenclature. *Systematic Biology*, **57**, 507–514.
- del Hoyo, J., Elliot, A. & Sargatal, J.** (eds). 1996. *Handbook of the Birds of the World. Volume 3. Hoatzins to Auks*. Lynx Edicions, Barcelona, 821 pp.
- Deméré, T. A.** 1982. Review of the lithostratigraphy, biostratigraphy, and age of the San Diego Formation. *Geologic Studies in San Diego*, **1982**, 127–134.
- Deméré, T. A.** 1983. The Neogene San Diego basin: a review of the marine Pliocene San Diego Formation. Pp. 187–195 in D. K. Larue & R. J. Steel (eds) *Cenozoic Marine Sedimentation, Pacific Margin U.S.A.* Society of Economic Paleontologists and Mineralogists.
- De Santo, T. L. & K. Nelson.** 1995. Reproductive ecology of the auks (Family Alcidae) with emphasis on the Marbled Murrelet. Pp. 33–47 in *USDA Forest Service General Technical Report*, PSW-152.
- Domning, D. P. & T. A. Deméré.** 1984. New material of *Hydrodamalis cuetiae* (Mammalia, Dugonidae) from the Miocene and Pliocene of San Diego County, California. *Transactions of the San Diego Society of Natural History*, **20**, 169–188.
- Dove, C. J.** 2000. A descriptive and phylogenetic analysis of plumulaceous feather characters in Charadriiformes. *Ornithological Monographs*, **51**, 1–163.
- Driesch, A. von den.** 1976. A guide to the measurement of animal bones from archaeological sites. *Peabody Museum Bulletin*, **1**, 103–129.
- Ericson, P. G. P., Envall, I., Irestedt, M. & Norman, J. A.** 2003. Inter-familial relationships of the shorebirds (Aves: Charadriiformes) based on nuclear DNA sequence data. *BMC Evolutionary Biology*, **3**, 3–16.
- Fain, M. G. & Houde, P.** 2007. Multilocus perspectives on the monophyly and phylogeny of the order Charadriiformes (Aves). *BMC Evolutionary Biology*, **7**, 35.
- Friesen, V., Baker, A. & Piatt, J.** 1996. Phylogenetic relationships within the Alcidae (Charadriiformes: Aves) inferred from total molecular evidence. *Molecular Biology and Evolution*, **13**, 359–367.
- Gmelin, J. F.** 1789. *Systema Naturae, per regna tria natura, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. 13th edition. Tome 1, pars II, pp. 501–1032. Lyon.
- Gradstein, F. M., Ogg, J. G. & Smith, A. G.** 2004. *A Geologic Timescale 2004*. Cambridge University Press, Cambridge, 589 pp.
- Howard, H.** 1929. The avifauna of Emeryville shellmound. *University of California Publications in Zoology*, **32**, 301–394.
- Howard, H.** 1949. New avian records for the Pliocene of California. *Carnegie Institute of Washington Publications, Contributions to Paleontology*, **584**, 177–199.
- Howard, H.** 1968. Tertiary birds from Laguna Hills, Orange County, California. *Los Angeles County Museum Contributions to Science*, **142**, 1–21.
- Howard, H.** 1978. Late Miocene marine birds from Orange County, California. *Natural History Museum of Los Angeles County Contributions to Science*, **290**, 1–26.

- Howard, H.** 1982. Fossil birds from the Tertiary marine beds at Oceanside, San Diego County, California, with descriptions of two new species of the genera *Uria* and *Cephus* (Aves: Alcidae). *Natural History Museum of Los Angeles County Contributions to Science*, **341**, 1–15.
- Hudson, G. E., Hoff, K. M., Vanden-Berge, J. & Trivette, E. C.** 1969. A numerical study of the wing and leg muscles of the Lari and Alcae. *Ibis*, **111**, 459–524.
- Huxley, T.** 1867. On the classification of birds: and on the taxonomic value of the modifications of certain of the cranial bones observable in the class. *Proceedings of the Zoological Society of London*, **1867**, 415–472.
- International Union for Conservation of Nature.** 2010. *Red list of threatened species v2101.4*. [updated at www.iucnredlist.org]; Last accessed 10/31/2012.
- Jones, I. L., Hunter, F. M. & Robertson, G. J.** 2002. Annual adult survival of Least Auklets (Aves, Alcidae) varies with large-scale climatic conditions of the North Pacific Ocean. *Oecologia*, **133**, 38–44.
- Kearney, M.** 2002. Fragmentary taxa, missing data, and ambiguity, mistaken assumptions and conclusions. *Systematic Biology*, **51**, 369–381.
- Kerr, K. C. R., Stoeckle, M. Y., Dove, C. J., Weigt, L. A., Francis, C. M. & Hebert, P. D. N.** 2007. Comprehensive DNA barcode coverage of North American birds. *Molecular Ecology Notes*, **7**, 535–543.
- Kitaysky, A. S. & Golubova, E. G.** 2000. Climate change causes contrasting trends in reproductive performance of planktivorous and piscivorous alcids. *Journal of Animal Ecology*, **69**, 248–262.
- Krijgsman, W., Langereis, C. G., Daams, R. & van der Meulen, A. J.** 1994. Magnetostratigraphic dating of the Middle Miocene climate change in the continental deposits of the aragonian type area in the Calatayud-Teruel basin (Central Spain). *Earth and Planetary Science Letters*, **128**, 513–526.
- Leach W. E.** 1820. Eleventh Room. Pp. 65–68 in *Synopsis of the Contents of the British Museum*, 17th edition. Richard & Arthur Taylor, London.
- Liebers, D., de Knijff, P. & Helbig, A. J.** 2004. The herring gull complex is not a ring species. *Proceedings Biological Sciences*, **271**, 893–901.
- Linnaeus, C.** 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Editio decima, reformata. Laurentii Salvii, Holmiae, 824 pp.
- Maddison D. R. & Maddison, W. P.** 2005. *MacClade v4.08*. Sinauer Associates, Sunderland, Massachusetts.
- Mayr, G.** 2011. The phylogeny of charadriiform birds (shorebirds and allies) – reassessing the conflict between morphology and molecules. *Zoological Journal of the Linnean Society*, **161**, 916–934.
- Merrem, B.** 1788. Versuch eines Grundrisses zur allgemeinen Geschichte und natürlichen Eintheilung der Vogel. *Tentamen Naturalis Systematis Avium*, **1**, 7, 13, 20.
- Miller, L.** 1956. A collection of bird remains from the Pliocene of San Diego California. *Proceedings of the California Academy of Sciences*, **28**, 615–621.
- Miller, L. & Bowman, R. I.** 1958. Further bird remains from the San Diego Pliocene. *Los Angeles County Museum Contributions in Science*, **20**, 4–15.
- Moum, T., Johansen, S., Erikstad, K. E. & Piatt, J. F.** 1994. Phylogeny and evolution of the auks (subfamily Alcinae) based on mitochondrial DNA sequences. *Proceedings of the National Academy of Sciences*, **91**, 7912–7916.
- Moum, T., Àrnason, U. & Àrnason, E.** 2002. Mitochondrial DNA sequence evolution and phylogeny of the Atlantic Alcidae, including the extinct Great Auk (*Pinguinus impennis*). *Molecular Biology and Evolution*, **19**, 1434–1439.
- Nixon, K. C. & Wheeler, Q. D.** 1992. Extinction and the origin of species. Pp. 119–143 in M. J. Novacek & Q. D. Wheeler (eds) *Extinction and Phylogeny*. Columbia University Press, New York.
- Norell, M. A.** 1992. The effect of phylogeny on temporal diversity and evolutionary tempo. Pp. 89–118 in M. J. Novacek & Q. D. Wheeler (eds) *Extinction and Phylogeny*. Columbia University Press, New York.
- Ogg, J. G., Ogg, G. & Gradstein, F. M.** 2008. *The Concise Geologic Timescale*. Cambridge University Press, Cambridge, 184 pp.
- Olson, S. L.** 1985. The fossil record of birds. Pp. 79–252 in D. S. Farmer & A. King (eds) *Avian Biology. Volume 8*. Academic Press. Orlando, Florida.
- Olson, S. L. & Rasmussen, P.** 2001. Miocene and Pliocene Birds from the Lee Creek Mine, North Carolina. *Smithsonian Contributions to Paleobiology*, **90**, 233–365.
- Pallas, P. S.** 1769. *Spicilegium zoologicum: quibus novae imprimis et obscurae animalium species iconibus, descriptionibus atque commentariis illustrantur*. Berolini, Lange.
- Pallas, P. S.** 1811. *Zoographia rosso-asiatica, sistens omnium animalium in extenso Iperio rossico, et adjacentibus maribus observatorum recensitionem, domicilia, mores et descriptiones, anatomen atque icons plurimorum*. In officina Caes, Academiae Scientiarum Impress, Petropoli.
- Paton, T. A. & Baker, A. J.** 2006. Sequences from 14 mitochondrial genes provide a well-supported phylogeny of the charadriiform birds congruent with the nuclear RAG-1 tree. *Molecular Phylogenetics and Evolution*, **39**, 657–667.
- Paton, T. A., Baker, A. J., Groth, J. G. & Barrowclough, G. F.** 2003. RAG-1 sequences resolve phylogenetic relationships within charadriiform birds. *Molecular Phylogenetics and Evolution*, **29**, 268–278.
- Pereira, S. L. & Baker, A. J.** 2008. DNA evidence for a Paleocene origin of the Alcidae (Aves: Charadriiformes) in the Pacific and multiple dispersals across northern oceans. *Molecular Phylogenetics and Evolution*, **46**, 430–455.
- Piatt, J. F. & Nettleship, D. N.** 1985. Diving depth of four alcids. *Auk*, **102**, 293–297.
- Pontoppidan, E.** 1763. *Den Danske atlas eller Konge-Riget Dannemark, med dets naturlige egenskaber, elementer, indbyggere, værter, dyr og andre afføddinger; dets gamle tildragelser og nærværende omstændigheder i alle provintzer, stæder, kirker, slotte og herre-gaarde. Forestillet ved en udførlig lands-beskrivelse, saa og oplyst med dertil forfærdigede land-kort over enhver provintz, samt ziret med stædernes prospecter, grund- ridser, og andre merkverdige kaabberstykker*. Tomus I (pp. 1–6, 1–XL [= 1–40], [1–4], 1–723, Tab. I–XXX [= 1–30]), Godiche, Kiøbenhavn.
- Prince, P. A. & Harris, M. P.** 1988. Food and feeding ecology of breeding Atlantic alcids and penguins. Pp. 1195–1204 in *Proceedings of the 19th International Ornithological Congress*. University of Ottawa Press, Ottawa, Canada.
- Rambaut, A.** 2002. *Se-AI v2.0a11*. [updated at http://tree.bio.ed.ac.uk/software/seal]; Last accessed 10/31/2012.
- Schoell, M., Schouten, S., Sinninghe Damste, J. S., de Leeuw, J. W. & Summons, R. E.** 1994. A molecular organic carbon isotope record of Miocene climate changes. *Science*, **263**, 1122–1124.

- Sibley C. G. & Ahlquist, J. E.** 1990. *Phylogeny and Classification of Birds: a study in molecular evolution*. Yale University Press, New Haven, 976 pp.
- Smith, N. A.** 2011a. Taxonomic revision and phylogenetic analysis of the flightless Mancallinae (Aves, Pan-Alcidae). *Zookeys*, **91**, 1–116.
- Smith, N. A.** 2011b. *Systematics and evolution of extinct and extant Pan-Alcidae (Aves, Charadriiformes): combined phylogenetic analyses, divergence estimation, and paleoclimatic interactions*. Unpublished PhD thesis, The University of Texas at Austin. 748pp.
- Smith, N. A. & Clarke, J. A.** 2011. An alphataxonomic revision of extinct and extant razorbills (Aves, Alcidae): a combined morphometric and phylogenetic approach. *Ornithological Monographs*, **72**, 1–61.
- Smith, N. A., Olson, S. L. & Clarke, J. A.** 2007. First Atlantic record of the puffin *Cerorhinca* (Aves, Alcidae) from the Pliocene of North Carolina. *Journal of Vertebrate Paleontology*, **27**, 1039–1042.
- Springer, A. M., Kondratyev, A. Y., Ogi, H., Shibaev, Y. V. & van Vliet, G. B.** 1993. Status, ecology, and conservation of *Synthliboramphus* murrelets and auklets. Pp. 187–201 in K. Vermeer, K. T. Briggs, K. H. Morgan & D. Siegel-Causey (eds) *The Status, Ecology, and Conservation of Marine Birds of the North Pacific*. Canadian Wildlife Service, ***.
- Storer, R. W.** 1945. Structural modifications in the hind limb in the Alcidae. *Ibis*, **87**, 433–456.
- Storer, R. W.** 1960. Evolution in the diving birds. Pp. 694–707 in G. Bergman, K. O. Donner & L. v. Haartman (eds.) *Proceedings of the Twelfth International Ornithological Congress*. Tilgmannin Kirjapaino, Helsinki.
- Strauch, J. G.** 1978. The phylogeny of the Charadriiformes (Aves): a new estimate using the method of character compatibility analysis. *Transactions of the Zoological Society of London*, **34**, 263–345.
- Strauch, J. G.** 1985. The phylogeny of the Alcidae. *Auk*, **102**, 520–539.
- Swofford, D. L.** 2002. *PAUP* Phylogenetic analysis using parsimony (*and other methods)*. Version 4.0, Sinauer Associates, Sunderland.
- Thomas, G., Wills, M. A. & Szekely, T.** 2004. Phylogeny of shorebirds, gulls and alcids (Aves: Charadrii) from the cytochrome-*b* gene, parsimony, Bayesian inference, minimum evolution and quartet puzzling. *Molecular Phylogenetics and Evolution*, **30**, 516–526.
- Thompson, J. D., Gibson, T. J., Plewniak, F., Jeanmougin, F. & Higgins, D. G.** 1997. The ClustalX windows interface, flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research*, **24**, 4876–4882.
- Thoresen, A. C.** 1985. Diurnal activity and social displays of Rhinoceros Auklets on Teuri Island, Japan. *Condor*, **85**, 373–375.
- Wagner, H. M., Riney, B. O., Deméré, T. A. & Prothero, D. R.** 2001. Magnetic stratigraphy and land mammal biochronology of the nonmarine facies of the Pliocene San Diego Formation, San Diego County, California. Pp. 359–368 in *Magnetic Stratigraphy of the Pacific Coast Cenozoic*. Pacific Section SEPM, Book 91.
- Walsh, H. E. & Friesen, V. L.** 2003. A comparison of intraspecific patterns of DNA sequence variation in mitochondrial DNA, α -enolase, and MHC class II B loci in auklets (Charadriiformes: Alcidae). *Journal of Molecular Evolution*, **57**, 681–693.
- Walsh, H. E., Jones, I. L. & Friesen, V. L.** 2005. A test of founder effect speciation using multiple loci in the auklets (*Aethia* spp.). *Genetics*, **171**, 1885–1894.
- Watada, M., Kakizawa, R., Kuroda, N. & Utida, S.** 1987. Genetic differentiation and phylogenetic relationships of an avian family, Alcidae (auks). *Journal of the Yamashina Institute of Ornithology*, **19**, 79–88.
- Watanuki, Y. & Burger, A. E.** 1999. Body mass and dive duration in alcids and penguins. *Canadian Journal of Zoology*, **77**, 1838–1842.
- Westerhold, T., Bickert, T. & Röhl, U.** 2005. Middle to Late Miocene oxygen isotope stratigraphy of ODP site 1085 (SE Atlantic): new constraints on Miocene climate variability and sea-level fluctuations. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **217**, 205–222.
- Wijnker, E. & Olson, S. L.** 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**, 471–487.
- Yamamoto, Y., Kakizawa, R. & Yamagishi, S.** 2005. *Mitochondrial Genome Project of Endangered Birds in Japan*. Hyogo College of Medicine, Department of Genetics, Nishinomiya.
- Yen, P. P. W., Sydeman, W. J. & Hyrenbach, K. D.** 2004. Marine bird and cetacean associations with bathymetric habitats and shallow-water topographies: implications for trophic transfer and conservation. *Journal of Marine Systems*, **50**, 79–99.
- You, Y., Huber, M., Muller, D., Poulson, C. J. & Ribbe, J.** 2009. Simulation of the Middle Miocene climate optimum. *Geophysical Research Letters*, **36**. doi: 10.1029/2008GL036571.