



## **An Alphataxonomic Revision of Extinct and Extant Razorbills (Aves, Alcidae): A Combined Morphometric and Phylogenetic Approach**

Authors: Smith, N. Adam, Department of Geological Sciences, Jackson School of Geosciences, University of Texas at Austin, Austin, Texas 78713, USA, and Clarke, Julia A., Department of Geological Sciences, Jackson School of Geosciences, University of Texas at Austin, Austin, Texas 78713, USA

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## AN ALPHATAXONOMIC REVISION OF EXTINCT AND EXTANT RAZORBILLS (AVES, ALCIDAE): A COMBINED MORPHOMETRIC AND PHYLOGENETIC APPROACH

N. ADAM SMITH<sup>1</sup> AND JULIA A. CLARKE

*Department of Geological Sciences, Jackson School of Geosciences, University of Texas at Austin,  
Austin, Texas 78713, USA*

**ABSTRACT.**—*Alca* (Aves, Alcidae) has a comparatively rich fossil record with respect to other Charadriiformes, consisting of thousands of specimens. Despite the abundance of fossil material, species richness in this clade has remained poorly understood, primarily because of the paucity of associated specimens. To address this issue, a combined morphometric and apomorphy-based method was developed that would allow referral of fragmentary and isolated specimens, which constitute ~97% of the *Alca* fossil record. Measurements of multiple variables from >2,000 *Alca* fossils were categorized by hierarchical cluster analysis and resulted in the recognition of “species clusters.” Discriminant function analysis was used to assess statistical support for these clusters and to identify the most informative measurements with respect to discriminating between species on the basis of size. The reliability of this method was tested using the same measurements taken from 13 extant alcid species and was found to be robust with respect to the accurate recovery of species-correlated groups of measurement data. With the exception of the similarly proportioned *Alca carolinensis* sp. nov. and *A. olsoni* sp. nov., the holotype specimens of all *Alca* species were recovered in separate, statistically supported clusters. These clusters of fossils were then evaluated for the presence of diagnostic morphological features, resulting in the recognition of three new *Alca* species. In contrast to previously described *Alca* species, two new species are described from holotype specimens that are associated partial skeletons. These associated specimens facilitated referral of isolated fossil material and phylogenetic estimation of *Alca* relationships. Amended diagnoses for *Alca* species are proposed, and 203 humeri are referred to species on the basis of unique suites of characters and size ranges identified through these analyses. This method has potential for assessing species diversity in other taxa known from abundant fragmentary and/or isolated remains.

The combined phylogenetic analysis includes the three new species described herein, nine extinct species in Alcini that have not been phylogenetically analyzed before, and six other extant or recently extinct (i.e., Great Auk [*Pinguinus impennis*]) Alcini species. The character matrix includes osteological characters and previously published molecular sequence data (ND2, ND5, ND6, COI, CYTB, 12S, 16S, RAG1). The results support the monophyly of an *Alca* + *Pinguinus* clade recovered as the sister taxon to a clade composed of *Uria*, *Miocepphus*, and *Alle*.

The description of three new species of auk from the Early Pliocene Yorktown Formation of North Carolina nearly doubles the number of known species in *Alca*, makes *Alca* the most speciose clade of Atlantic alcids, and supports previous hypotheses of high species richness in this clade. The sole extant species, the Razorbill Auk (*Alca torda*), may accordingly be viewed as the only survivor of a diverse Atlantic Ocean clade that was species-rich a mere 4 million years ago. These new fossils refine our knowledge of alcid paleodiversity, provide information regarding ancestral osteological states within *Alca*, and allow for increased understanding of radiation, extinction, and biogeography within this clade. Received 4 October 2010, accepted 8 April 2011.

Key words: *Alca*, auks, Cenozoic, climate change, fossil birds, intraspecific variation, systematics.

<sup>1</sup>E-mail: [adam\\_smith@mail.utexas.edu](mailto:adam_smith@mail.utexas.edu)

## Revisión Alfataxonómica de Taxones Extintos y Vivientes de *Alca* (Aves, Alcidae): Un Enfoque Combinado de Morfometría y Filogenética

RESUMEN.—*Alca* (Aves, Alcidae) presenta un registro fósil comparativamente rico con respecto a otros Charadriiformes, que consiste de miles de especímenes. A pesar de la abundancia de material fósil, la riqueza de especies de este clado ha permanecido pobremente comprendida, principalmente debido a la escasez de especímenes adecuadamente preservados. Para abordar este asunto se desarrolló un método que, mediante una combinación de morfometría y análisis de apomorfías, permitiría establecer la identidad taxonómica de especímenes fragmentarios y aislados, que constituyen cerca del 97% del registro fósil de *Alca*. Se categorizaron medidas de múltiples variables tomadas en más de 2000 fósiles de *Alca* mediante análisis jerárquicos de conglomerados, lo que condujo al reconocimiento de "conglomerados de especies". Se empleó un análisis de funciones discriminantes para evaluar el respaldo estadístico de esos conglomerados y para identificar las mediciones que brindan más información con respecto a la discriminación entre especies basada en el tamaño. La confiabilidad de este método fue puesta a prueba utilizando las mismas medidas tomadas en 13 especies vivientes de álcidos y se encontró que el método es robusto con respecto a la identificación exacta de grupos correlacionados con especies a partir de las medidas. Con la excepción de dos especies que presentan proporciones similares, *Alca carolinensis* sp. nov. y *A. olsoni* sp. nov., los especímenes holótipo de todas las especies de *Alca* se asignaron a conglomerados distintos apoyados estadísticamente. Luego se examinaron estos conglomerados de fósiles para evaluar la presencia de rasgos morfológicos diagnósticos, lo que condujo al reconocimiento de tres especies nuevas de *Alca*. En contraste con las especies de *Alca* previamente descritas, se describen dos especies a partir de holótipos que son esqueletos parciales. Estos especímenes facilitaron la clasificación de material fósil aislado y la estimación de las relaciones filogenéticas en *Alca*. Se proponen diagnósis corregidas para las especies de *Alca*, y 203 húmeros son referidos a las especies correspondientes con base en conjuntos únicos de rasgos y en rangos de tamaño identificados mediante los análisis. Este método tiene potencial para evaluar la diversidad de especies en otros taxones conocidos por abundantes restos fragmentarios y/o aislados.

El análisis filogenético combinado incluye las tres especies nuevas aquí descritas, nueve especies extintas de Alcini que no habían sido analizadas filogenéticamente con anterioridad y otras seis especies vivientes o recientemente extintas (i.e., *Pinguinus impennis*) de Alcini. La matriz de caracteres incluye rasgos osteológicos y datos moleculares de secuencias previamente publicadas (ND2, ND5, ND6, CO1, CYTB, 12S, 16S, RAG1). Los datos apoyan la monofilia de un clado *Alca* + *Pinguinus*, que fue recobrado como el grupo hermano de un clado compuesto por *Uria*, *Miocepphus* y *Alle*.

La descripción de tres especies nuevas de la formación Yorktown del Plioceno Temprano de Carolina del Norte casi duplica el número conocido de especies de *Alca*, posiciona a *Alca* como el clado de álcidos del Atlántico con más especies y apoya las hipótesis previas que sugerían una alta riqueza de especies en este clado. La única especie viviente, *Alca torda*, podría pues considerarse como la única sobreviviente de un clado del océano Atlántico que era rico en especies hace sólo 4 millones de años. Estos nuevos fósiles permiten afinar nuestro conocimiento sobre la paleodiversidad de los álcidos y permiten comprender mejor la radiación, extinción y biogeografía de este clado.

### INTRODUCTION

ALCIDAE IS A clade of pelagic charadriiforms including auks, auklets, puffins, guillemots, murre, and murrelets. Alcids have been proposed to fill the same wing-propelled diving niche in the Northern Hemisphere as occupied by penguins in the Southern Hemisphere (Ridgway 1919). Extant diversity within Alcidae consists of 23 species of exclusively Holarctic distribution (del Hoyo et al. 1996). Just as the ranges of all extant alcids are

correlated with cold-water upwelling zones that provide abundant feeding opportunities for these underwater predators (Prince and Harris 1988, del Hoyo et al. 1996), hypotheses regarding the paleodiversity and biogeographic history of extinct alcids have centered on geological and associated paleoclimatic explanations also related to cold-water upwelling (Warheit 1992a, Emslie 1998). Furthermore, alcid-fossil-bearing deposits from eastern and western North America as well as western Europe have been interpreted as

cold-water marine deposits on the basis of microfossil and lithologic evidence (Herman et al. 1974, Deméré 1982, Riggs 1984, Snyder et al. 2001), which suggests that alcids have been dependent on cold, nutrient-rich ocean systems since at least the Miocene.

With respect to other charadriiforms, Alcidae have a comparatively rich fossil record along the margins of both the Atlantic and Pacific oceans (Olson 1985). Specimens referred to the alcid taxon *Alca* are the most numerous (Olson and Rasmussen 2001). The range of the only extant species of auk, the Razorbill (*Alca torda*), and all known *Alca* fossils are restricted to the northern Atlantic Ocean basin (Brodkorb 1967, Olson 1985; but see Howard 1968 and discussion below; Fig. 1). Extinct *Alca* have been described from Miocene deposits in Virginia (Olson and Rasmussen 2001, Wijnker and Olson 2009) and from Pliocene deposits in Italy, Florida, North Carolina, Spain, Belgium, and Morocco (Portis 1888, 1891; Brodkorb 1955; Martin et al. 2001; Olson and Rasmussen 2001; Sanchez-Marco 2003; Dyke and Walker 2005; Mourer-Chauviré and Geraads 2010; Fig. 1).

The richest of these deposits is the Early Pliocene Yorktown Formation, a shallow marine deposit geologically linked with cold-water upwelling (Gibson 1967, Snyder et al. 2001) exposed at the PCS Phosphate Mine in Aurora, North Carolina (formerly known as the Lee Creek Mine; Ray 1983, Olson and Rasmussen 2001, Smith et al. 2007; Fig. 1). Although ~8,000 fossils from this locality, consisting primarily of ulnae, humeri, and coracoids, have been referred to *Alca*, a recent reassessment of this material indicates that only ~3% of these specimens are represented by undamaged skeletal elements (e.g., complete humeri), and only 23 specimens consist of associated material (18 of the 23 associated specimens are >90% incomplete; Smith 2007).

Previously recognized alcid diversity from the Yorktown Formation includes *Miocepphus mcclungi*, *M. bohaski*, *M. mergulellus*, *Fratercula cirrhata*, *F. arctica*, *Alca torda*, *A. ausonia*, *A. grandis*, *A. stewarti*, *Pinguinus alfrednewtoni*, and *Cerorhinca* sp. (Olson 1977, Martin et al. 2001, Olson and Rasmussen 2001, Smith et al. 2007, Wijnker and Olson 2009). The addition of three new *Alca* species described here increases the number of known *Alca*

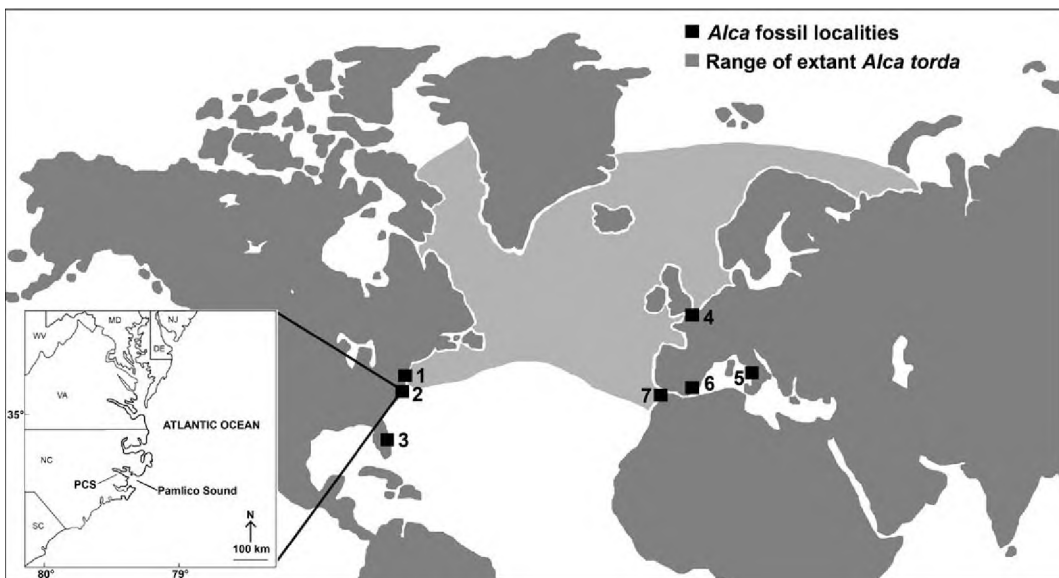


FIG. 1. Maps indicating the modern range of extant *Alca torda* and *Alca* fossil localities. (1) Eastover Formation, Virginia. (2) Yorktown Formation, North Carolina. (3) Bone Valley Formation, Florida. (4) Kallo Sands Formation, Belgium. (5) Oriano Pisano, Italy (formation unknown). (6) Puerto de Mazarron Formation, Murcia, Spain. (7) Ahl al Oughlam Quarry, Casablanca, Morocco. Inset map of the eastern United States indicates the locality of PCS Phosphate Mine near Aurora, North Carolina, where the holotype specimens of *A. carolinensis*, *A. minor*, and *A. olsoni* were collected. Range map altered from del Hoyo et al. (1996); inset map altered from Gibson (1983).

to 7, and the total number alcid fossils known from this locality to 14. Microfaunal analysis has confirmed the Pliocene Yorktown Formation provenience of many avian fossils from this locality (Gibson unpubl. data in Olson and Rasmussen 2001). However, the lack of associated sediments leaves the probable provenience of many fossils from this locality in question (Smith et al. 2007, Wijnker and Olson 2009).

PCS Phosphate Mine is located near the south shore of the Pamlico River (Fig. 1) and exposes sediments of Miocene, Pliocene, and Pleistocene age (Gibson 1983). The Pliocene Yorktown Formation unconformably overlies the Miocene Pungo River Formation and is composed primarily of clay-rich sands (i.e., marls), with the basal-most unit containing reworked phosphate pebbles from the underlying Pungo River Formation (Gibson 1983). An age of  $4.4 \pm 0.2$  Ma (Early Pliocene) was assigned to the Yorktown Formation at PCS Phosphate Mine on the basis of K/Ar dating of the *Orionina vaughani* assemblage zone and correlated with planktonic foraminifera Zone N19 (Hazel 1983). Yorktown Formation sediments from the PCS Phosphate Mine are interpreted to be the result of moderate-depth (~150 m) outer neritic marine deposition at the southwestern end of the Aurora Embayment (Popenoe 1985, Snyder et al. 2001). The Aurora Embayment was a deep depression that allowed cold waters to upwell 100 km west of the margin of the Pliocene continental shelf (Riggs 1984). That upwelling resulted in a nutrient-rich marine environment interpreted as "a marine vertebrate high-use feeding area" by Purdy et al. (2001:188). As noted above, the distribution of extant alcid fossils also coincides with cold-water upwelling zones (Prince and Harris 1988, del Hoyo et al. 1996), which suggests that the environmental preferences of alcid fossils have remained relatively stable since the early Pliocene. The Yorktown Formation contains abundant remains of marine vertebrates (e.g., Chondrichthyes, Osteichthyes, Cetacea, Sirenia, Pinnipedia, Testudines, Crocodylia; Ray 1983, 1987; Ray and Bohaska 2001; Ray et al. 2008) and

invertebrates (e.g., Echinodermata, Hexagonaria, Porifera, Mollusca, Foraminifera; Ray 1983, 1987). In addition to the taxa listed above, the remains of a diverse avifauna representing ~100 other avian species are known from this location (Olson and Rasmussen 2001, Storer 2001, Smith et al. 2007, Wijnker and Olson 2009).

The paucity of associated fossil specimens, incomplete preservation of the overwhelming majority of specimens, and morphological similarity of *Alca* species combined to complicate previous referral of *Alca* fossils to species (Olson and Rasmussen 2001). Further compounding the difficulties of referring additional elements to species, the holotype and paratype material of all three previously described extinct *Alca* species (*A. grandis*, *A. ausonia*, and *A. stewarti*; Table 1 and Fig. 2) are isolated skeletal elements. Osteologically distinguishing between modern species in a species-rich or sub-species-rich taxon can be difficult or impossible (Stewart 2002, 2007). The same difficulties can also be present in assemblages of closely related fossil taxa. Previous researchers (Olson and Rasmussen 2001) assigned specimens to species on the basis of humeral size classes determined through principal component analysis (PCA). Because PCA does not account for covarying character complexes (i.e., principal axes not orthogonal), we chose not to use that method.

The results of the analysis of fossil *Alca* distal humeri from the Yorktown Formation conducted by Olson and Rasmussen (2001) using the K-means method of clustering supported the presence of four size-based species in genus *Alca*. That method relied on previous authors' assumptions about the number of species expected given the overall size variance based on a modified version of the phenetic technique proposed by Warheit (1992b). Extant diversity in *Alca* is limited to a single species; therefore, the expected range of size variance is not well constrained for fossil taxa and there is no logical method of *a priori* establishing means. Many fossil birds from the Yorktown Formation are known from a single specimen, or only a few

TABLE 1. Previously published extinct *Alca* holotype material.

Taxon	Material	Provenience	Age	Reference
<i>Alca ausonia</i>	Distal humerus	Italy	Middle Pliocene	Portis 1888
<i>A. grandis</i>	Humerus	USA	Early Pliocene	Marsh 1870
<i>A. stewarti</i>	Ulna	Belgium	Early Pliocene	Martin et al. 2001



FIG. 2. Comparison of *Alca* and *Pinguinus* humeri in anterior view. (A) Paratype cast of *Alca stewarti* (NHMUK PV A 7052; specimen image reversed for comparison). (B) Holotype humerus of *A. olsoni* (USNM 454590). (C) Holotype humerus of *A. carolinensis* (NCSM 13734). (D) Holotype specimen of *A. grandis* (ANSP 13357). (E) Cast of *A. ausonia* holotype specimen (IGF 14875). (F) Referred specimen of *A. ausonia* (USNM 446692). (G) *A. torda* (USNM 502382; extant). (H) Holotype specimen of *A. minor* (USNM 302324). (I) *Pinguinus impennis* (USNM 623465). (J) *P. alfrednewtoni* (USNM 366630; specimen image reversed for comparison).

isolated specimens (e.g., *Cerorhinca* sp.,  $n = 3$ ; Smith et al. 2007). Whether or not those individual specimens are representative of the average size for those species or perhaps represent

smaller-than-average or larger-than-average individuals cannot be determined on the basis of such small sample sizes. Because *K*-means analyses can be sensitive to choice of mean and small sample sizes (Kaufman and Rousseeuw 1990), a hierarchical clustering approach was taken that did not require prior assumptions about the number of clusters or variance.

A method for differentiating species was used that took into account the non-independence of osteological variables while allowing for the analysis of fragmentary material and potentially small sample sizes. This method is an improvement on previous methods that rely solely on measurement data to differentiate between species because it also employs intragroup and intergroup morphological analyses of morphometrically determined clusters and allows for identification of discrete morphological characters for phylogenetic analysis and diagnosis of species. Thus, only statistically supported clusters of fossils that can also be morphologically differentiated from one another are accepted, preventing the potential overestimation of species richness.

Interspecific size variation has been used successfully to differentiate between extant and extinct avian species (Livezey 1988, 1989; Warheit 1992b), and knowledge of interspecific size variation has a long history of use as a criterion for estimating diversity among fossil material (see Warheit 1992b). However, the application of interspecific models to delimit proposed size classes of fossil specimens assumes that qualitative features of phylogenetic value are conserved despite relative size differences among species (Warheit 1992b). Thus, referral of fossil specimens solely on the basis of size data is not recommended. This does not mean that morphometric data, including size, cannot play a role in the identification of fossils; instead, morphometric data should be used in conjunction with discrete morphological characters in a phylogenetic context.

The ability to quantify the diversity represented by fossil assemblages known from fragmentary taxa holds potential to inform both paleoecological trends and paleobiogeographic patterns that are currently understudied or undescribed. Alcidae is recognized as one of the dominant groups of seabirds during the Pliocene (Olson 1985). Increasing knowledge of extinct alcid diversity, relative abundance of species, and estimates of species longevity will clarify our presently poor understanding of alcid paleobiogeographic patterns. Additionally,

evaluation of extinct species richness with respect to latitudinal gradients will allow for comparisons with extant latitudinal distribution of alcid species. Furthermore, insights gained through more detailed evaluation of the alcid fossil record may result in a refined understanding of the extent to which previously hypothesized (Warheit 1992a, Emslie 1998, Olson and Rasmussen 2001, Smith et al. 2007, Pereira and Baker 2008, Smith 2011) paleoclimatic drivers contributed to radiations and extinctions in Alcidae.

Although recently sequenced molecular data have resulted in strongly supported phylogenetic hypotheses of extant alcid relationships (Moum et al. 1994, 2002; Friesen et al. 1996; Thomas et al. 2004; Baker et al. 2007; Pereira and Baker 2008), extinct alcid species were largely excluded in analyses of morphological data (Strauch 1985, Chandler 1990, Chu 1998). Analyses of morphological (Strauch 1985, Chandler 1990) and molecular sequence data (Moum et al. 2002, Baker et al. 2007, Pereira and Baker 2008) place extant *A. torda* as the sister taxon to the recently extinct *Pinguinus impennis*. *Alca* and *Pinguinus* are part of Alcini, which also includes *Uria*, *Alle*, and *Miocepphus*. Extinct *Alca* species, *Pinguinus alfrednewtoni* Olson 1977, and *Miocepphus* species have never been included in a phylogenetic analysis. This study is the first to include all known extant and extinct Alcini in a combined phylogenetic analysis of morphological (i.e., osteological) and molecular sequence data.

To assess the monophyly of *Alca* and evaluate the relationships among all Alcini, osteological variation among the thousands of fossils that have been referred to *Alca* was investigated. Estimates of species richness resulting from this investigation form a more complete picture of morphological variation between *Alca* species, and between *Alca* and *Pinguinus*. The discovery of an associated partial *Alca* skeleton (the most complete fossil *Alca* presently known) from the Pliocene Yorktown Formation of North Carolina prompted an extensive review of the *Alca* fossil record and a reexamination of *Alca* diversity that resulted in the recognition of three new species of *Alca*. Descriptions of these new species and amended diagnoses for previously recognized *Alca* species are presented along with species referrals for 203 isolated specimens and phylogenetic analysis of relationships within Alcini.

## MATERIALS AND METHODS

Description of anatomical features primarily follows the English equivalents of the Latin osteological nomenclature summarized by Baumel and Witmer (1993). The terminology of Howard (1929) is followed for features not treated by Baumel and Witmer (1993). Taxonomy of extant North American Charadriiformes follows that of the 7th edition of the American Ornithologists' Union (AOU) *Check-list of North American Birds* (AOU 1998). Measurements follow those of von den Driesch (1976). All measurements were taken using digital calipers and rounded to the nearest 0.1 mm. Ages of geological time intervals are based on the International Geologic Timescale (Gradstein et al. 2004, Ogg et al. 2008).

## INSTITUTIONAL ABBREVIATIONS

Alam = Asociación Cultural Paleontológica Murciana, Murcia, Spain; ANSP = Academy of Natural Sciences of Philadelphia; GCVP = Georgia College Vertebrate Paleontology Collection, Milledgeville, Georgia; IGF = Museo di Storia Naturale, Firenze, Italy; LACM = Natural History Museum of Los Angeles County, Los Angeles, California; NCSM = North Carolina Museum of Natural Sciences, Raleigh, North Carolina; NHMUK (formerly BMNH) = Natural History Museum, London; UCMP = University of California Museum of Paleontology, Berkeley, California; UF-PB = Florida Museum of Natural History-Pierce Brodkorb Collection, Gainesville, Florida; and USNM = National Museum of Natural History, Smithsonian Institution, Washington, D.C.

## COMPARATIVE SKELETAL MATERIAL USED IN THE PHYLOGENETIC ANALYSIS

See Appendix 1 for extant specimens used in the morphometric analyses. *Alca torda* Razorbill Auk NCSM 20058, 20502; USNM 18062, 347946, 501644, 502378, 502382, 502387, 502388, 502389, 502549, 555666, 555668; *Alle alle* Dovekie NCSM 18374; USNM 344740, 344748, 499471, 560929; *Cephus columba* Pigeon Guillemot NCSM 18094, 18095, 18096, 18097; USNM 610936; *Pinguinus impennis* Great Auk USNM 346387 (composite), 557975 (composite), 623465 (composite), additional series of disarticulated USNM material from the Lucas expedition to Funk Island (Lucas

1890); *Uria aalge* Common Murre NCSM 17822, 18116, 18117, 18118, 18234; *Uria lomvia* Thick-billed Murre NCSM 18114, 19414; USNM 344435, 561265.

#### MORPHOMETRIC ANALYSES

Measurements of 66 osteological variables (e.g., greatest length of humerus) were taken from 67 skeletons representing 12 extant alcid species and the recently extinct flightless species *Pinguinus impennis* (Appendix 1). Inclusion of measurement data from extant auklets (i.e., *Aethia* and *Ptychoramphus*) provided a test of the robustness of this method with respect to differentiating between members of a single clade, the monophyly of which is supported by analyses of both morphological (Strauch 1985, Chandler 1990, Smith 2011) and molecular data (Friesen et al. 1996, Pereira and Baker 2008).

Owing to the relative incompleteness of associated *Alca* fossils, it was necessary to evaluate not only how this method performed when measurements from complete skeletons of extant alcids were included, but more importantly how the method performed when more limited sets of data were available. Additional analyses were conducted using subsets of measurement data (e.g., distal humeri data only) from extant alcids to gauge how this method might perform when applied to isolated and fragmentary fossils.

A hierarchical cluster analysis was performed on raw measurement data using the statistical software package SPSS, version 16 (SPSS, Chicago, Illinois). This analysis employed single linkage, nearest-neighbor joining, and Euclidean distance. Resulting phenogram topology was evaluated to infer potential clusters of specimens (i.e., clusters of measurement data). Statistical support for cluster membership was determined by conducting canonical discriminant function analyses on measurement data assigned to categories based on phenogram topology (Fig. 3).

Measurement data from extant alcids were also used to determine the typical range of intraspecific size variation of extant alcid species so that this metric could be applied as an additional criterion in the acceptance or rejection of clusters of *Alca* fossils. As suggested by Warheit (1992b), this procedure provided a phylogenetic context for the estimation of average size for extinct *Alca*. Because size alone can be misleading when delimiting species (Stewart 2007), whenever available,

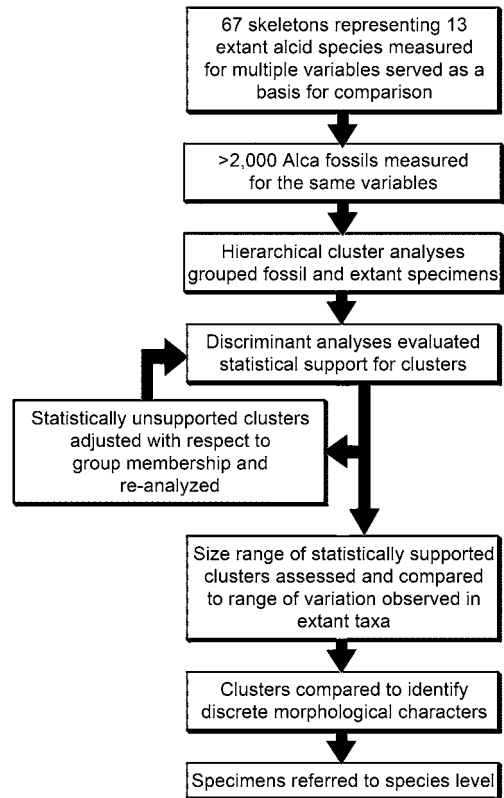


FIG. 3. Flow chart depicting a simplified explanation of the combined morphometric and morphological method used to refer specimens to species.

specimens from multiple locations within the geographic range of extant species (e.g., extant *Alca torda* specimens from the eastern and western Atlantic) were used to calculate the intraspecific size-variation values that were used as a criterion to evaluate the size ranges of clustered fossils. This value was calculated by assessing the difference between the median of measurements of the greatest length of the humerus and the length of the longest and shortest specimens for each extant species. Comparing the differences between the known ranges of variation between closely related extant alcids (e.g., auklets) with the range in size of statistically supported clusters of fossils provided an additional criterion with which to evaluate support for clustered groups of fossils (Warheit 1992b). Only clusters with a size range of specimens not significantly exceeding that of the predetermined range of intraspecific size variation for Alcidae were accepted. Although



in practice this method mistakenly assumes that no two fossil species fall within the same size range, morphological comparison of statistically clustered specimens guarded against the possibility of underestimating the number of species represented by a single size class. The possibility that a subset of the humeral data might represent two species that possess statistically insignificant size differences and are morphologically indistinguishable could be verified only in cases in which associated specimens with other morphologically distinct elements were preserved.

The same procedure as described above was applied to data from 203 *Alca* humeri, including the type specimens of all previously described species of *Alca*, and additional *Alca* humeri from both eastern and western Atlantic fossil localities (Appendix 2). Although 946 *Alca* fossil humeri were examined and measured, only specimens in which at least three of the six humeral variables could be measured, and that preserved diagnostic morphological details, were included in the final analysis. The holotype or paratype specimens of all three previously described species of extinct *Alca* are humeri (Table 1 and Fig. 2), and humeri are the second-most-frequently represented skeletal element among collections of fossil *Alca*. Although ulnae are more abundant, this element lacks morphologically distinguishing characters, compared with *Alca* humeri.

As with extant specimens, cluster membership of fossil specimens was determined by evaluating phenogram topology resulting from cluster analysis and grouping topologically adjacent specimens. Statistical support values (i.e., number of cases correctly classified) obtained from canonical discriminant function analysis of extant alcids were used as a metric to accept or reject clusters of fossils. Clusters that received <90% statistical support (the lowest support resulting from analysis of extant taxa) were rejected. A caveat to this method is that as the number of specimens being analyzed increases, the interpretation of phenogram topology into distinct clusters (i.e., categorization of fossils) becomes increasingly complicated. For example, even though analysis of the distal humeri of extant alcids showed that this metric accurately clusters specimens into species groups, analysis of 621 distal humerus fossils produced a phenogram of such complexity that clusters could not be reliably delimited. The largest number of successfully analyzed specimens in this analysis was 146. However, numbers of

specimens included for analysis were more commonly limited by the completeness of the fossil specimens themselves (e.g., only 66 complete fossil *Alca* humeri) rather than by the complexity of interpreting results. Data analyzed using this method cannot contain any missing entries (i.e., values unmeasurable because of incompleteness or damage to fossils). However, limiting the quantities of specimens analyzed using this method should not present a significant problem, because the method itself is not biased by small sample sizes. However, the possibility that a small sample size may represent individuals that are skewed toward one size extreme or another within a species (e.g., only three complete *Alca stewarti* humeri available for analysis) should be considered.

The results of analyses in which some clusters of fossils were rejected on the basis of the criteria outlined above (i.e., statistical support and range of size variation as compared with extant alcids) were discarded. Phenogram topology was then reevaluated, outliers (i.e., smallest or largest specimens within a cluster) were reassigned to topologically adjacent clusters, and then the entire data set was reanalyzed to determine whether an alternative clustering scheme would receive stronger statistical support (Fig. 3). When reassigning specimens to different categories, only adjacently placed specimens and groups of specimens (i.e., those specimens with linked Euclidean distances) were combined into new potential categories. No specimens with Euclidean distance values intermediate between those of specimens placed adjacently in phenogram topology were excluded.

Statistically supported clusters of fossils were compared to identify shared intragroup morphological characters and intergroup morphological differences, which could be used to differentiate *Alca* species and facilitate referral of specimens to species. Additionally, the morphology of specimens clustered with the holotype or paratype specimens of previously recognized species were compared with those name-bearing type specimens to identify previously unrecognized morphological variation and to document characteristics not visible in the type specimens because of damage. The range of size variation within fossil clusters was compared to values obtained from extant alcid taxa as described above. Intraspecific size variations within alcid species that are attributable to latitude are well documented (Storer

1952, Spring 1971, Moen 1991, Burness and Montevocchi 1992). Additional analyses of measurement data collected from *Alca* fossils deposited in a single stratigraphic layer (Early Pliocene Yorktown Formation) exposed at a single geographic locality (Aurora, North Carolina) were performed to address this issue.

#### PHYLOGENETIC ANALYSIS

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 on the basis of 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 geographic variation.

A total of 131 morphological characters, including 126 unordered binary characters, two multistate unordered characters, and three multistate ordered characters were scored for 18 taxa (5 extant and 13 extinct alcids; see Appendix 3 for morphological character descriptions and Appendix 4 for morphological character scorings used in the phylogenetic analysis). Ninety-three characters were newly identified. The other 38 characters are from the work of Strauch (1978, 1985;  $n = 13$ ), Chandler (1990;  $n = 22$ ), and Chu (1998;  $n = 3$ ).

The primary goal of the present study was to accurately evaluate diversity within *Alca* so that all species within Alcini could be included in a phylogenetic analysis. Because of the isolated nature of all but four extinct Alcini holotype specimens (i.e., associated holotype specimens of *Miocepphus blowi*, *M. bohaski*, *A. carolinensis*, and *A. olsoni*), resolution of systematic relationships was facilitated by combination of all available referable specimens into supraspecific terminals, thus decreasing the amount of missing data in the phylogenetic analysis. Taxonomic referrals of all holotype and previously referred specimens were reevaluated using an apomorphy-based approach. Characters for all extinct taxa were coded from direct observation. Characters for *Pinguinus alfrednewtoni* were scored from the hypodigm of that species (USNM specimen numbers: 179226, 179277, 192497, 193101, 193334, 206362, 275780, 366630, 430935, 430943, 430947, 459391; Olson and Rasmussen 2001). Characters for *A. grandis* were

scored from the holotype specimen as well as from two previously referred specimens (USNM 215454, USNM 336379; Olson and Rasmussen 2001) and one specimen referred herein (USNM 236802). Characters for *A. ausonia* were scored from two high-quality casts of the holotype retained in the USNM and UF-PB collections as well as a representative specimen referred herein (USNM 446692). Characters for *A. stewarti* were scored from the holotype (NHMUK PV A 7050; formerly BMNH A 7050), the paratype humerus (NHMUK PV A 7052; formerly BMNH A 7052; Martin et al. 2001), a previously referred specimen (USNM 242238; Wijnker and Olson 2009), and an additional specimen documented by Olson and Rasmussen (2001; USNM 446650) as *Alca* "undescribed species" and referred to *A. stewarti* herein. Characters for *A. carolinensis* sp. nov. and *A. olsoni* sp. nov. were scored from the holotype specimens, whereas *A. minor* sp. nov. was scored from the hypodigm of that species (USNM 302324, 192879, 495600). *Miocepphus* species were scored directly from the holotype specimens representing those taxa.

*Pseudocepphus teres* Wijnker and Olson, 2009 was not included in the phylogenetic analysis because results of a comprehensive analysis including all extinct and extant Alcidae (A. Smith unpubl. data) place that species outside Alcini. Additionally, recent reevaluation of the holotype specimen of *Uria paleohesperis* Howard, 1982 (UCMP 88704) failed to identify any apomorphies that would allow for its referral to *Uria*. Contra Howard (1982), the size of UCMP 88704 is consistent in all dimensions with the holotype specimen of *U. brodkorbi* Howard, 1981 (UF-PB 7690). Additionally, the late Miocene (~6.7–10 Ma) age of the San Luis Rey River Local Fauna of the San Mateo Formation from which UCMP 88704 was recovered is consistent with the Late Miocene age assigned to the Sisquoc Formation from which the holotype of *U. brodkorbi* was recovered (Domning and Deméré 1984, Dumont and Barron 1995). Furthermore, UCMP 88704 and *U. brodkorbi* share a concave sternal margin of the procoracoid process of the coracoid. This margin is convex in *U. aalge*, *U. lomvia*, *Synthliboramphus*, *Fratercula*, and all *Alca* except *A. carolinensis*, and concave in *Aethia*, *Ptychoramphus*, *Brachyramphus*, and *M. bohaski*. However, because the holotype specimen of *U. brodkorbi* consists of impressions on two slabs of diatomite, many morphological details that might further elucidate potential

affinity of these species are obscured by matrix or not preserved. Because size and a single potential synapomorphy are not considered sufficient evidence for synonymy, the possibility that *U. paleohesperis* may be a junior synonym of *U. brodkorbi* should be reconsidered upon recovery of additional remains.

Previously published molecular sequence data (mitochondrial: ND2, ND5, ND6, CO1, CYTB; ribosomal RNA: 12S, 16S; and nuclear: RAG1) were downloaded from GenBank ([www.ncbi.nlm.nih.gov/genbank](http://www.ncbi.nlm.nih.gov/genbank); Appendix 5). Sequence data for all genes were available for the total taxonomic sample with the exception of two species. ND5 sequence data for *Cephus columba*, as well as ND2, CO1, 16S, and RAG-1 sequence data for *Pinguinus impennis* were not available. Preliminary sequence alignments were obtained using the program CLUSTALX, version 2.0.6 (Thompson et al. 1997) and then manually adjusted using the program SE-AL, version 2.0A11 (Rambaut 2002). Alignment and concatenation of sequence data resulted in a final molecular matrix with a maximum length of 11,503 base pairs (including gaps). Molecular sequence data were combined with 131 morphological characters for a matrix of 11,634 characters.

The phylogenetic analysis used a branch-and-bound search strategy implemented in PAUP\*, version 4.0b10 (Swofford 2002). All characters were equally weighted, and multistate scorings represented polymorphism. Branches recovered with a minimum length = 0 were collapsed. Bootstrap values from 1,000 replicates (100 random addition sequences per replicate) and descriptive tree statistics (e.g., CI, RI, RC) were also calculated using PAUP\*. Bremer support values were calculated using a script generated in MACCLADE, version 4.08 (Maddison and Maddison 2005), and implemented in PAUP\*. The tree was rooted with *C. columba* on the basis of this taxon's placement outside of Alcini in previous analyses (Strauch 1985, Chandler 1990, Moum et al. 1994, Baker et al. 2007, Pereira and Baker 2008, Smith 2011).

## RESULTS

### MORPHOMETRIC RESULTS

*Extant Alcidae*.—Morphometric analysis including all 66 skeletal variables effectively discerned between different species of closely related extant alcids and *Pinguinus impennis* (Fig. 4). Cluster analyses

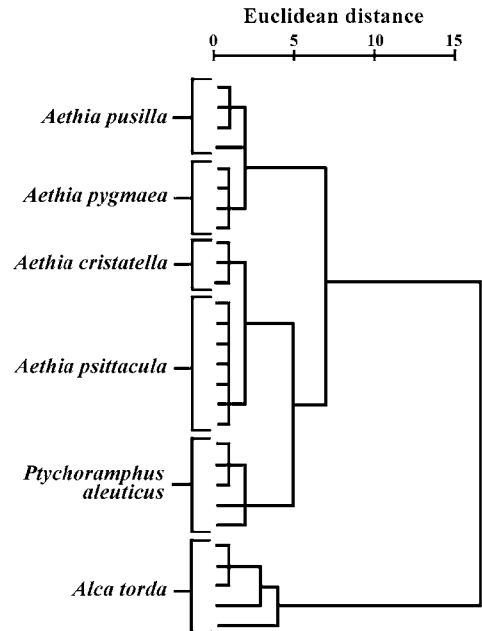


FIG. 4. Example phenogram depicting the results of cluster analysis of extant alcid species based on humeral measurements. Each terminal represents a separate specimen of a particular species. Note that species relationships shown reflect size similarity, not phylogeny.

correctly classified all 67 extant skeletal specimens into distinct species groups in 100% of cases (Table 2). When subjected to discriminant function analysis, group membership of specimen clusters representing extant species received 100% statistical support (i.e., 100% of cases correctly classified).

Additional analyses of single skeletal elements (e.g., humeri) and partial elements (e.g., proximal ends of humeri) of extant alcids had varying results (Table 2). Analyses of coracoids and of complete and partial humeri resulted in correctly classified and statistically supported clusters, whereas analyses of ulnae and carpometacarpus resulted in statistically significant percentages of incorrectly classified specimens (Table 2). In addition to providing measures of statistical support for groups of measurement data categorized by cluster analysis, discriminant function analysis identifies the variables that have the most influence on the resulting classification. Discriminant analysis of extant alcid measurement data identified the medial length of the coracoid as the most informative classificatory variable included in the analysis, followed in order of decreasing utility by the greatest length of the humerus.

TABLE 2. Summary of morphometric analyses and results. Taxonomic categories include the following species: extant Alcidae = all taxa listed in Appendix 1; extant Atlantic = *U. aalge*, *U. lomvia*, *A. torda*, *C. grylle*, *C. columba*, *A. alle*, *P. impennis*, and *F. arctica*; auklets and *Alca* = *A. cristatella*, *A. psittacula*, *A. pusilla*, *A. pygmaea*, *P. aleuticus*, and *A. torda*; *Alca* fossils = fossils referred to *Alca* from both eastern and western Atlantic localities as well as extant *A. torda* specimens used as a control group of specimens with known species identity. Note that accuracy of inclusion is only applicable for analyses of known (i.e., extant) species.

Alcid taxa	Number of species	Number of specimens	Number of variables	Data type	Number of clusters recovered	Accuracy of inclusion	Statistical support
Extant Alcidae	13	61	4	Carpometacarpi	4–10	73%	<90%
Extant Alcidae	13	67	6	Complete ulnae	5–9	69%	<90%
Extant Atlantic	8	40	66	Entire skeleton	8	100%	100%
Extant Atlantic	8	40	6	Complete Humeri	8	92%	97%
Auklets and <i>Alca</i>	6	28	53	Entire skeleton	6	100%	100%
Auklets and <i>Alca</i>	6	28	6	Complete Humeri	6	96%	96%
Auklets and <i>Alca</i>	6	28	3	Proximal Humeri	6	82%	94%
Auklets and <i>Alca</i>	6	28	3	Distal humeri	6	93%	90%
<i>Alca</i> fossils	?	121	4	Carpometacarpi	5–7	NA	<90%
<i>Alca</i> fossils	?	116	6	Complete ulnae	4–7	NA	<90%
<i>Alca</i> fossils	?	58	1	Coracoids	7	NA	97%
<i>Alca</i> fossils	?	79	6	Complete Humeri	6	NA	93%
<i>Alca</i> fossils	?	146	3	Proximal Humeri	6	NA	92%
<i>Alca</i> fossils	?	117	3	Distal humeri	6	NA	93%

The range of intraspecific size variation among extant Alcini (based on the median value of greatest length of humeri for each species) was calculated to vary from  $\pm 1.1\%$  in *Uria lomvia* to  $\pm 6.0\%$  in *Alca torda* (Table 3). The calculated range of size differences between species of auklets varied from  $\pm 0.3\%$  from the median between *Aethia pusilla* and *A. psittacula*, to  $\pm 2.8\%$  between *A. pygmaea* and *Ptychoramphus aleuticus*.

*Extinct Alca*.—After the robustness of this method for differentiating between extant species of alcids was evaluated, the same procedure (Fig. 3) was applied to measurement data collected from *Alca* fossils. As with extant species of alcids, morphometric analyses of measurement data from fossil carpometacarpi and ulnae did not result in distinctly clustered or statistically supported groups of fossils (Table 2). Analysis of coracoid measurement data resulted in seven well-supported clusters of fossils (Table 2) that likely correspond to the seven species of *Alca*. *Alca* coracoids do not display sufficient interspecific morphological differences to allow differentiation of all species within the clade; however, the coracoids of *A. stewarti*, *A. carolinensis*, *A. torda*, and *A. olsoni* can be differentiated by morphological and mensural means. Although there are

TABLE 3. Comparison of size variation in alcids. All data are from greatest length of the humerus except for data for *Australca*, which are measurements of the greatest width of the distal humerus. Integer values are in millimeters and have been rounded to the nearest 10th.

Taxon	Size range	Median value	Variation from median value
<i>Fratercula arctica</i>	7.7	65.1	5.6%
<i>Ptychoramphus aleuticus</i>	3.8	45.4	9.2%
<i>Aethia psittacula</i>	2.3	54.4	2.1%
<i>A. pusilla</i>	1.7	34.8	2.4%
<i>A. cristatella</i>	3.7	52.5	3.4%
<i>A. pygmaea</i>	0.9	37.9	1.2%
<i>Cephus grylle</i>	3.9	59.8	3.4%
<i>C. columba</i>	4.2	66.7	3.3%
<i>Uria aalge</i>	7.3	85.6	4.5%
<i>U. lomvia</i>	1.9	88.5	1.1%
<i>Alle alle</i>	3.1	41.9	3.8%
<i>Pinguinus impennis</i>	4.5	104.1	2.1%
<i>Alca torda</i> (extant)	9.9	77.9	6.0%
<i>A. torda</i> (fossils)	12.3	77.4	8.6%
<i>A. grandis</i>	15.2	92.0	7.6%
<i>A. carolinensis</i>	1.8	101.9	0.9%
<i>A. ausonia</i>	2.8	105.4	1.3%
<i>A. stewarti</i>	0.8	111.6	0.4%

no associated specimens of *A. ausonia* or *A. minor* that permitted confident referral of coracoids to these species, the smallest *Alca* coracoids from the Yorktown Formation are likely representative of *A. minor*, and the size class of coracoids that are larger than *A. torda* yet smaller than *A. grandis* likely represent *A. ausonia*.

Analyses of complete, proximal, and distal ends of humeri all resulted in clusters with high degrees of statistical support (Table 2) and distinct morphologies. Cluster and discriminant analyses of complete, proximal, and distal ends of humeri recovered six statistically supported size-based groups of fossils (Fig. 5 and Table 2). The holotype and paratype humeri of *A. grandis*, *A. stewarti*, *A. torda*, *A. minor*, and *A. ausonia* were recovered in separate statistically supported clusters (Fig. 5). The similarly proportioned *A. olsoni* and *A. carolinensis* clustered together. Although *A. carolinensis* and *A. olsoni* can be differentiated on the basis of characteristics of the coracoid, ulna, radius, and furcula, the humeri of these two species are morphologically similar and are essentially equal in greatest humeral length. Although *A. olsoni* is slightly more robust with respect to other proportions (Table 4), greatest length of the humerus was identified as the second most informative measurement in the discriminant analysis, thus permitting six size classes corresponding to seven species. Rather than trying to separate humeri representing these two species on the basis of statistically insignificant size differences, referrals of isolated humeri to these species were left ambiguous (Appendix 2). Adding further support to the hypothesis that six distinct size classes are represented by the proximal and distal humerus measurement data, iterative analyses of fossil measurements clustered into two, three, four, five, seven, and eight clusters did not receive strong (i.e., >90%) statistical support.

Additional morphometric analyses were conducted including mensural data from specimens of extant *A. torda* in order to identify fossil specimens potentially referable to that species, and to further test the validity of previously recovered clusters containing the holotype specimens of other *Alca* species. Extant *A. torda* specimens were recovered in a single cluster that did not contain the holotype or paratype specimens of any other *Alca* species, allowing for potential identification of Pliocene examples of this taxon. Pliocene examples of this taxon were slightly larger, on

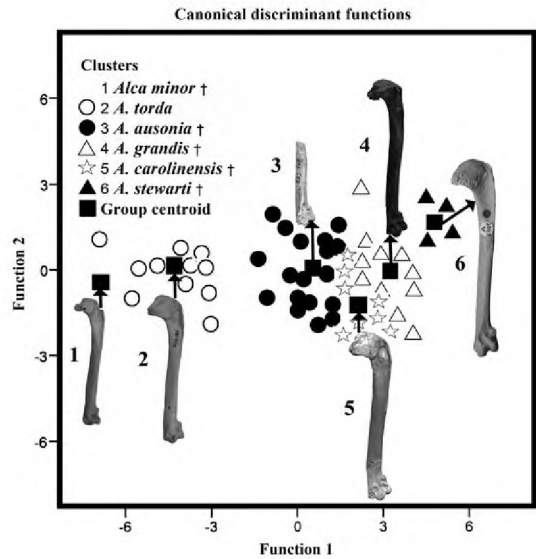


FIG. 5. Graphic representation of results from discriminant function analysis of *Alca* humeri. Plot depicts *Alca* species clusters and representative humeri. (1) *A. minor* holotype specimen (USNM 302324). (2) *A. torda* (USNM 502382). (3) *A. ausonia* cast of holotype specimen (IGF 14875). (4) *A. grandis* holotype specimen (ANSP 13357). (5) *A. carolinensis* (NCSM 13734). (6) *A. stewarti* cast of paratype specimen (NHMUK PV A 7052). *A. olsoni* not shown owing to overlap in size range with *A. carolinensis*. Note that *A. minor* is represented only by the centroid because only one complete humerus is known from that taxon. Values on vertical and horizontal axes represent the coefficients of the variables of the discriminant axes, where discriminant function 1 represents the maximum amount of variation in the data.

average, than extant examples (Table 4) but are otherwise morphologically identical to the extant sample with respect to humeral morphology.

Adding further support to the hypothesis that at least six species in *Alca* are represented among fossils sampled, the range of size variation based on greatest length of the humerus within five of the six clusters is congruent with the size range established on the basis of extant alcids (Table 3). Only values for *A. stewarti* showed a range significantly different from that observed in other alcids. This may be an artifact, because only three complete humeri are known from this taxon. Values of size variation calculated using measurements from distal humeri referred to *A. stewarti* ( $n = 10$ ) vary 5.3% from the median, a value similar to estimates of size variation for other *Alca* (Table 3).

TABLE 4. Measurements of *Alca humeri* (mm). Abbreviations: Bd = breadth of the distal end, Bp = breadth of proximal end, Dd = distal diagonal, Dip = diagonal of proximal end, Gl = greatest length, and Sc = smallest dorsoventral breadth of corpus (shaft). Extant *Alca torda* specimen numbers listed in Appendix 1.

Taxon	Specimen	Bd	Bp	Dd	Dip	Gl	Sc
<i>Alca ausonia</i>	IGF 14875	12.4	–	9.2	–	–	7.5
<i>A. carolinensis</i>	NCSM 13734	14.9	20.8	10.4	21.0	102.4	9.2
<i>A. grandis</i>	ANSP 13357	13.9	19.7	9.4	18.8	97.2	8.2
<i>A. minor</i>	USNM 302324	–	13.8	–	–	63.7	5.7
	USNM 192879	–	13.2	–	–	–	–
	USNM 495600	9.1	–	7.0	–	–	5.8
<i>A. olsoni</i>	USNM 454590	15.4	22.8	11.0	21.7	104.0	8.8
<i>A. stewarti</i>	NHMUK PV A 7052	15.5	22.8	12.1	21.8	111.2	8.9
<i>A. torda</i> (extant)	Average ( $n = 13$ )	11.2	16.4	8.1	15.7	78.4	7.0
<i>A. torda</i> (fossils)	Average ( $n$ )	11.5	16.5	8.4	15.5	78.8	6.8
		( $n = 14$ )	( $n = 44$ )	( $n = 14$ )	( $n = 43$ )	( $n = 17$ )	( $n = 44$ )

Morphological comparison of the six clusters of fossils revealed previously undocumented morphological variation, which allowed for referral of three associated *Alca* specimens to species. Humeri of *A. carolinensis* and *A. olsoni* could not be discriminated on the basis of morphological differences. *Alca* diversity would therefore be underestimated if it were not for the association of other elements (e.g., ulnae) in the holotype specimens of those species, which display distinct morphological differences. Combination of holotype and referred specimens into supraspecific terminals decreased the amount of missing data for *Alca* species terminals and facilitated phylogenetic analysis.

Additional analyses performed on a subset of fossil measurement data collected from the Early Pliocene Yorktown Formation also recovered six statistically supported clusters of complete and partial humeri. Morphological evaluation of specimens from this locality confirms that all seven *Alca* species were present in North Carolina during the Pliocene.

Specimens from the Early Pliocene Bone Valley Formation of southern Florida (i.e., '*Australca grandis*' sensu Brodkorb 1955) were assigned to three distinct size classes and displayed a large range of size variation (based on measurements of distal humeri; 14.5%), which suggests that more than one species is represented by this assemblage. The principal component analysis by Olson and Rasmussen (2001) obtained a similar result. Only one complete humerus (GCVP 5691) is known from this location. That specimen was recovered within the

cluster representing *Alca grandis* (i.e., '*Australca grandis*' sensu Brodkorb 1955). However, analysis of 45 proximal and distal humeri from that location grouped '*Australca*' specimens in clusters corresponding to *Alca grandis*, *A. torda*, and *A. ausonia* (Appendix 2).

Strong statistical support for morphometrically derived clusters of fossils and congruence between those groups and those based on discrete morphological characters permitted referral of 203 *Alca* humeri to species (Appendix 2). Additionally, specimens were consistently clustered together in analysis of multiple subsets of data. For example, the holotype humerus of *A. carolinensis* was clustered with the same specimens in analyses of complete humeri, proximal humeri, and distal humeri. Nineteen complete humeri (e.g., USNM 446692; Appendix 2) can now be confidently referred to *A. ausonia*, which was previously known only from the holotype specimen, a distal humerus. Two associated specimens (USNM 336379, USNM 215454) are referred to *A. grandis*, greatly increasing the number of characters available for phylogenetic analysis of that taxon. An additional associated specimen (USNM 242238) is referred to *A. stewarti*.

The referral of *Alca* humeri via the combined morphometric and phylogenetic analyses allowed for the calculation of tentative estimates of relative species abundance from the Yorktown Formation. The most abundantly represented taxon, evidently, is *A. grandis* (25.7%), although humeri representing *A. carolinensis* and *A. olsoni* (27.6%) are combined owing to the morphological similarity of the humeri of

those species. Remains of *A. minor* (3.9%) and *A. stewarti* (2.0%) are the least frequently represented. The remainder of the sample was composed of the remains of *A. ausonia* (18.4%) and *A. torda* (22.4%). These estimates of relative species abundance assume that all seven species lived contemporaneously and that the Yorktown Formation is not significantly time-averaged with respect to adjacent geological units. Chronological evaluation of *Alca* species diversity within the Yorktown Formation will require direct sampling of in situ *Alca* fossils. Exposures of the Yorktown Formation outside the PCS Phosphate Mine are rare, and permission to sample directly from in situ strata at the PCS Mine has not been obtained.

The possibility of the presence of a Pliocene auk even larger than *A. stewarti* was mentioned by Olson and Rasmussen (2001) and Dyke and Walker (2005). The specimen mentioned by Olson and Rasmussen (2001; USNM 181090) was evaluated and found to be within the statistically supported size range of *A. stewarti*. A very large maxilla (NHMUK PV A 9033; formerly BMNH A 9033) with the mediolateral compression and dorsal expansion characteristic of *Alca* and *Pinguinus* maxillae was reported by Dyke and Walker (2005). Given the very large quantities of Pliocene *Alca* fossils and the lack of statistical support for an *Alca* species larger than *A. stewarti*, it seems likely that this specimen represents the first record of *Pinguinus* from the Early Pliocene Kallu Sands Formation of

Belgium. Although fragmentary, the curvature and size of NHMUK PV A 9033 agrees more with specimens of *Pinguinus* than with those known for *Alca*.

#### PHYLOGENETIC ANALYSIS

Phylogenetic analysis of the combined matrix resulted in a single most parsimonious tree of 1,931 steps (consistency index 0.80, retention index 0.47, rescaled consistency index 0.38; Fig. 6). Bootstrap and Bremer support values were highest for clades with higher proportions of extant taxa and, thus, available molecular data (i.e., *Pinguinus* and *Uria*) and were fairly low for clades including abundant extinct taxa with significant amounts of missing data (i.e., *Alca* and *Miocepphus*). Optimized characters that support recovered clades are listed in Table 5.

As in previous studies (Strauch 1985, Chandler 1990, Moum et al. 2002, Baker et al. 2007, Pereira and Baker 2008, Smith 2011), the present study recovered strong support for a clade composed of *Alca* and *Pinguinus*, although relationships between *Alca* species remained partially unresolved. *Alca torda* and *A. minor* were recovered as sister taxa, and *A. stewarti*, *A. carolinensis*, and *A. olsoni* were recovered as successive outgroups to this clade. The positions of *A. grandis* and *A. ausonia* remain unresolved at the base of *Alca*. Although the sister relationship of *Pinguinus impennis* and *P. alfrednewtoni* is strongly supported by these

TABLE 5. Unambiguously optimized morphological apomorphies supporting alcid clades in the resultant phylogenetic tree (Fig. 6). Character numbers from Appendix 3 are followed by character state symbols (e.g., (23:0) corresponds with character 23, state 0). Characters followed by an asterisk are locally optimized apomorphies with a CI <1.0. All other characters have a consistency index = 1.0.

Clade	Character numbers and states that support monophyly
Alcini:	(9:0); (44:0); (46:0); (47:0); (58:0); (63:0); (64:0); (71:0); (75:0); (77:0); (78:0); (85:1); (101:1); (103:0); (105:1); (115:1); (117:1); (119:1); (130:1).
<i>Alca</i> + <i>Pinguinus</i> :	(13:1); (22:1); (61:1); (114:0).
<i>Alca</i> :	(122:0)*.
<i>Pinguinus</i> :	(55:1); (93:1); (121:0); (125:0).
<i>Uria</i> + <i>Alle</i> + <i>Miocepphus</i> :	(4:1); (18:0); (24:1); (25:0); (96:1).
<i>Uria</i> :	(92:1)*; (102:1)*; (110:1)*.
<i>Alle</i> + <i>Miocepphus</i> :	(49:1); (91:0).
<i>Alle</i> + <i>Miocepphus mergulellus</i> :	(62:1)*; (68:0)*.
<i>Alca torda</i> + <i>A. minor</i> + <i>A. stewarti</i> + <i>A. carolinensis</i> + <i>A. olsoni</i> :	(36:1); (102:1)*.
<i>A. torda</i> + <i>A. minor</i> + <i>A. stewarti</i> :	(53:0)*; (67:0)*; (94:1)*.
<i>A. torda</i> + <i>A. minor</i> :	(65:1)*.

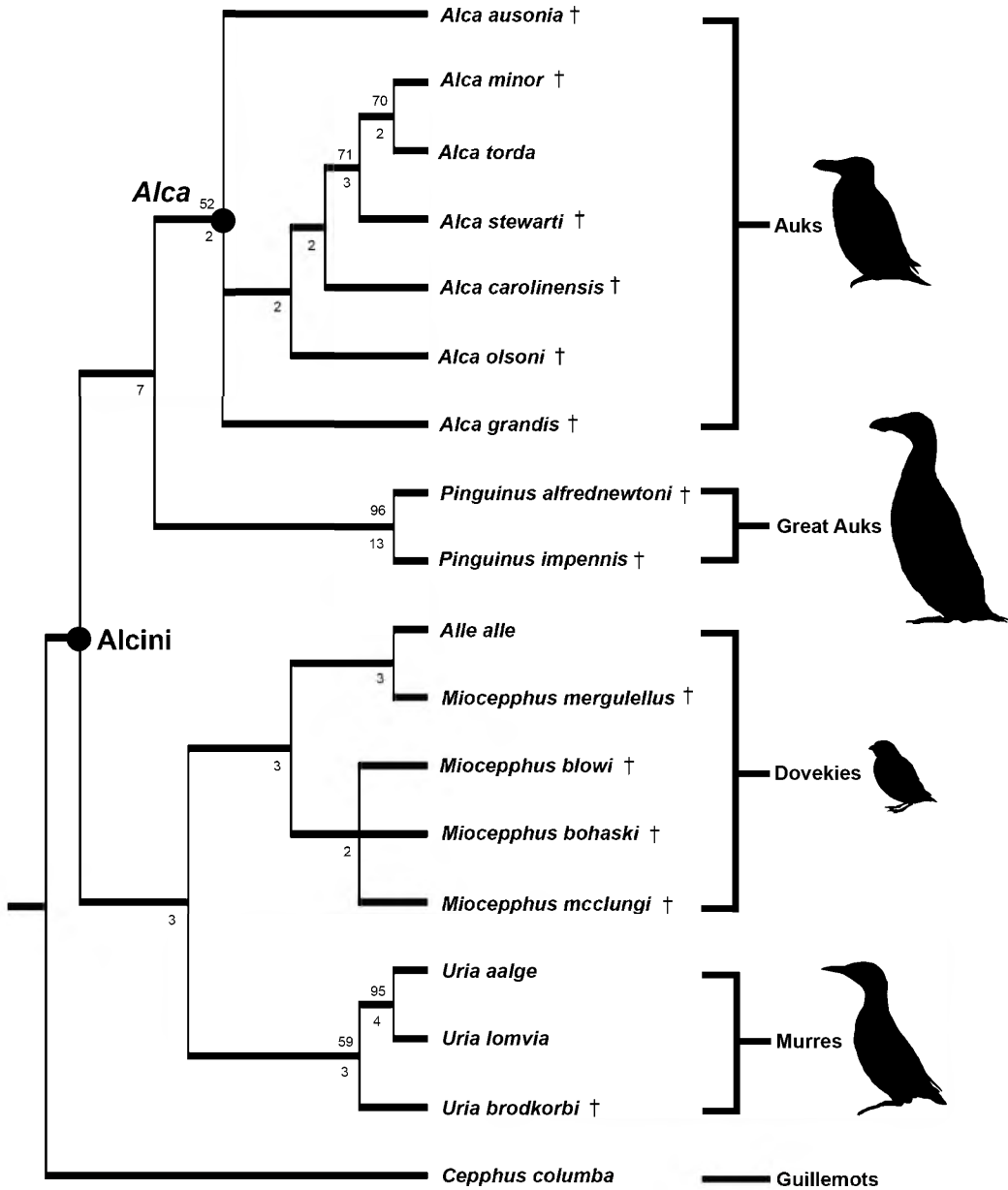


FIG. 6. Cladogram of Alcini relationships (single most parsimonious tree of length 1,931 steps; consistency index 0.80, retention index 0.47, rescaled consistency index 0.38). Bootstrap support values >50% are presented above and Bremer support values are presented below the node they refer to.

results, the monophyly of *Alca* with respect to *Pinguinus* is weakly supported. We identified four unambiguously optimized morphological characters that unite *Alca* and *Pinguinus*, but only a single locally optimized apomorphy that supports the monophyly of *Alca* (Table 5).

Further clarification of the systematic relationship between *Alca* and *Pinguinus*, and support for *Alca* monophyly, will require discovery of additional associated *Alca* fossil specimens referable to species. Although there are documented integumentary differences between



*A. torda* and *P. impennis* (Strauch 1985, Chandler 1990, Smith 2011), there are no known fossils that preserve integumentary details of additional extinct *Alca* and *Pinguinus* species that might provide these missing data, data that might further clarify the relationship between species in *Alca* and *Pinguinus*.

The *Alca* + *Pinguinus* clade was recovered as the sister to *Uria*, *Miocepphus*, and *Alle*. *Uria* was recovered as monophyletic, with *U. brodkorbi* placed as an outgroup to sister taxa *U. aalge* and *U. lomvia*. *Uria* is placed as the sister taxon to a clade composed of *Miocepphus* and *Alle*. *Alle alle* is placed as the sister taxon to *Miocepphus mergulellus*. *Alle alle* and *M. mergulellus* were recovered as the sister taxon to an unresolved clade composed of the other *Miocepphus* species (i.e., *M. blowi*, *M. bohaski*, and *M. mcclungi*).

Because this was the first phylogenetic analysis to include all 17 Alcini species, 12 of which had not been phylogenetically analyzed before, comparison of these results with those of previous analyses is necessarily somewhat limited. *Alca torda* has been recovered as the sister taxon to *P. impennis* in every analysis that has included both taxa (Strauch 1985, Chandler 1990, Moum et al. 2002, Baker et al. 2007, Pereira and Baker 2008, Smith 2011). However, extinct *Alca* species, *Miocepphus* species, *Uria brodkorbi*, and *P. alfrednewtoni* have not been included in previous phylogenetic analyses. The sister relationship between *Alca* plus *Pinguinus* and *Uria* is also strongly supported by the results of previous analyses (Strauch 1985, Chandler 1990, Moum et al. 2002, Baker et al. 2007, Pereira and Baker 2008, Smith 2011).

The systematic position of *Alle alle* is one of the most contentious issues in alcid systematics because this taxon has been recovered as sister to *Alca* (Moum et al. 1994), outgroup to *Alca* and *Pinguinus* (Moum et al. 2002, Baker et al. 2007), sister to *Alca* and *Pinguinus* plus *Uria* (Strauch 1985), sister to *Uria* (Thomas et al. 2004, Pereira and Baker 2008, Smith 2011), sister to Fraterculinae (Chandler 1990), and sister to *Cephus*, *Aethia*, and *Brachyramphus* (Chu 1998). The nested placement of *Alle* along with *Miocepphus* species supports the hypothesized affinity between these taxa (Wijnker and Olson 2009). The placement of *Alle* and *Miocepphus* as the sister taxon to *Uria* is also congruent with the molecular-based results of Pereira and Baker (2008) and Thomas et al. (2004) in which *Alle alle* was placed as the sister to *Uria*.

#### SYSTEMATIC PALEONTOLOGY

Aves Linnaeus, 1758  
Charadriiformes Huxley, 1867  
Alcidae Leach, 1820  
Alcini Storer, 1960  
*Alca* Linnaeus, 1758

*Diagnosis*.—*Alca* is referable to Alcidae based on dorsoventral compression of the humerus (78:0), radius, and ulna (101:0). The shafts of these elements are more rounded in cross section in all other Charadriiformes. The humeral, radial, and ulnar shafts of *Cephus* and *Pseudocepphus teres* are intermediate with respect to shaft-roundness (78:1; 101:1) as compared to all other Alcidae and Charadriiformes systematically placed outside of Alcidae. As in all alcids except Mancallinae Brodkorb, 1967, the dorsal cotylar process of the ulna is anteriorly expanded to a degree exceeding that of other Charadriiformes (Smith 2011). As in all Alcidae, the sternum is elongated in comparison with the relatively shorter sterna of other Charadriiformes. *Alca* is referable to Alcini (contents = *Alca* + *Pinguinus* + *Uria* + *Alle* + *Miocepphus*) based on anterior flattening of the extensor process of the carpo-metacarpus (105:1). *Alca* is differentiated from *Pinguinus* by the restriction of the deltopectoral crest to the proximal half of the humeral shaft (55:0). The coracobrachial nerve sulcus of *Alca* and *Pinguinus* is a closed duct (61:1), rather than an open sulcus (61:0) as in other Alcini. *Alca* and *Pinguinus* are differentiated from *Uria*, *Alle*, and *Miocepphus mergulellus* on the basis of the equal width of the tricipital sulci of the distal humerus (82:1). The humerotricipital sulcus is wider than the scapulo-tricipital sulcus in *Uria* (82:0) and *M. mergulellus*. The scapulo-tricipital sulcus is wider than the humerotricipital sulcus in *Alle* (82:2).

*Remarks*.—Despite a long history of study, no osteological apomorphies specific to *Alca* have been identified. This lack of osteological distinction from *Pinguinus* calls into question the monophyly of *Pinguinus* with respect to *Alca*. *Alca* (sensu Linnaeus, 1758) originally contained the Great Auk, which was then known as *Alca impennis*. Both Strauch (1985) and Chandler (1990) recommended that *Pinguinus* be synonymized with *Alca*; however, both the AOU and the British Ornithologists' Union have followed the recommendations of Salomonsen (1944) and Olson (1977) in maintaining the generic status of

*Pinguinus*. Although *P. impennis* is characterized by many apomorphies with respect to *A. tarda*, the monophyly of *Alca* to the exclusion of *Pinguinus* is weakly supported by current osteological data. However, knowledge of the skeletal anatomy of extinct *Alca* that might bolster support for *Alca* monophyly is currently incomplete for most species in the clade.

The original diagnosis of *Alca* Linnaeus, 1758 was as a member of the Order Natatore (anseriforms, podicipediforms, gaviiforms, sphenisciforms, pelicaniforms, and charadriiforms), which was defined by "the backward position of the legs, which are thrown entirely behind the equilibrium of their body, and with wings considerably shorter, and less covered with feathers than those of any other birds" (Vigors 1825:497). Family "Alcadae" (sensu Vigors, 1825) was differentiated and later separated from other Natatore (sensu Linnaeus, 1758) on the basis of the tridactyl configuration of the feet (i.e., absence of a hallux) and differentiated from sphenisciforms by the mediolateral compression of the bill. Close relationship of alcids with penguins was a common misconception (e.g., Linnaeus 1758, Verheyen 1958, Gysels and Rabaey 1964). Originally, *Alca* (sensu Linnaeus, 1758) included six species: *A. impennis*, *A. tarda*, *A. pica*, *A. arctica*, *A. lomvia*, and *A. alle*. *Alca pica*, upon further study, turned out to be *A. tarda* in winter plumage (Coues 1868). The other five species are still recognized, though only *tarda* is placed within *Alca* in modern classifications (e.g., AOU 1998).

Unlike the preceding classifications, that of Gadow (1892) considered osteological and behavioral characteristics in making distinctions between avian taxa. Alcidae was placed along with Laridae in Suborder Gaviae of the Order Charadriiformes on the basis of five characters: aquatic lifestyle, complex coloration of down in nestlings, ossified supraorbital rims, and hypotarsus with two grooves (Gadow 1892). Among Gaviae, Gadow (1892) diagnosed Alcidae on the basis of five additional characters: "Periarctic" (i.e., Holarctic) distribution, coracoids not fused, dorsal supracondylar process absent (this feature is not absent but merely reduced in alcids compared with larids), presence of a procoracoid process, and sternum with only two notches posteriorly (i.e., medial sternal notches absent; contra Gadow 1892, medial sternal notches are present in puffins [Smith

2011]). *Alca* (including *Pinguinus*) was further distinguished from other Alcidae by Beddard (1898) on the basis of three characters: foramen at the anterior end of the supra-orbital groove, lack of a medial notch of the sternum (in contrast with puffins), and two *brevis* tendons (i.e., m. brachialis with two heads) that pass over the extensors and insert on the ulna. The oological study of Dawson (1920) differentiated *Alca* and *Uria* from other alcids on the basis of four characters: single-egg clutches, ovate shape, dull luster, and granular texture. In a study of Alcidae hind-limb osteology, Storer (1945) united *Alca*, *Pinguinus*, and *Uria* in Alcini and cited the following characteristics: long and narrow postacetabular ilium; narrow, tapering posterior ischium; leg of medium length, with thick joints; moderately heavy toes with short, broad claws; and especially heavy tarsometatarsus with a groove on its upper surface.

More recent osteological studies (Strauch 1985, Chandler 1990) have resulted in an increasing suite of proposed diagnostic characters for *Alca* and *Pinguinus*. The compatibility analysis of Strauch (1985) identified a clade composed of *A. tarda* and *P. impennis*, which was defined by the presence of a coracoid foramen, a flat extensor process of the carpometacarpus, first tendinal canal of the hypotarsus a narrow groove, completely feathered nostrils, one incubation patch, intermediate posthatching development pattern, nesting in the open, and pointed retrices. The phylogenetic analysis of Chandler (1990) identified five additional apomorphies that unite *Alca* and *Pinguinus*: enlarged premaxilla, nasal bar extending beneath premaxilla, ventral cotyla of the ulna with a lateral crest that is separate from the ventral collateral ligament tubercle, and a crest that extends from the shaft of the femur to the lateral edge of the ventral cotyla.

The earliest known fossil referred to Alcidae was also proposed to have affinities with *Alca*. This specimen (GCVP 5690) was reported from the Late Eocene (34.2–36 Ma) Clinchfield Formation of Wilkinson County, Georgia (Chandler and Parmley 2002), and consists of an isolated and weathered distal humerus. The equal width of the tricripital sulci are consistent with the morphology of *Alca* and *Pinguinus*; however, owing to the weathered and fragmentary nature of this isolated specimen, it cannot be confidently referred at this time. It is best considered Alcidae *incertae sedis*.

Two specimens from Late Miocene deposits in Laguna Hills, California, were tentatively referred to *Alca* (Howard 1968). These specimens consist of a fragment of coracoid (LACM 18282) and a poorly preserved distal humerus (LACM 18283). Recent reexamination of these specimens failed to identify any apomorphies that would support referral to any Alcini taxon. Furthermore, no additional material has been referred to *Alca* from Pacific localities in the intervening 40 years. Thus, *Alca* affinities of these specimens are considered unreliable, and these fossils are best considered *Alcidae incertae sedis*.

Although previously referred *Alca* cranial material is largely restricted to bills (Olson and Rasmussen 2001, Dyke and Walker 2005), two fossilized skulls from Pliocene deposits have been referred to *Alca* (Fig. 7). The first specimen (Alam 0001) is housed in the collections of the Asociación Cultural Paleontológica Murciana in Murcia, Spain, and was described by Sanchez-Marco (2003). Recent reexamination of this specimen confirms its referral to *Alca* on the basis of the mediolaterally compressed and dorsoventrally expanded premaxilla and deeply incised salt-gland fossae. The second skull (NCSM 24139) was recovered from the Yorktown Formation exposed at Aurora, North Carolina, and is reported here for the first time (Fig. 7). These two skulls are both comparable in size and morphological characteristics to *A. torda*, although they lack any associated postcranial material, preventing referral of these specimens to species at this time. There is currently only a single associated *Alca* fossil specimen with both cranial and postcranial elements preserved (USNM 336380; Olson and Rasmussen 2001) that might allow diagnosis of cranial characters for extinct *Alca* species. The only cranial element preserved by USNM 336380 is the premaxilla, and no discrete morphological variation was identified among that specimen, the two skulls described above, and extant *A. torda* specimens.

#### *Alca torda* Linnaeus, 1758

**Diagnosis.**—*Alca torda* is differentiated from other species of *Alca* by the following humeral characteristics: distal margin of posterior humeral head rounded as in *A. stewarti* and *A. minor* (53:0; pointed in *A. olsoni*, *A. stewarti*, *A. ausonia*, and *A. grandis*); dorsal margin of the primary pneumotricipital fossa (i.e., fossa pneumotricipitalis ventrale; Baumel and Witmer 1993) of *A. torda*

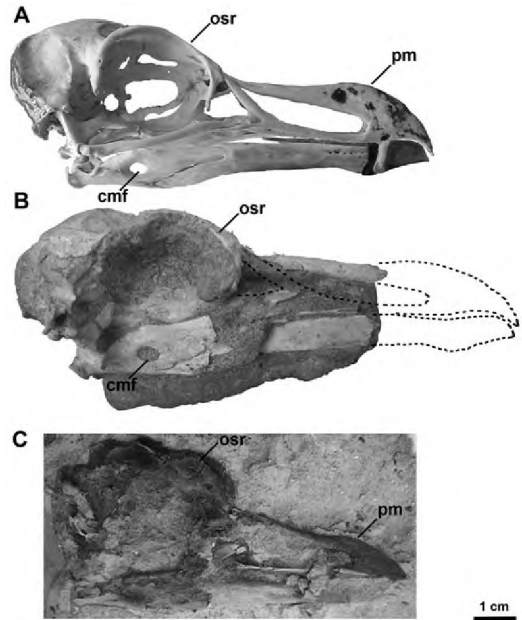


FIG. 7. Comparison of *Alca* skulls in right lateral view. (A) *A. torda* NCSM 20058. (B) Alam-001. (C) NCSM 24139. Anatomical abbreviations: cmf = caudal mandibular fenestra, osr = ossified supraorbital rim, and pm = dorsally expanded premaxilla.

and *A. minor* extends farther distally (65:1) than in all other *Alca*; primary pneumotricipital fossa rounded as in *A. minor* and *A. stewarti* (67:0; oval in all other *Alca*); distal edge of the primary pneumotricipital fossa straight as in *A. carolinensis*, *A. grandis*, *A. olsoni*, and *A. stewarti* (70:1; concave in *A. minor* and *A. ausonia*). The size of *A. torda* is intermediate between that of the smaller *A. minor* and the larger *A. ausonia* (Table 4 and Fig. 2).

**Remarks.**—Remains of at least four species of *Alca* from Early Pliocene deposits in North Carolina (*Alca* aff. *torda*, *A. ausonia*, *A. grandis*, *Alca* sp.) were reported by Olson and Rasmussen (2001). Among these fossils are specimens that agree in both size and morphological characteristics with examples of extant *A. torda* (Fig. 2). Furthermore, Miocene-aged (5–10 Ma) specimens from deposits in Maryland and Virginia were recently referred to *Alca* cf. *torda* by Wijnker and Olson (2009). Although estimates of the average geological longevity of species are variable (May et al. 1995), the existence of *A. torda* throughout the last 10 Ma would constitute an example of extreme species-longevity. Issues related to the diagnosability of

fossils that are morphologically similar or indistinguishable from extant taxa have been previously discussed in detail (Stewart 2002, 2007; Stewart and Beech 2006). Incomplete fossil remains sometimes do not preserve the key skeletal elements that are required to recognize different species with ecomorphologies similar to those of living species (Stewart 2002). The extension of the temporal range of an extant species into the Miocene prompts questions about both the longevity and diagnosability of species, though no discrete differences in size or morphology between Miocene and Pliocene fossils attributed to *A. torda* and extant *A. torda* specimens were noted in specimens examined.

***Alca grandis* (Marsh, 1870)**

*Holotype*.—Left humerus (ANSP 13357; Figs. 2 and 5).

*Referred material*.—Right coracoid, right distal humerus (USNM 215454; specimen referred to *A. grandis* by Olson and Rasmussen 2001; Fig. 8); partial sternum, right distal humerus, right proximal radius, right ulna, right distal carpometacarpus, right digit 1 phalanx 1, right digit II phalanx 1, right digit II phalanx 2, partial pelvis, right femur, right proximal tibiotarsus (USNM 336379; specimen referred to *A. grandis* by Olson and Rasmussen 2001; Fig. 9). See Appendix 2 for referral of isolated humeri.

*Original diagnosis*.—Originally described by Marsh (1870:213–214) as *Cataractes antiquus* (see Olson 2007) and diagnosed in relation to *Uria lomvia* on the basis of the following osteological characteristics: humeral head more obtusely rounded; tricipital grooves of roughly equal width; small posterodorsally projecting tubercle on the posterodistal margin of the ventral tubercle (Fig. 10); ventral condyle anteroposteriorly narrow.

*Amended diagnosis*.—*Alca grandis* is characterized by a small posterodorsally projecting tubercle on the posterodistal margin of the ventral tubercle of the humerus (84:1), which is absent in all other *Alca* species but is present in *Pinguinus* (Fig. 10). As in all *Alca*, restriction of the deltopectoral crest to the proximal half of the humeral shaft (55:0) differentiates *A. grandis* from *Pinguinus*. *Alca grandis* is further differentiated from other *Alca* by the following characteristics: dorsal margin of the medial sternal process of coracoid notched (51:1) as in *A. torda* and *A. carolinensis* (absent in other *Alca* for which the coracoid is known;

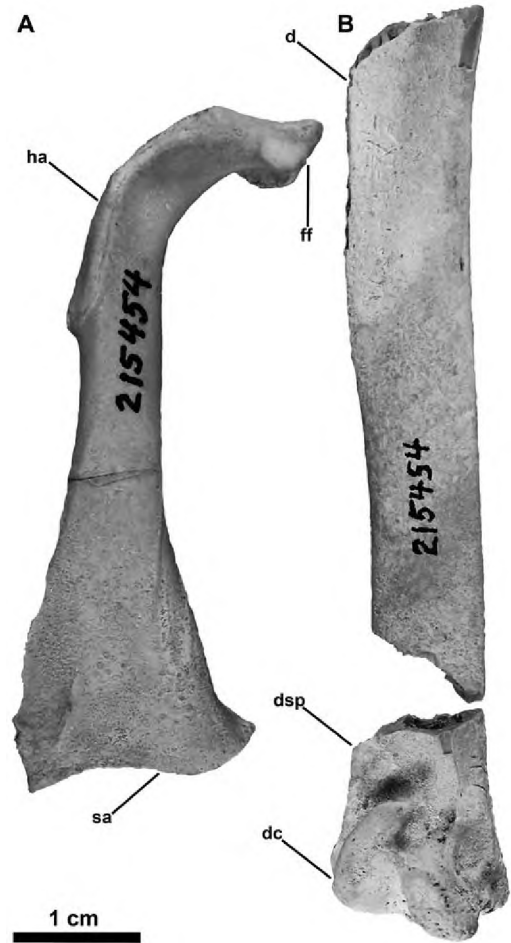


FIG. 8. *Alca grandis* referred associated specimen (USNM 215454). (A) Right coracoid, (mediolateral view). (B) Distal left humerus in two pieces (anterior view). Anatomical abbreviations: d = deltopectoral crest, dc = dorsal condyle, dsp = dorsal supracondylar process, ff = furcular facet, ha = humeral articulation facet, and sa = sternal articular surface of coracoid.

i.e., *A. stewarti* and *A. olsoni*); distal margin of posterior humeral head pointed (53:1; rounded in *A. stewarti*, *A. minor*, and *A. torda*); primary pneumotricipital fossa of humerus oval (67:1) as in *A. ausonia*, *A. carolinensis*, and *A. olsoni* (rounded in other *Alca*); olecranon curves posteriorly (94:0) as in *A. carolinensis* and *A. olsoni* (curves anteriorly in *A. stewarti* and *A. torda*); anterior margin of dorsal cotylar prominence of ulna rounded (97:0) as in *A. carolinensis* and *A. torda* (margin straight in *A. olsoni* and *A. stewarti*); dorsal condyle of ulna rounded (102:0) as

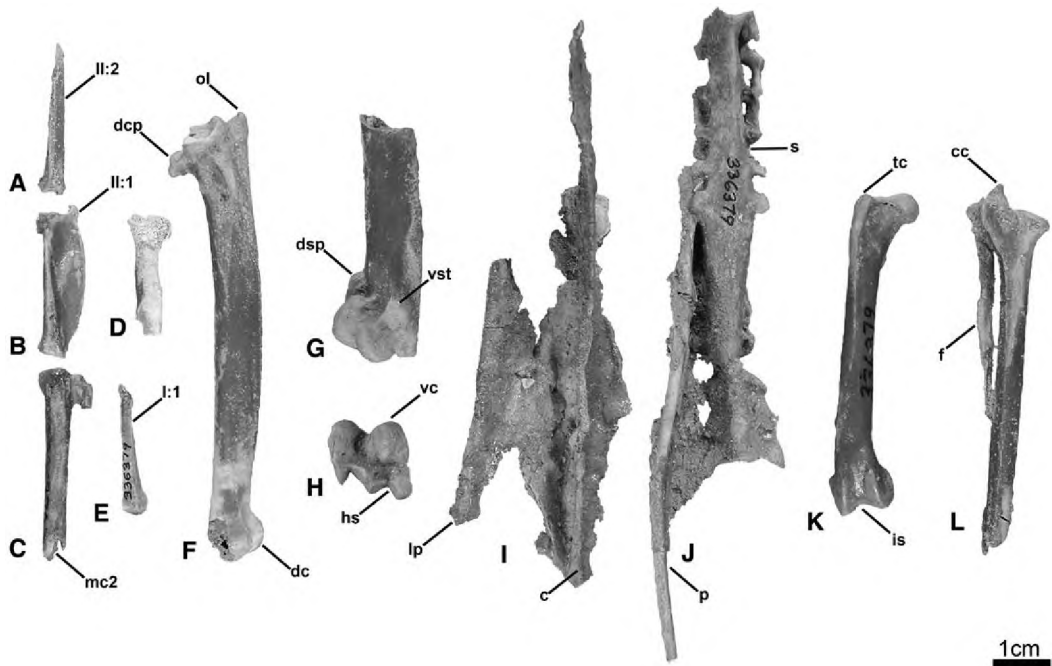


FIG. 9. *Alca grandis* referred associated specimen (USNM 336379), prepared from matrix since original description (see Olson and Rasmussen 2001:fig. 13). (A) Digit II phalanx 2 (dorsal view). (B) Digit II phalanx 1 (dorsal view). (C) Right distal carpometacarpus (ventral view). (D) Right proximal radius (ventral view). (E) Digit I phalanx 1 (dorsal view). (F) Right ulna (ventral view). (G) Distal right humerus (anterior view). (H) Right humerus (distal view). (I) Partial sternum (ventral view). (J) Partial pelvis (ventral view). (K) Right femur (anterior view). (L) Right proximal tibiotarsus and fibula (anteromedial view). Anatomical abbreviations: I:1 = manual phalanx I:1, II:1 = manual phalanx II:1, II:2 = manual phalanx II:2, c = carina, cc = cnemial crest, dc = dorsal condyle, dcp = dorsal cotylar process, dsp = dorsal supracondylar process, f = fibula, hs = humerotricipital sulcus, is = intercondylar sulcus, lp = lateral process, mc2 = metacarpal 2, ol = olecranon process, p = pubis, s = sacrum, tc = trochanteric crest, vst = ventral supracondylar tubercle, and vc = ventral condyle.

in *A. olsoni* (angled in *A. torda* and *A. stewarti*); distal tendinal groove of carpometacarpus a sulcus (108:0) as in *A. torda* rather than a closed canal as in *A. carolinensis*. In size, *A. grandis* is between the smaller *A. ausonia* and the larger *A. carolinensis* (Table 4 and Fig. 2).

**Remarks.**—*Catarractes antiquus* was described by Marsh in 1870 on the basis of a left humerus with minor damage to the bicipital crest from Pliocene deposits in North Carolina (Fig. 2). Characteristics of this fossil prompted Olson and Rasmussen (2001) to create a new combination for this species, *Alca antiqua* (Marsh, 1870). *Alca antiqua* became *A. grandis* (Marsh, 1870), because the previous name was “a secondary homonym preoccupied by *Alca antiqua* Gmelin, 1789, a basonym of the extant Ancient Murrelet *Synthliboramphus antiquus*, and was therefore unavailable for the fossil species”

(Olson 2007:225). The species name *grandis* stems from *Australca grandis* Brodkorb, 1955, which was recognized as a junior synonym of *Alca antiqua* by Olson and Rasmussen (2001). Numerous examples of this species are known from Yorktown Formation deposits at PCS Phosphate Mine (Olson and Rasmussen 2001). The morphology and size of the coracoid referred to *Alca grandis* herein (USNM 215454) is comparable to that of the holotype specimen of *Australca grandis* (UF/PB 141). These data support the synonymy of *Australca grandis* Brodkorb, 1955 and *Alca antiqua* Marsh, 1870 by Olson and Rasmussen (2001). Numerous examples of *Alca grandis* are known from Yorktown Formation deposits at PCS Phosphate Mine (Olson and Rasmussen 2001), and *Alca grandis* has also been reported from the Pliocene of Belgium (Dyke and Walker 2005).

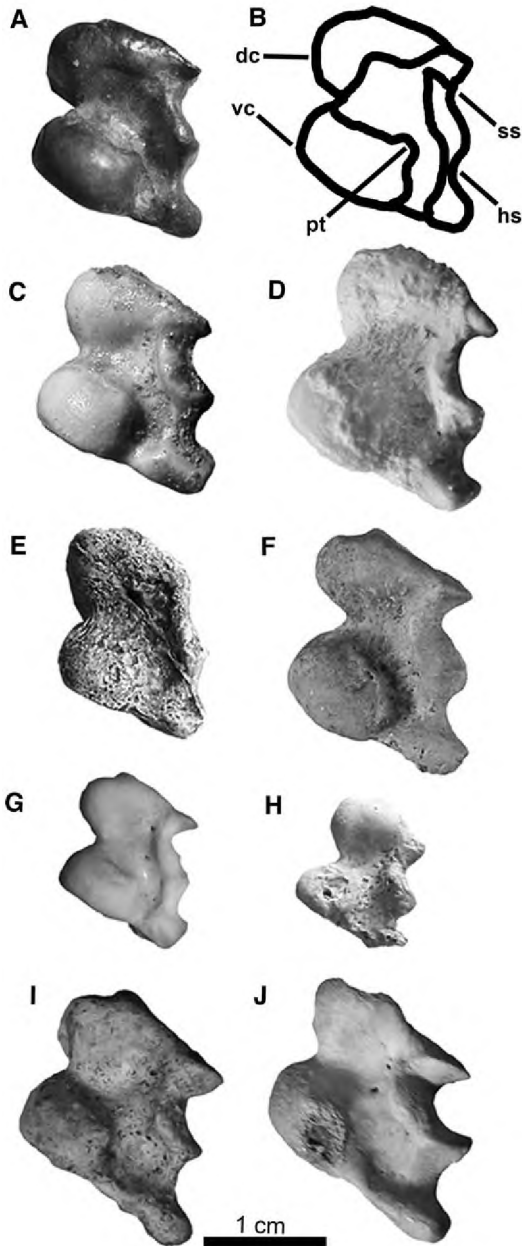


FIG. 10. Distal view of *Alca* and *Pinguinus* humeri. (A) *A. grandis* (ANSP 13357). (B) Line drawing of *A. grandis*. (C) *A. carolinensis* (NCSM 13734). (D) *A. stewarti* (NHMUK PV A 7052). (E) *A. ausonia* (IGF 14875). (F) *A. olsoni* (USNM 454590). (G) *A. torda* (USNM 502382). (H) *A. minor* (USNM 495600). (I) *P. impennis* (USNM 623465). (J) *P. alfrednewtoni* (USNM 366630). Anatomical abbreviations: dc = dorsal condyle, hs = humerotricipital sulcus, pt = proximodistal tubercle, ss = scapulo-tricipital sulcus, and vc = ventral condyle.

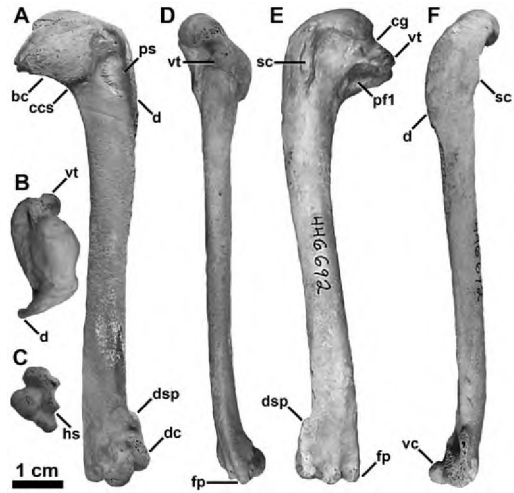


FIG. 11. *Alca ausonia* referred left humerus (USNM 446692): (A) anterior view, (B) proximal view, (C) distal view, (D) ventral view, (E) posterior view, and (F) dorsal view. Anatomical abbreviations: bc = bicipital crest, ccs = coracobrachial sulcus, cg = capital groove, d = deltopectoral crest, dc = dorsal condyle, dsp = dorsal supracondylar process, fp = flexor process, hs = humerotricipital sulcus, pfl = primary pneumotricipital fossa, ps = pectoralis scar, sc = supracoracoidal crest, vc = ventral condyle, and vt = ventral tubercle.

***Alca ausonia* (Portis, 1888)**

*Holotype*.—Right distal humerus (IGF 14875; Figs. 2 and 5).

*Referred material*.—Left humerus (USNM 446692; specimen previously referred to *Alca grandis* by Olson and Rasmussen, 2001; Figs. 2 and 11; Table 4). See Appendix 2 for referral of additional isolated specimens.

*Original diagnosis*.—Originally described as *Uria ausonia* by Portis (1888). Diagnostic characteristics relative to other Alcini taxa were not provided in the original description (Portis 1888) or subsequent publication (Portis 1891).

*Amended diagnosis*.—Although no autapomorphic characters are present in the humerus of *A. ausonia*, this species is differentiated from other *Alca* by the presence of a unique combination of characteristics. Owing to lack of associated specimens referable to *A. ausonia*, only humeri can be confidently referred to this species. The humeral shaft of *A. ausonia* is relatively more gracile than that of other *Alca* (ratio of greatest width at mid-shaft to greatest distal width = 1.65 *A. ausonia*; 1.69 *A. torda* fossils; 1.70 *A. grandis*). The coracobrachial

sulcus forms the dorsal and lateral margin of the bicipital surface, and the point at which the sulcus curves ventrally is variable in *Alca*. This area of curvature of the coracobrachial sulcus is located more dorsally in *A. ausonia* and *A. grandis* (62:0; positioned ventrally in other *Alca*). The shape of the distal edge of the primary pneumotricipital fossa is concave (70:0) in *A. minor* and *A. ausonia* (straight in other *Alca*). As in *A. carolinensis*, *A. grandis*, and *A. olsoni*, the posteriorly overturned portion of the humeral head is distally pointed (53:1; i.e., roughly triangular) in *A. ausonia*, whereas the profile of this feature is more rounded in *A. stewarti*, *A. minor*, and *A. torda*. The size of *A. ausonia* falls between the smaller *A. torda* and the larger *A. grandis* (Table 4 and Fig. 2).

**Remarks.**—A distal humerus (IGF 14875) from the Pliocene of Italy was described by Portis (1888, 1891). This fragmentary specimen (Fig. 2) was designated as the holotype of a new taxon *U. ausonia* Portis, 1888. *Uria ausonia* was diagnosed with respect to *U. aalge* solely on the basis of size (Portis 1888). A more complete description of this specimen followed (Portis 1891); however, the poor preservation of IGF 14875 prevented character-based diagnosis in relation to other closely related taxa (e.g., *A. torda* and *U. aalge*). Olson and Rasmussen (2001) referred this specimen to *Alca*. These authors (Olson and Rasmussen 2001) noted that the holotype specimen of *A. ausonia* agrees with characters that Marsh (1870) used to diagnose *A. grandis*, and that its size range falls between the smaller *A. torda* and the larger *A. grandis* (Fig. 2). Additional material from Italy representing this species is not known, although specimens of *A. ausonia* are common within the Early Pliocene Yorktown Formation exposed at PCS Phosphate Mine in Aurora, North Carolina, and have been reported from the Pliocene of Belgium (Dyke and Walker 2005). Recently, remains from Late Pliocene deposits in Morocco were referred to *A. ausonia* (Mourer-Chauviré and Geraads 2010) on the basis of size.

#### *Alca stewarti* Martin et al., 2001

**Holotype.**—Left ulna (NHMUK PV A 7050).

**Paratype.**—Right humerus cast (NHMUK PV A 7052; Figs. 2 and 5).

**Referred material.**—Partial sternum, left coracoid, right humerus, right radius, right ulna (USNM 242238; Fig. 12). This specimen was previously documented by Olson (1984, 1985), Olson and Rasmussen (2001), and Wijnker and Olson (2009). See Appendix 2 for referral of isolated specimens.

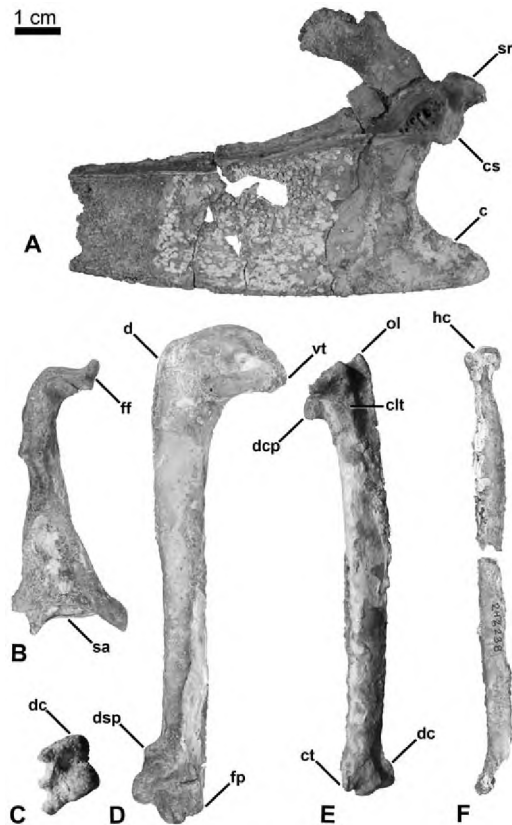


FIG. 12. *Alca stewarti* referred associated specimen (USNM 242238): (A) partial sternum (right lateral view), (B) left coracoid (posteromedial view), (C) right humerus (distal view), (D) right humerus (anterior view), (E) right ulna (ventral view), and (F) right radius (dorsal view). Anatomical abbreviations: c = carina, clt = ventral collateral ligament tubercle, cs = coracoidal sulcus, ct = carpal tubercle, d = deltopectoral crest, dc = dorsal condyle, dcp = dorsal cotylar process, dsp = dorsal supracondylar process, ff = furcular facet, fp = flexor process, hc = humeral styloid of radius, ol = olecranon process, sa = sternal articular surface of coracoid, sr = sternal rostrum, and vt = ventral tubercle.

**Original diagnosis.**—Proposed diagnostic characters cited in the original description of *A. stewarti* included deltopectoral crest less rounded; ventral tubercle of humerus more ventrally deflected; crus dorsale fossa of humerus positioned more obliquely; dorsal supracondylar process narrow, and extending farther proximally; humerotricipital sulcus broader than scapulotricipital sulcus.

**Amended diagnosis.**—Although missing data for other *Alca* species (e.g., *A. ausonia*) prevents the unambiguous optimization of all the characters listed below, examination of the holotype,

paratype, and additional referred material (USNM 242238, USNM 446650) identified the following unique suite of characteristics in which *A. stewarti* differs from other species of *Alca*: notch in medial sternal process of coracoid absent (51:0) as in *A. olsoni*; sternocoracoidal facet of coracoid angled  $\sim 135^\circ$  (52:1) as in *A. carolinensis*; dorsal humeral shaft between deltopectoral crest and dorsal tubercle slightly concave (57:0); capital incisure of humerus broader, and expanded farther ventrally; ventral tubercle of humerus more ventrally deflected than other *Alca* (76:1). Contra Martin et al. (2001), the tricipital sulci of the distal humerus are approximately equal in width, as in other *Alca*. *Alca stewarti* is larger (e.g., greatest length of humerus longer; Table 4 and Fig. 2) than all other known *Alca* heretofore described.

*Remarks.*—*Alca stewarti* was described from the Early Pliocene of Belgium by Martin et al. (2001). Although this species was originally diagnosed in relation to *A. torda* and Pliocene ‘*Australca*’ (i.e., Pliocene *Alca*), Martin et al. (2001) neither made mention of fossil comparative material examined nor referred to previously published figures of Pliocene species of *Alca* (Portis 1891, Shufeldt 1915, Brodkorb 1955). At the time of description, the ulna designated as the holotype specimen of *A. stewarti* (NHMUK PV A 7050) by Martin et al. (2001) was not directly comparable to the holotype specimens of previously described extinct species of *Alca*, all of which were humeri. Also, there were no associated *Alca* specimens referred to species on the basis of criteria other than size (Olson and Rasmussen 2001) that would allow for comparisons between holotype and additional fossil material referred to *A. stewarti* by Dyke and Walker (2005). None of the alcid remains described by Martin et al. (2001) or Dyke and Walker (2005) were associated; thus, referrals of elements other than ulnae to *A. stewarti* were based only on size, locality, and age. However, the humerus designated as the paratype specimen of *A. stewarti* (Fig. 2) by Martin et al. (2001) is diagnosably distinct from those of other *Alca*. Additionally, an associated specimen from the Late Miocene Eastover Formation of Virginia (USNM 242238; Fig. 12) is referable to *A. stewarti* on the basis of both size and diagnostic morphology. This specimen was documented previously but not assigned to species by Olson (1984, 1985) or Olson and Rasmussen (2001). In a recent review of Alcidae known from the Miocene of the northwestern

Atlantic Ocean basin, Wijnker and Olson (2009) referred this specimen to *A. stewarti* on the basis of its larger size in comparison with other known *Alca*. USNM 242238 comprises multiple associated elements, including a humerus and ulna, and therefore allows for confirmation of referrals of humeri to *A. stewarti* by Martin et al. (2001) and Dyke and Walker (2005), and also facilitates description of additional skeletal elements representing this taxon. Furthermore, USNM 242238 is the earliest known occurrence of *A. stewarti* (Wijnker and Olson 2009).

#### *Alca carolinensis*, sp. nov.

*Holotype.*—NCSM 13734: a partial postcranial skeleton comprising the following elements: furcula, sternum, ribs, left coracoid, right and left scapulae, right and left humeri, right and left ulnae, right radius, left radius missing proximal terminus, partial right ulnare, right carpometacarpus, and right manual phalanx I:1 (Figs. 2, 5, and 13). Although discovered partially articulated, all elements were prepared from the matrix to allow for detailed examination, description, and measurement of osteological features (Tables 4 and 6). The holotype specimen of *A. carolinensis* (NCSM 13734) was collected by Vince and Judy Schneider from the spoil piles at the PCS Phosphate Mine in Aurora, North Carolina, during a 1996 field expedition of the North Carolina Museum of Natural Sciences and was prepared by V. Schneider.

*Etymology.*—The species name *carolinensis* refers to the provenience of the holotype specimen in North Carolina.

*Locality and horizon.*—Aurora, Beaufort County, North Carolina; PCS Phosphate Mine (35°23' N; 76°47' 30" W; Fig. 1), Rushmere Member of the Yorktown Formation, Lower Pliocene (Berggren et al. 1995, Woodburne and Swisher 1995). Sedimentary characteristics of the matrix surrounding NCSM 13734, such as grain size, mineralogical composition, degree of induration, color, abundance of echinoderm fragments, and lack of phosphate nodules, are consistent with the sedimentology of the Rushmere Member of the Yorktown Formation (Snyder et al. 2001). Independent analysis of the foraminiferal assemblage identified the presence of *Elphidium* species and absence of *Parafissurina bidens* and also supports the referral of this specimen to the Rushmere Member (S. Snyder pers. comm.).

*Diagnosis.*—Proposed autapomorphies of *Alca carolinensis* include the presence of a dorsally



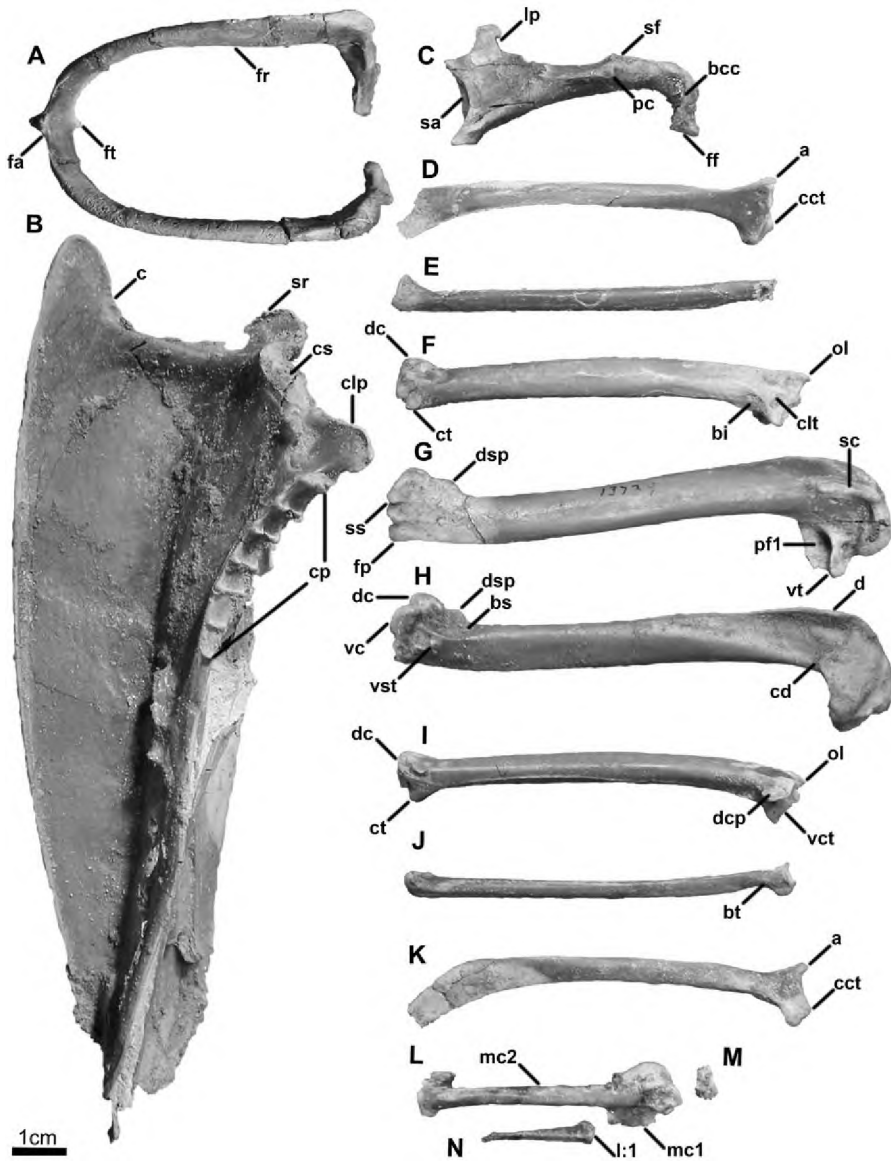


FIG. 13. Holotype specimen of *Alca carolinensis* (NCSM 13734) after preparation from matrix: (A) furcula (anterior view), (B) sternum (left lateral view), (C) left coracoid (posteromedial view), (D) left scapula (medial view), (E) left radius missing proximal end (ventral view), (F) left ulna (ventral view), (G) left humerus (posterior view), (H) right humerus (anterior view), (I) right ulna (dorsal view), (J) right radius (dorsal view), (K) right scapula (lateral view), (L) right carpometacarpus (dorsal view), (M) right ulnare (distal view), and (N) right digit 1:phalanx 1 (dorsal view). Anatomical abbreviations: I:1 = manual phalanx I:1, a = acromion, bcc = bicipital crest of coracoid, bi = brachial impression, bs = brachialis scar, bt = bicipital tubercle, c = carina, cct = coracoidal tubercle, cd = coracobrachial duct, clp = craniolateral process, clt = ventral collateral ligament tubercle, cp = costal processes of sternum, cs = coracoidal sulcus, ct = carpal tubercle, d = deltopectoral crest, dc = dorsal condyle, dcp = dorsal cotylar process, dsp = dorsal supracondylar process, fa = furcular apophysis, ff = furcular facet, fp = flexor process, fr = furcular ramus, ft = furcular tubercle, lp = lateral process, ol = olecranon process, pc = procoracoid process, pf1 = primary pneumotricipital fossa, mc1 = metacarpal 1, mc2 = metacarpal 2, sa = sternal articular surface of coracoid, sc = supracoracoidal crest, sf = scapular facet, sr = sternal rostrum, ss = scapulotricipital sulcus, vc = ventral condyle, vct = ventral cotyla, vst = ventral supracondylar tubercle, and vt = ventral tubercle.

TABLE 6. Measurements of associated *Alca* holotype specimens (mm; – = missing data owing to damage or lack of comparable element; ~ = approximate measurement because of damage).

Measurements	<i>Alca olsoni</i>	<i>A. carolinensis</i>
	USNM	NCSM
	454590	13734
<b>Sternum</b>		
Medial length	–	~137.0
Dorsal length	–	126.0
Medial length of rostrum sterni	10.0	11.0
Length of carina	–	~144.0
Smallest width between costal processes	–	5.4
<b>Furcula</b>		
Dorsoventral height of apophysis	7.5	9.2
Length of omal extremity	–	29.3
<b>Coracoid</b>		
Greatest length	48.5	48.8
Medial length	46.8	46.5
Basal breadth	–	26.1
Breadth of sternal articulation	20.3	20.9
<b>Scapula</b>		
Greatest proximal height	–	14.8
<b>Humerus</b>		
Greatest length	104.0	102.4
Breadth of proximal end	21.7	20.8
Breadth of shaft	8.8	9.2
Breadth of distal end	15.3	14.9
<b>Radius</b>		
Greatest length	77.0	79.2
Breadth of proximal end	6.5	6.7
Breadth of shaft	5.0	4.6
Breadth of distal end	6.8	7.1
<b>Ulna</b>		
Greatest length	87.5	83.0
Breadth of proximal end	16.4	16.0
Breadth of shaft	7.0	7.9
Breadth of distal end	11.1	10.8
<b>Carpometacarpus</b>		
Greatest length	–	53.4
Length of metacarpal 1	–	9.7

projecting tubercle on the posterior apophysis of the furcula (37:1) and bicipital tubercle of the proximal radius positioned distal to and separated from the proximal ligamental papilla (90:1; sensu Howard 1929). These features are not seen in any other extant Alcidae or in any extinct Pan-Alcidae for which these elements are known. However, among other *Alca*, furculae are known only from *A. torda* and *A. olsoni*, and radii are known only from *A. torda*, *A. olsoni*, and *A. stewarti*. *Alca carolinensis* can be differentiated from *A. olsoni* by the absence of a distinct ridge that borders the m. brachialis scar on the ventral surface of the proximal ulna (98:1). Like *A. torda* and *A. grandis*, the ulna of *A. carolinensis* has a rounded anterior margin of the dorsal cotylar prominence (97:0), rather than a straight margin as in *A. olsoni* and *A. stewarti*. The intercondylar sulcus is less deeply incised than in *A. olsoni*, *A. stewarti*, *A. grandis*, and *A. torda* (104:1). *Alca carolinensis* is further differentiated from *A. grandis* by the lack of a posterodorsally projecting tubercle on the distal surface of the ventral condyle (84:0; Fig. 10). *Alca carolinensis* is further differentiated by the concave ventral/sternal margin of the procoracoid process of the coracoid (50:0). This margin is convex in *A. torda*, *A. stewarti*, *A. olsoni*, and *A. grandis*. Associated specimens that would allow referral of coracoids to *A. ausonia* and *A. minor* are not known. The dorsal margin of the primary pneumotricipital fossa (i.e., crus dorsale fossae; Baumel and Witmer 1993) of *A. carolinensis* and other *Alca* except *A. torda* and *A. minor* ends proximal to the junction of the bicipital crest with the humeral shaft (65:0). The distal margin of the primary pneumotricipital fossa (i.e., crus ventrale fossae; Baumel and Witmer 1993) of *A. carolinensis* and other *Alca* except *A. minor* and specimens referred to *A. ausonia* is straight rather than concave (70:1). With the exception of *A. olsoni*, with which it shares similar proportions, *A. carolinensis* can be differentiated from other *Alca* on the basis of size (Table 4; difference between greatest length of humeri: ~61% > *A. minor*; ~30.6% > *A. torda*; ~15.1% > *A. ausonia*; 5.3% > *A. grandis*; 8.6% < *A. stewarti*).

*Anatomical description.*—The sternum is the most complete known for extinct *Alca* (Fig. 13). Complete *Alca* sterni are known only from extant *A. torda*; however, partial sterni are known from *A. grandis*, *A. stewarti*, and *A. olsoni*. As in all alcids, the sternum is long and narrow, although the width of the sternum immediately distal to

the costal processes is relatively thinner than in *A. torda*. The dorsally directed cranio-lateral processes are rounded, rather than pointed as in *A. torda*. The carinal apex projects anterior to the mediolaterally compressed sternal rostrum, which is more ventrally expanded than in extant *A. torda* and is characterized by a ventrally projecting spine. The dorsal and ventral rostral spines are fused and separate the anteroposteriorly broad coracoidal sulci. As in *A. torda*, there are seven costal processes. Two complete vertebral ribs and three sternal ribs are preserved.

The furcula was recovered in five pieces and subsequently repaired. It is the first complete furcula known for extinct *Alca* (Fig. 13). Comparisons of *Alca* furculae are limited to extant *A. torda* and the partial furcula (apophysis and adjacent portions of rami; omal extremities not preserved) of the holotype specimen of *A. olsoni*. As with all alcids for which the furcula is known, and many other charadriiforms (e.g., *Larus marinus*), the omal ends of the furcular rami are mediolaterally compressed posterior to the coracoidal facet. The posterior omal extremity is elongate compared with most other charadriiforms (e.g., *L. marinus*) and surveyed specimens of *A. torda*. Additionally, the distance from the furcular apophysis to the coracoidal facet is relatively longer than that of *A. torda*. The furcular apophysis expands anteriorly, posteriorly, and ventrally, to form a semicircular projection. Both anterior and posterior extensions of the apophysis bear a dorsally projecting tubercle. The posterior tubercle is absent in all other alcids for which the furcula is known, although an anterior tubercle is present in *A. torda*. Cristae are present along the anterior shafts of the rami dorsal to the apophysis and are less distinct than those of *A. torda*.

The scapulae are missing only their distal tips, with the right scapula preserving slightly more of the original length of this element (Fig. 13). Associated specimens of other extinct *Alca* that would allow for referral of isolated scapulae are not known. As in *A. torda*, the tip of the acromion is rounded and directed anterodorsally. However, the acromion projects farther dorsally and contacts the shaft of the scapula at a more acute angle than in *A. torda*. The scapular blade is mediolaterally compressed along its entire length, unlike the more rounded condition in some charadriiforms (e.g., *L. argentatus*). The scapular blade broadens distally toward the ventrally deflected distal extremity, which is dorsoventrally narrower in *A. torda*.

The left coracoid is complete (Fig. 13) and is characterized by a rounded scapular cotyla, triangular procoracoid process with a concave sternal margin (convex in other *Alca*), and a distinctly ovoid m. supracoracoideus nerve foramen. The lateral process is dorsoventrally broad with an anterodorsally directed "hook" along its dorsal margin. As in *A. torda*, the medial end of the sternal articular surface curves posteriorly and broadens anteroposteriorly to form an approximately perpendicular (i.e.,  $\sim 90^\circ$ ) angle in proximal view. This angle is less acute (i.e.,  $\sim 135^\circ$ ) in some alcids (e.g., *Cephus* and *Synthliboramphus*) and more acute (i.e.,  $\sim 75^\circ$ ) in others (e.g., *Aethia* and *Ptychoramphus*). As in all *Alca* except *A. olsoni*, the brachial tuberosity of the coracoid is not deeply pneumatized. The medial sternal process of the coracoid of *A. carolinensis*, *A. torda*, and *A. grandis* is notched, rather than smooth as in *A. olsoni* and *A. stewarti*.

Before preparation, both humeri (Fig. 13) were preserved in articulation with the radii and ulnae. The humeral head is smoothly rounded in comparison with *Uria aalge*. As in *A. grandis*, the distal margin of the humeral head in posterior view is slightly pointed, whereas this feature is rounded in *A. torda*. The m. coracobrachialis impression is small compared with that of charadriiforms such as *L. argentatus*, triangular, and separated from a well-defined m. pectoralis attachment scar that is comparatively shallower in *A. grandis*. The deltopectoral crest is prominent, slightly undercut dorsally by the m. pectoralis attachment scar, and, unlike the condition in *Pinguinus*, restricted to the proximal half of the shaft. The deltopectoral crest merges smoothly with the anterior surface of the dorsal tubercle, which is separated from the humeral head in proximal view only by a slight notch. In posterior view, the dorsal tubercle is distally elongated into what Fürbringer (1888) termed a supracoracoidal crest (see Baumel and Witmer 1993:98). The capital groove is less deeply incised than in *A. torda*. The posterior surface of the ventral tubercle is less flattened and laterally deflected than in *A. grandis*, and mediolaterally narrower than in *A. torda*. The primary pneumotricipital fossa is shallower than in *Cephus*, *Cerorhinca*, and *Fratercula*. The primary pneumotricipital fossa is rounded, rather than oval as in *A. torda* and *A. minor*. Like other Alcini, *A. carolinensis* has a weakly developed secondary pneumotricipital fossa (i.e., absent). The capital

incisure is relatively narrow compared with that of *A. stewarti*. The ventral tubercle is robust, with a well-developed pit for insertion of *m. subcoracoideus* at the junction of the distal margin of the ventral tubercle and the ventral margin of the primary pneumotricipital fossa. The width of the shaft just distal to the deltopectoral crest is relatively broader than that of *A. stewarti*. The morphology of the distal humerus agrees with other *Alca* in having tricripital grooves of equal width. The *m. brachialis* scar extends proximal to the dorsal supracondylar prominence, whereas it is more distally restricted in *A. ausonia*. As in all pan-alcids other than Mancallinae, the anterior surface of the ventral condyle is flattened (Smith 2011), although more rounded and anteriorly projected than in specimens here referred to *A. ausonia*. The distal margin of the dorsal condyle is proximal to that of the ventral condyle. The proximal tip of the dorsal condyle is narrower and deflected more anteriorly than that of *A. grandis*. The dorsal epicondyle and dorsal supracondylar process are continuous, forming an anteroposteriorly compressed crest along the dorsal margin of the shaft. The dorsal supracondylar process projects less than in some specimens of *A. torda*. The distal margin of the ventral epicondyle is level with that of the ventral condyle, whereas this margin is distal to the ventral condyle in *Pinguinus*.

The right radius is complete and the left radius is missing the distal end (Fig. 13). Radii are also known from *A. torda*, *A. olsoni*, and *A. stewarti*. Compared with the radial shaft of *Pinguinus*, which is strongly bowed and dorsoventrally compressed to a degree exceeding that of volant alcids, the radial shaft of *A. carolinensis* is comparably straight and less compressed, although more compressed than in *A. torda*. The proximal end distal to the humeral cotyla and adjacent to the capital tuberosity is more excavated than in *A. torda*. Unlike all other alcids for which the radius is known, the bicripital tubercle is separated from the ligamental papilla and positioned more distally. A distinct intramuscular line is present along the entire length of the shaft and the distal end of the radius is relatively broader than in *A. torda*.

Both ulnae are complete (Fig. 13). *Alca* ulnae are also known from *A. torda*, *A. stewarti*, *A. olsoni*, and *A. grandis*. The olecranon is prominent, pointed, and deflected slightly ventrally. As in *A. torda* and *A. grandis*, the dorsal cotylar

prominence has a rounded anterior margin that borders the dorsal cotyla (straight in *A. stewarti* and *A. olsoni*) and partially bounds the proximal radial depression. The ventral collateral ligament tubercle is anteroposteriorly broader than that of *A. stewarti* and more distally extended than that of *A. torda*. The anterior shaft is characterized by a distinct intermuscular line that extends the length of the shaft, and the posterior shaft displays distinct feather papillae. As in *A. stewarti* and *A. torda*, the anterior margin of the dorsal condyle is straight. The intercondylar sulcus is only slightly depressed compared to other *Alca*.

The holotype specimen of *A. carolinensis* (NCSM 13734) preserves the second manual phalanx I:1 (also present in *A. grandis* USNM 336379; Fig. 9) and the first partial ulnare from an extinct *Alca* species (Fig. 13). Like the carpometacarpus, these elements are larger but otherwise morphologically indistinguishable from those of *A. torda*. The right carpometacarpus of NCSM 13734 lacks most of the shaft of metacarpal III (Fig. 13). Metacarpal I is elongate with the anteriorly flattened extensor process characteristic of all Alcini. The ventral margin of the carpal trochlea extends posterior to the dorsal trochlear margin. The infra-trochlear fossa is well defined and bordered distally by the distinct and anteriorly deflected pisiform process. The intermetacarpal spatium extends proximal to the distal extent of metacarpal I. Metacarpals II and III are equal in distal extent and the anteriorly projecting tuberosity of metacarpal II (sensu Howard 1929) is rectangular in shape.

#### *Alca minor*, sp. nov.

*Holotype*.—USNM 302324: a left humerus (Figs. 2, 5, and 14; Table 4) missing the dorsal tubercle and the proximal-most portion of the deltopectoral crest. The holotype specimen was collected by Peter J. Harmatuk from the spoil piles at the PCS Phosphate Mine in Aurora, North Carolina, and donated to the Smithsonian Institution National Museum of Natural History in 1979.

*Etymology*.—The species name *minor* reflects the diminutive size of this taxon compared with other known species of *Alca*.

*Locality and horizon*.—Aurora, Beaufort County, North Carolina; PCS Phosphate Mine (35°23' N; 76°47' 30" W; Fig. 1), Yorktown Formation, Lower Pliocene (Berggren et al. 1995, Woodburne and Swisher 1995). No associated sediment was

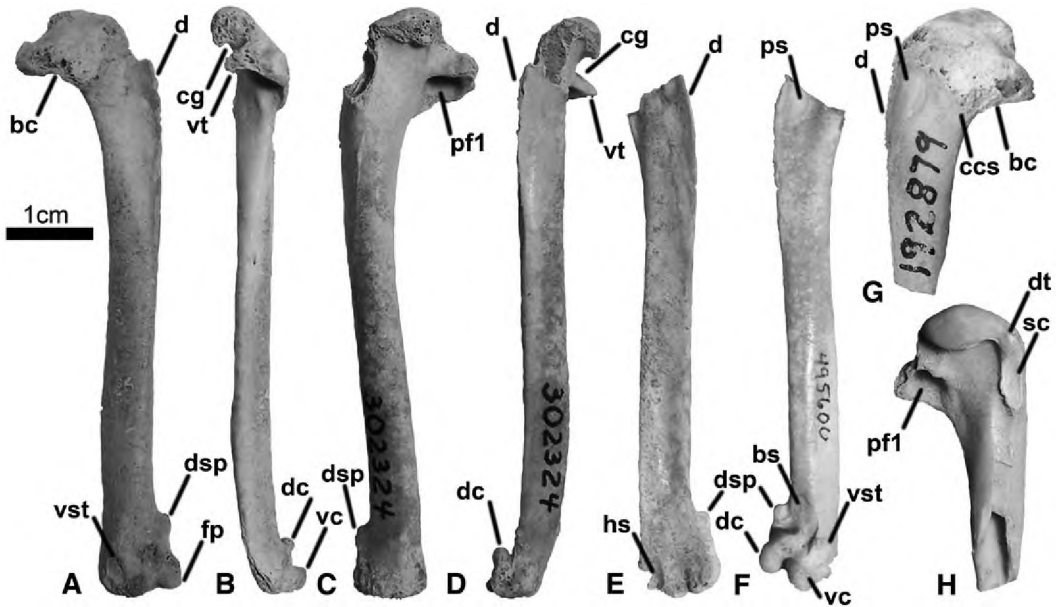


FIG. 14. Holotype and referred specimens of *Alca minor*. Holotype left humerus USNM 302324: (A) anterior view, (B) ventral view, (C) posterior view, and (D) dorsal view. Referred distal right humerus USNM 495600: (E) posterior view and (F) anterior view. Referred right proximal humerus USNM 192879: (G) anterior view and (H) posterior view. Anatomical abbreviations: bc = bicipital crest, bs = brachialis scar, ccs = coracobrachial sulcus, cg = capital groove, d = deltopectoral crest, dc = dorsal condyle, dsp = dorsal supracondylar process, dt = dorsal tubercle, fp = flexor process, hs = humerotricipital sulcus, pfl = primary pneumotricipital fossa, ps = m. pectoralis scar; sc = supratoracoidal crest, vc = ventral condyle, vst = ventral supracondylar tubercle, and vt = ventral tubercle.

recovered with USNM 302324 that would permit microfaunal analysis. The gray color and lack of phosphatic patina of this specimen agrees with the preservation of other Pliocene Yorktown Formation specimens; however, the possibility that this specimen is from the underlying Miocene Pungo River Formation cannot be excluded.

*Referred specimens.*—USNM 192879 (proximal right humerus; Fig. 14); USNM 495600 (distal right humerus; Fig. 14).

*Diagnosis.*—Although this smallest known species of *Alca* (Table 4) can be morphologically differentiated from other known species of *Alca*, there are no autapomorphic characters preserved in the three specimens referred to this species. Unlike all other *Alca*, and similar to the condition observed in *Uria*, the coracobrachial nerve appears to be transmitted in a sulcus rather than in a closed canal; however, the possibility that the coracobrachial nerve passage was exposed owing to weathering cannot be excluded. The holotype (USNM 302324) and referred specimens (USNM 192879 and USNM 495600) of *A. minor* were previously referred to “*Miocepphus* undescribed species”

(Olson and Rasmussen 2001:270). *Alca minor* is differentiated from *Miocepphus* by the equal width of the tricipital sulci (82:1), and by the relative robustness of the humerus. In *A. minor* the average dorsoventral height of the proximal humerus is 2.33× wider than the shaft and the average dorsoventral height of distal humerus is 1.57× wider than the shaft. The tricipital sulci of *Miocepphus* are of different widths, the humeral shaft is thicker, and the proximal and distal ends of the humerus are more dorsoventrally expanded. In *Miocepphus* the average dorsoventral height of the proximal humerus is 2.68× wider than the shaft (ratio derived from measurements of *M. blowi* and *M. mergulellus*), and the average dorsoventral height of distal humerus is 1.75× wider than the shaft (ratio derived from measurements of *Miocepphus* holotype specimens). *Alca minor* is differentiated from *Alle alle*, the smallest member of the Alcini, by its larger size, equal width of the tricipital sulci (82:1), and dorsally curving ventral margin of the distal humerus (*Alle alle* characterized by ~52% shorter greatest length, scapulothoracic sulcus wider than humerotricipital sulcus; ventrally flared ventral margin of distal

humerus). *Alca minor* is differentiated from similarly sized *Synthliboramphus* and *Brachyramphus* by the rounded shape (67:0) and shallow depth of the primary pneumotricipital fossa (66:0). Because of the fragmentary nature of the holotype specimen of *A. ausonia* (IGF 14875; Fig. 2), discernable differences between that specimen and *A. minor* are limited to size. The greatest width at the midpoint of the humeral shaft of *A. minor* is ~32% smaller than that of *Alca ausonia* (Table 4). This is significantly outside the range of intraspecific variation documented for other alcids (Moen 1991, Burness and Montevecchi 1992, Table 3). *Alca minor* is further differentiated from *A. grandis* by the lack of a posterodorsally projecting tubercle on the posterior margin of the ventral condyle (84:0; Fig. 10). In contrast to other *Alca* in which the primary pneumotricipital fossa is deeper and more ovoid, the primary pneumotricipital fossa is relatively shallow and more rounded. As in specimens referred to *A. ausonia*, the distal margin of the primary pneumotricipital fossa is concave (70:0) rather than straight as in other *Alca*. *Alca minor* is differentiated from all other species of *Alca* by its overall smaller size (Table 4; greatest length of humerus: ~75% < *A. stewarti*; ~63% < *A. olsoni*; ~61% < *A. carolinensis*; ~53% < *A. grandis*; ~27% < *A. torda*).

**Anatomical description.**—The proximal end of the humerus is broken proximal to the scar for attachment of *m. pectoralis* and the posterior surface of the head, the ventral tubercle, and the condyles on the distal end of the humerus are abraded, obscuring fine morphological details in these areas (Fig. 14A–D). The referred proximal right humerus (USNM 192879; Fig. 14G, H) is broken at approximately midshaft, has minor abrasions on the anterior bicipital surface, and is missing the ventral tubercle. The referred distal humerus (USNM 495600; Fig. 14E, F) is broken proximal to the *m. pectoralis* attachment scar and the flexor process is missing.

The humerus of *A. minor* is smaller in all dimensions than that of *A. torda* (Fig. 2 and Table 4). As in other *Alca*, the humeral head is proximally rounded and projects distally in relation to the shallowly excavated secondary pneumotricipital fossa. The coracobrachial nerve is transmitted in a sulcus rather than in a closed canal. The deltopectoral crest merges smoothly with the humeral shaft proximal to midshaft. The *m. latissimus dorsi* scar is prominent, extends distally from the supracoracoidal crest, is restricted to the proximal shaft, confined to the anterior surface of the

shaft, and does not curve onto the dorsal surface of the humerus as in *Cephus*. As in other *Alca*, the tricipital sulci are of equal width and the dorsal supracondylar process is a rounded dorsally projected tubercle (less dorsally projected in *Uria*).

***Alca olsoni*, sp. nov.**

**Holotype.**—USNM 454590: a partial postcranial skeleton comprising the following elements: partial furcula, partial sternum, left coracoid, left humerus, distal right humerus, right ulna, and right radius (Figs. 2, 6, and 15; Tables 4 and 6). The holotype specimen of *A. olsoni* (USNM 454590) was collected by Reginald Titmas from the spoil piles at the PCS Phosphate Mine in Aurora, North Carolina, and donated to the Smithsonian Institution National Museum of Natural History in 1992.

**Etymology.**—This new species is named in recognition of the many contributions to the systematics of extinct Alcidae by Storrs L. Olson.

**Locality and horizon.**—Aurora, Beaufort County, North Carolina; PCS Phosphate Mine (35°23'N; 76°47'30" W; Fig. 1), Yorktown Formation, Lower Pliocene (Berggren et al. 1995, Woodburne and Swisher 1995). No associated sediment was recovered with USNM 454590 that would allow for microfaunal analysis. The brown to gray color and lack of phosphatic patina of this specimen agree with the preservation of other Pliocene Yorktown Formation specimens; however, the possibility that this specimen is from the underlying Miocene Pungo River Formation cannot be excluded.

**Diagnosis.**—*Alca olsoni* is diagnosed from all other species of *Alca* in which the ulna is known (i.e., *A. torda*, *A. stewarti*, *A. carolinensis*, *A. grandis*) by the presence of a distinct ridge that borders the *m. brachialis* scar on the ventral surface of the proximal ulna (98:1). Associated specimens of *A. minor* and *A. ausonia* that would allow for referral of ulnae to these taxa, and evaluation of this proposed autapomorphy are not known. The ventral extension of this ridge along the *m. brachialis* scar makes the brachialis scar appear as a deep pit or fovea rather than the shallow depression that is characteristic of other Alcidae (Fig. 15). An additional proposed autapomorphy of *A. olsoni* is a furcular apophysis that is expanded ventrally but anteroposteriorly narrow (Fig. 15). This feature is not seen in any extant Alcidae, or in any extinct Alcidae for which these elements are known (i.e., *A. torda* and *A. carolinensis*). Although the ulnae of *A. olsoni* and *A. carolinensis* are morphologically distinct, the humeri of these species are similar in

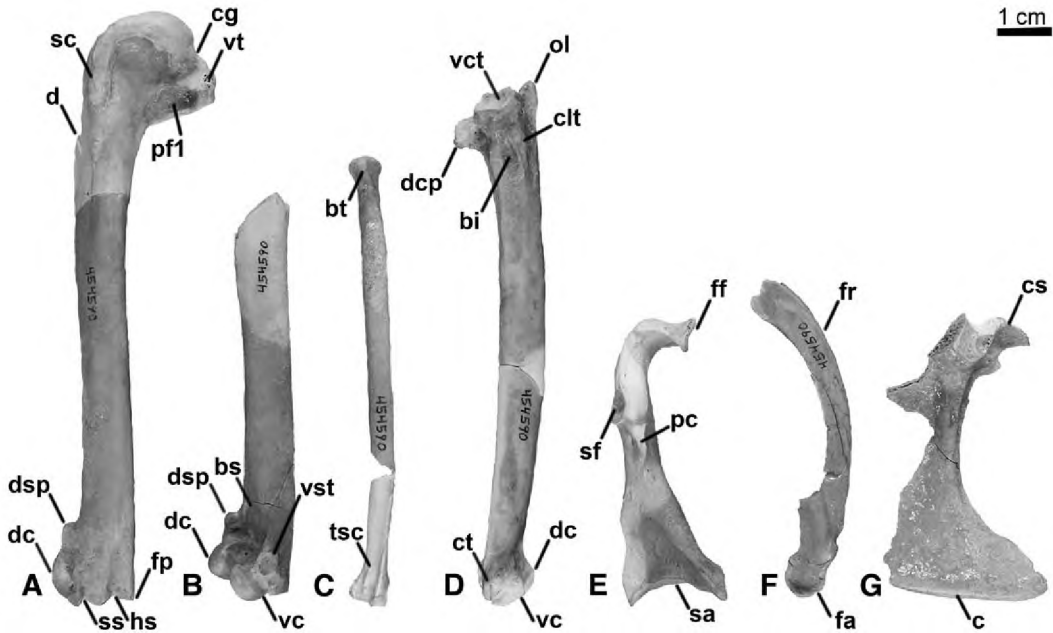


FIG. 15. Holotype specimen of *Alca olsoni* (USNM 454590): (A) left humerus (posterior view), (B) right distal humerus (anterior view), (C) right radius (dorsal view), (D) right ulna (ventral view), (E) left coracoid (posteromedial view), (F) partial furcula (right lateral view), and (G) partial sternum (right lateral view). Anatomical abbreviations: bi = brachial impression, bs = brachialis scar, c = carina, cg = capital groove, clt = ventral collateral ligament tubercle, cs = coracoidal sulcus, ct = carpal tubercle, d = deltopectoral crest, dc = dorsal condyle, dcp = dorsal cotylar process, dsp = dorsal supracondylar process, fa = furcular apophysis, ff = furcular facet, fp = flexor process, fr = furcular ramus, hs = humerotricipital sulcus, ol = olecranon process, pc = procoracoid process, pf1 = primary pneumotricipital fossa, sa = sternal articular surface of coracoid, sc = supracoracoidal crest, sf = scapular facet, sr = sternal rostrum, ss = scapulo-tricipital sulcus, tsc = tendinal sulcus crest, vc = ventral condyle, vct = ventral cotyla, vst = ventral supracondylar tubercle, and vt = ventral tubercle.

both size and morphological characteristics (Table 4). However, *A. olsoni* is differentiated from *A. carolinensis* by the curvature of the sternal margin of the procoracoid process of the coracoid, which is convex (50:1) in the former but concave in the latter. The brachial tuberosity is less deeply undercut than that of *A. stewarti* and *A. torda* (41:1), and as in *A. torda* and *A. grandis* the medial end of the sternal articular surface of the coracoid curves posteriorly to form a  $\sim 90^\circ$  angle in sternal view (52:2;  $\sim 135^\circ$  in *A. stewarti*). On the basis of the greatest length of the humerus, *A. olsoni* is larger than *A. grandis* ( $\sim 7\%>$ ), *A. torda* ( $\sim 32\%>$ ), and *A. minor* ( $\sim 63\%>$ ) and smaller than *A. stewarti* ( $\sim 6.5\%<$ ; Table 4). The width of the humeral shaft of *A. ausonia* is  $\sim 17\%$  smaller than that of *A. olsoni*.

*Anatomical description.*—The furcular apophysis and left furcular ramus distal to the omal extremity are preserved (Fig. 15). As in all other alcids and many other charadriiforms (e.g., *Larus*

*marinus*), the furcular ramus is mediolaterally compressed. Unlike other *Alca* species for which the furcula is known (i.e., *A. torda*, *A. carolinensis*), the apophysis lacks either an anterior or posterior tubercle and is expanded further ventrally than in other *Alca*. These features were not observed to vary in specimens of extant *A. torda* examined.

The proximal sternum including the right coracoidal sulcus, medial portion of the left coracoidal sulcus, sternal rostrum, and anterior carina are preserved (Fig. 15). The posterior margins of the coracoidal sulci are bordered by a distinct ridge. This ridge is less distinct in *A. torda* and *A. carolinensis*. As in *A. stewarti* and *A. carolinensis*, the sulci broaden medially and nearly contact the sternal rostrum. The left coracoid lacks only the lateral process (Fig. 15) and is characterized by a rounded scapular cotyla, a triangular procoracoid process (square in *Alle*), and an ovoid m. supracoracoideus nerve foramen.

The complete left and distal right humeri are preserved (Fig. 15). The left humerus was collected in two pieces and repaired. A portion of the deltopectoral crest is missing. The depth of the m. coracobrachialis impression on the proximal humerus is shallower than in *Alca stewarti*, and the attachment scar of m. subcoracoideus on the posterior surface of the ventral tubercle is deeper than in *A. stewarti*. The distal margin of the humeral head in posterior view is slightly pointed, rather than rounded as in *A. torda*. The posterior tip of the ventral tubercle of *A. olsoni* is not ventrally deflected as in *A. stewarti*. All other morphological features of the humerus agree with those of *A. carolinensis*.

The right ulna is complete (Fig. 15). As in *A. stewarti*, the anterior margin of the dorsal cotylar prominence is straight, rather than rounded as in *A. torda* and *A. carolinensis*. A distinct ridge borders the m. brachialis scar on the anterior surface of the proximal ulna, which gives the m. brachialis scar a narrow, "eye-shaped" appearance and makes this feature appear as a deep pit rather than a shallow scar. This conformation is not seen in any other *Alca* from which the ulna is known (e.g., *A. torda*, *A. stewarti*, and *A. carolinensis*). This ridge along the anterior margin of the m. brachialis scar is as wide as the muscle scar and results in an anteriorly curving bulge along the length of the m. brachialis scar. Interestingly, this condition resembles that of *Mancalla emlongi* Olson, 1981, a flightless alcid that is not hypothesized to be closely related to *Alca* (Chandler 1990, Smith 2011). As in other *Alca*, the shaft of the ulna is dorsoventrally compressed. The posterior margin of the dorsal condyle just distal to its contact with the ulnar shaft is rounded, whereas the contact with the shaft is more angular in *A. torda* and *A. stewarti*. The intercondylar sulcus is more deeply incised than in *A. carolinensis*.

The complete right radius is preserved (Fig. 15). Unlike the condition in *A. carolinensis*, the bicapital tubercle contacts the ligamental papilla. As in other Alcidae, the shaft of the radius is dorsoventrally compressed and tapered to a distinct crest along the anterior margin. The distal tendinal sulcus is divided lengthwise into two distinct sulci by a distinct crest, a character shared by all Alcini taxa except *Alle alle* and *Miocepphus bohaski*.

## DISCUSSION

The identification of three new species of *Alca* brings the total number of *Alca* species known

from the western Atlantic Ocean to seven, making *Alca* the most speciose clade of Atlantic alcids and the most species-rich clade of Pliocene Atlantic seabirds known. Analytical results indicate that fossil remains from the Bone Valley Formation previously referred to '*Australca grandis*' represent three species of *Alca* (*A. grandis*, *A. torda*, and *A. ausonia*), and that *Alca* fossil material from the eastern Atlantic Ocean represents at least four species (*A. ausonia*, *A. grandis*, *A. stewarti*, and *A. carolinensis* or *A. olsoni*). However, *A. minor* may also be present in the Pliocene of the Netherlands (E. Wijnker pers. comm.). The inclusion of these extinct *Alca* species and additional extinct Alcini species in a phylogenetic analysis supports the monophyly of *Alca* and its sister taxon *Pinguinus*, and also supports placement of *Alle alle* nested within *Miocepphus*. Additionally, assessment of *Alca* paleodiversity with respect to latitude reveals an apparent trend of higher *Alca* diversity at higher latitudes that is consistent with the distribution of extant alcids.

Known diversity of extinct Atlantic alcids now approaches that of extinct Pacific alcids (about 16–19 species ranging from Miocene to Pleistocene age from each ocean basin). Hypotheses concerning Pacific ancestral origination of alcids based on proposed greater Pacific species diversity should accordingly be reevaluated. Extant diversity in the Pacific may be a poor indicator of origination area, and the two oldest known alcid fossils are both from Atlantic deposits (Wetmore 1940, Chandler and Parmley 2002, Wijnker and Olson 2009). Regardless of the ancestral area of the clade, similarly diverse lineages of alcids inhabited the eastern and western coasts of North America during the Pliocene, given that at least six species of flightless Mancallinae (Aves, Pan-Alcidae) lineage are known from approximately coeval Early Pliocene deposits of California and Mexico (Smith 2011). In comparison, the five species of auklets (*Aethia cristatella*, *A. pusilla*, *A. psittacula*, *A. pygmaea*, and *Ptychoramphus aleuticus*) are the most speciose clade of extant alcids and are restricted to the Pacific Ocean basin (del Hoyo et al. 1996).

The possibility that all of the *Alca* species from North Carolina contemporaneously shared overlapping ranges is consistent with data on the ranges of extant alcids (e.g., auklets; del Hoyo et al. 1996). Depositional duration of the Yorktown Formation is estimated at approximately 1 million years (3.7–4.8 Ma; Hazel 1983), but there is little information on the relative stratigraphic occurrence of *Alca* remains within the deposit. Considering that the only *Alca* fossils from Middle to Late Pleistocene and



younger deposits are referred to the extant species *A. torda* (Tyrberg 1998, Harrison and Stewart 1999), extinction of the other six species of *Alca* is inferred to have taken place during the last 2 million years of the Pliocene (i.e., sometime between the end of Yorktown Formation deposition and the beginning of the Pleistocene). However, there are no records of *Alca* from the Early Pleistocene (Tyrberg 1998), and whether there is unrecognized *Alca* diversity among Middle and Late Pleistocene fossils merits further investigation. At least one species of the flightless Pacific taxon *Mancalla* survived until the Pleistocene (Howard 1976), and *Pinguinus*, the sister taxon of *Alca*, was driven to extinction by humans less than 200 years ago (Bengston 1984). Middle and Late Pliocene records of *Alca* and *Pinguinus* that would potentially elucidate whether decreases in diversity were gradual or abrupt (owing to paleoclimatic changes in the Late Pliocene) are currently limited to the reported presence of *A. ausonia* from the Late Pliocene (~2.5 Ma) of Morocco (Mourer-Chauviré and Geraads 2010).

Potential biases including sample size, collection bias, ontogeny, sexual dimorphism, and intraspecific size variation were considered. Sample size does not present a potential bias because the morphometric method described here is not negatively affected by small sample size. Although larger specimens are more likely to be seen and collected, the unusually large sample size used in the present study, compounded by specimens having been sampled from the North Carolina locality over a ~30-year period, should negate any potential effect of collection bias. Ontogeny is not a complicating factor with respect to this analysis because only specimens assessed as adult on the basis of degree of ossification (Chapman 1965) were included in our study. Extant alcids do not display statistically significant degrees of sexual dimorphism in their size, plumage, or osteological morphology (Storer 1952, Nettleship and Birkhead 1985, Székely et al. 2000). Thus, we can reasonably assume that extinct alcids were also not sexually dimorphic, given that the proposed sister taxon of Alcidae, the Stercorariidae (Ericson et al. 2003, Thomas et al. 2004, Baker et al. 2007, Pereira and Baker 2008, Smith 2011), as well as the closely related Laridae, are also not sexually dimorphic.

Small degrees of intraspecific size variation owing to latitude have been previously documented among alcid species (Storer 1952, Spring 1971, Moen 1991, Burness and Montevecchi 1992). However, as noted by Olson and Rasmussen (2001), the possibility that the Aurora, North

Carolina, locality may have served as a wintering ground for multiple geographic races (i.e., subspecies with geographically variable size) cannot be ruled out. Although there are clear differences in size between *Alca* species, size alone is not a sufficiently robust criterion to diagnose a species (discussed by Stewart 2002, 2007). Rather, statistically determined size classes were examined to determine shared morphological characteristics that could be used to diagnose or differentiate species. Additionally, the ranges of size documented for statistically supported clusters of fossils are consistent with those estimated for extant alcids. Inherent in this statement is the assumption that the range of size variation within *Alca* species has not evolved, such as that documented in *Lagopus* by Stewart (2007).

The relationships recovered among *Alca*, although partially unresolved, suggest that intermediate body size would be optimized as pleisiomorphic for *Alca*, with more derived (i.e., much larger and much smaller) forms such as *A. stewarti* (estimated body mass = 1,941 g; Martin et al. 2001) and the smaller *A. minor* nested within the clade. *Alca torda* is also smaller (average body mass = 707 g; del Hoyo et al. 1996) than more basally recovered *Alca* species (Table 4). Among *Alca*, fossils representing *A. stewarti* and *A. minor* are the most rare. However, the possibility that these species, which represent extremes of body size, may have been more common in other localities should be considered. The range of *Alca* sizes recovered in distinct localities may reflect the same factors interpreted as driving size variation in extant seabirds, such as competition for nesting sites and niche partitioning (Ainley 1990). "If coevolution is indeed the process that structures seabird communities, it appears that coexistence of species is greatly advanced through adjustment of body size" (Ainley 1990:362).

The systematic position of *Uria brodkorbi* as the sister to extant *U. aalge* and *U. lomvia* is consistent with the Miocene age of that taxon and the lack of other more recent fossils referred to that clade. Additionally, *U. affinis* Marsh, 1872 (ANSP 13358) from the Pleistocene of Maine lacks any characters that differentiate it from modern *Uria* and may represent a Pleistocene occurrence of one of those modern forms.

The systematic placement of *Alle alle* nested within *Miocepphus* as the sister taxon of *M. mergulellus* may provide an explanation for the widely varying previous hypotheses regarding the affinities of *Alle*. Based on the age of *Miocepphus bohaski*

Wijnker and Olson, 2009, the split between the lineages leading to *Uria* and *Alle* occurred at least 20 mya. Much like *Alca torda*, *Alle alle* is the only surviving member of a clade including at least four additional extinct species. The inclusion of these extinct congeners (i.e., *Miocepphus*) results in a phylogenetic hypothesis that partially explains the unique suite of characters present in *Alle* and *Miocepphus* with respect to other Alcini. These characters that may have misled previous analyses, and the systematic position of *Alle*, can now be viewed in evolutionary context.

Pliocene *Alca* diversity, when evaluated with respect to latitude, evidently declined in more southern localities. Yorktown Formation deposits from North Carolina (~35°23'N latitude; Fig. 1) record the presence of all seven species of *Alca*, whereas the similarly sampled deposits from the Bone Valley Formation of Florida (~27°45' N latitude) record the presence of only three species. Although age estimates for the Bone Valley Formation of Florida are slightly older (4.5–5.2 Ma) than those for the Yorktown Formation (Hulbert 2001), whether the decreased diversity represented by the Bone Valley assemblage is a function of the different age of the deposits, the

geographic range of *Alca* paleospecies, or a latitudinal species diversity gradient is not known. Although *Alca* fossil localities in Europe are not as heavily sampled as those in North America, the same apparent pattern is observed in the Eastern Atlantic. Four species of *Alca* are known from deposits in Belgium (Martin et al. 2001, Dyke and Walker 2005; 51°15'N latitude), whereas only a single species has been reported from Italy and Morocco (Portis 1888, Mourer-Chauviré and Garaads 2010; ~43°N latitude). The apparent pattern of lower *Alca* diversity in southerly latitudes observed in the occurrence of *Alca* fossils is consistent with the latitudinal distribution of extant alcids (Fig. 16). Only 4 of the 23 extant alcid species have ranges that extend below the Tropic of Cancer (i.e., below 23.5°N latitude). The ranges of *Cepphus carbo* and *Synthliboramphus antiquus* in the Western Pacific Ocean extend south to the Ryuku Islands, and the ranges of *S. hypoleucus* and *S. craveri* in the Eastern Pacific Ocean extend just south of the southern tip of Baja California (del Hoyo et al. 1996). Confirmation of this same trend of higher diversity in northern latitudes among other extinct alcids will require further study. Just as extant alcid distribution is closely

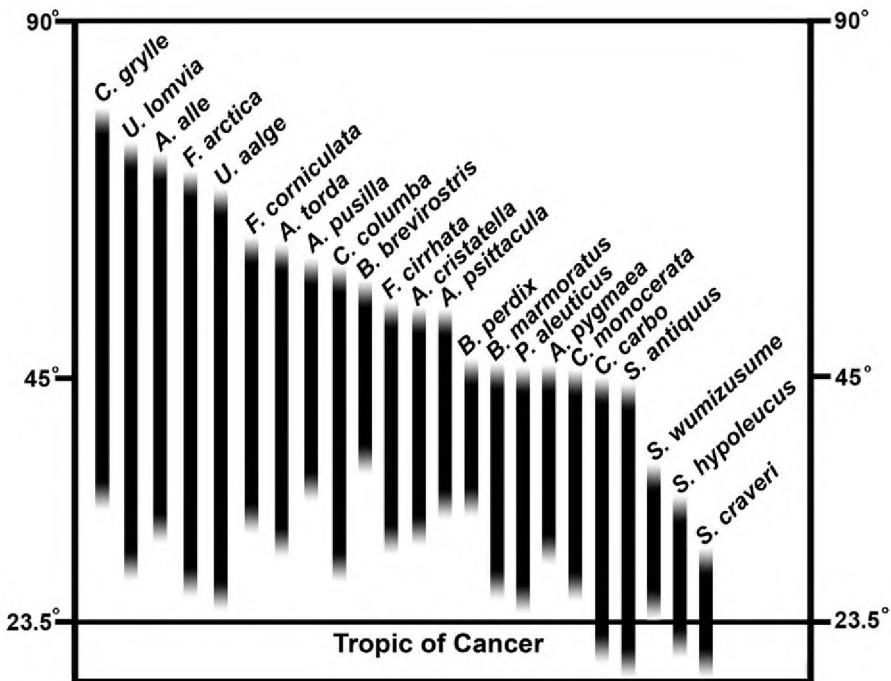


FIG. 16. Latitudinal ranges of extant alcids (ranges based on del Hoyo et al. 1996). Note that the ranges of only four species extend south of the Tropic of Cancer and that overall species diversity decreases in higher and lower latitudes.

associated with nutrient-rich, cold-water upwelling ocean systems, the apparent latitudinal diversity trend observed in *Alca* may represent changes in the abundance of feeding opportunities at different geographic locations at different points in geologic time.

Pelagic seabirds such as alcids are an excellent proxy for the study of interactions between the marine and terrestrial environments because they depend on the ocean for sustenance but must return to shore to reproduce. Changes in climate that affect sea level have potential to influence the availability of suitable breeding sites, and changes in ocean temperatures have potential to influence the distribution and availability of food. As such, it has often been hypothesized that radiations and extinctions of pelagic seabirds are linked with climatic changes that are commonly the result of large-scale geologic processes. Potential environmental drivers of alcid evolution have been extensively discussed (Warheit 1992a, Allmon et al. 1996, Emslie 1998, Olson and Rasmussen 2001, Smith et al. 2007, Pereira and Baker 2008, Smith 2011) and include (1) the Mid-Miocene Climatic Optimum (MMCO; ~11–16 mya) that may have been a factor in radiation of Alcidae; (2) reorganization of ocean currents after the final emergence of the Panamanian Isthmus and closure of the Central American Seaway (~2.6 mya), which resulted in changes in salinity, temperature, and pelagic invertebrate fauna that may have negatively affected Pliocene alcid diversity (Warheit 1992a, Allmon et al. 1996, Bartoli et al. 2005, Head et al. 2008, Sarnthein et al. 2009); (3) periods of Pleistocene glaciation and environmental change possibly affecting distribution and diversity in Alcidae (Warheit 1992a, Emslie 1998). El Niño Southern Oscillation (ENSO) events also have a documented record of impacts on extant seabird populations (Hatch 1987, Duffy et al. 1988, Ainley 1990, Hyrenbach and Veit 2003), and recent research indicates that ENSO-like conditions may have existed in the Pliocene (Ravelo et al. 2006). However, evidence of short-term oceanic disturbances is rare in the fossil record (Emslie and Morgan 1994, Emslie et al. 1996), and known alcid-bearing deposits do not appear to be death assemblages. Comparison of alcid evolutionary history with the timing of the MMCO and with the rising and lowering of sea level in relation to the Panamanian Isthmus will require resolution of phylogenetic relationships of extinct alcid taxa and estimation of clade origins based on reliably dated and phylogenetically evaluated alcid and

other charadriiform fossils. Unfortunately, the fossil record of the clade so far lacks sufficient resolution to test hypotheses on the scale of glacial cycles and ENSO events.

However, the absence of *Alca* from Pliocene Pacific Ocean deposits may not be linked to geological or climatic factors. Colonization of the Pacific Ocean by *Alca* may have been prevented by the occupation of wing-propelled diving niches (Volterra 1926, Hardin 1960, Levin 1970) by other relatively diverse clades of alcids (e.g., *Mancalla*, *Uria*; Howard 1976, 1981, 1982) regardless of the potential for dispersal through ocean passages. Although potential drivers of alcid radiation may be difficult to identify, the profound worldwide climate change that accompanied the final emergence of the Panamanian Isthmus (Sarnthein et al. 2009) offers a potential explanation for the significant decrease in Pliocene *Alca* diversity as compared with extant diversity in the clade. The negative impact of this climatic transition on other marine organisms is well documented (Versteegh 1997, Kameo and Sato 2000, Bartoli et al. 2005). Furthermore, the timing of the disappearance of *Alca* from the coast of Florida (3.5–2.5 mya) coincides with oceanographic changes linked with the emergence of the Panamanian Isthmus and associated decreases in biological productivity (Allmon et al. 1996). The extant Razorbill Auk *Alca torda* is recognized as the only survivor of a once diverse lineage of seabirds with a fossil record extending back to the Miocene. The timing and pattern of radiation, extinction, range retraction, and the absence of *Alca* in the Pacific Ocean warrant further investigation.

Body size in extant alcids has been correlated with dive depth and feeding ecology (Prince and Harris 1988, Watanuki and Burger 1999), and moderate body size in extant alcids has been associated with more generalist feeding strategies (e.g., moderately sized *Cepphus* commonly prey on both vertebrates and invertebrates; Bradstreet and Brown 1985). Thus, the size range observed in extinct *Alca* species may indicate a similar partitioning of resources related to differences in prey items available at varying depths. In a recent study, Gaston and Woo (2008) proposed that *A. torda* is capable of rapidly adapting to environmental changes that affect its food supply by expanding and contracting its breeding and foraging range. Compared with smaller (i.e., *A. minor*) and larger (e.g., *A. stewarti*) congeners, the more moderate body size of *A. torda* may be linked to its apparently enhanced ability to

respond to environmental changes both past and present. Termed “variability selection” by Potts (1998), this mechanism of adaptation to relatively frequent environmental perturbations offers a potential explanation for the adaptive ability of extant *A. torda* and may have played a role in its differential survival compared with its congeners. The presence of three relatively moderately sized species of *Alca* from the southernmost known *Alca* fossil locality (i.e., *A. torda*, *A. ausonia*, and *A. grandis* from the Bone Valley Formation) and the absence of larger and smaller congeners (e.g., *A. minor* and *A. stewarti*) in that locality may also be a reflection of adaptive advantage of moderately sized *Alca*.

The geographic ranges and feeding ecology of extant seabirds that are changing rapidly in response to the current global warming trend (Kitaysky and Golubova 2000, Hyrenbach and Veit 2003, Gaston and Woo 2008) may be best contextualized by insight from the past. Knowledge of extinct seabird diversity can have direct influence on our interpretation of the severity of these changes in extant seabird populations. Additional investigation of changes in extant seabird populations can facilitate a more detailed understanding of the processes that may have affected seabird diversity in the past. Increased global warming and its future effects on seabird diversity might be used as a corollary for conditions experienced by Pliocene alcids because global warming and cooling can both contribute to range retraction and reduced nesting site and prey availability. Just as the rise of the Panamanian Isthmus disrupted nutrient-rich cold-water upwelling in the Atlantic Ocean that Pliocene alcids would have depended on for food, the increased ocean temperatures associated with global warming may result in northward retraction of ranges and similar disruption of seabird food supplies and reproduction. Declines in seabird populations related to ocean warming have already been documented (Hyrenbach and Veit 2003). The combination of an evermore detailed understanding of extant avian ecology with new paleontological discoveries offers the potential for new insights into the effects of climate change on avian evolution and seabird conservation.

#### CONCLUSIONS

The resolution of phylogenetic relationships is facilitated by the referral of previously unknown skeletal elements to species, making this method

a potentially valuable tool when traditional morphology-only based methods of specimen referral are complicated by large quantities of isolated or fragmentary or morphologically similar specimens. However, the application of this method to fossil data is predicated on the identification of statistically robust recovery of species groups based on measurements of extant analogues, and on determination of phylogenetically contextualized size variances in extant analogues. Although the application of this combined morphometric and morphologic method to fossils without extant analogues (e.g., non-avian dinosaurs) is not recommended, application of this method to other fossil remains with extant analogues (e.g., turtles, crocodylians, mammals, squamates) may provide a refined assessment of diversity in those clades. Additionally, the potential ability to accurately cluster small numbers of specimens may be of use when dealing with fossil taxa known from limited quantities of material. The application of this method to other speciose clades within Alcidae (e.g., *Mancalla*) or to other birds may also provide new insights into the diversity of those clades, and the mensural data reported herein from both extant and extinct *Alca* is a resource that might be used to explore additional morphometric parameters (e.g., allometry) in Alcidae.

The phylogenetic hypothesis of Alcini relationships presented here represents the most inclusive sampling of this clade to date and provides evolutionary context for further studies involving ecological interactions among Alcini species, other alcids, other seabirds, and other marine organisms. The results of the combined phylogenetic analysis of morphological and molecular sequence data demonstrate the value of fossils in resolving systematic relationships among both extant and extinct organisms. The reduction in species diversity in both *Alca* and *Miocepphus*, which has left only a single extant representative of each of these clades, may provide compelling examples of extinction related to climatic changes that could have bearing on the plight of seabirds in the face of current global warming and pressures from overfishing. Evaluation of the potential relationship between alcid extinctions and paleoclimatic changes will require divergence estimation for Pan-Alcidae utilizing rigorously dated and phylogenetically analyzed fossils, such as *Alca carolinensis*.

Detailed evaluation of fossil Pan-Alcidae has resulted in estimates of species richness that continue to increase (Olson and Rasmussen 2001, Warheit 2002, Wijnker and Olson 2009, Smith 2011). Diverse

assemblages of alcids are now known from the Pliocene of the Atlantic (Olson and Rasmussen 2001), the Miocene of the Atlantic (Wijnker and Olson 2009), and the Pliocene of the Pacific (Howard 1982, Smith 2011). The combined morphometric and morphological-character-based method provides quantification of previously hypothesized (Olson and Rasmussen 2001) high diversity in *Alca*. Recent evaluation of fossil Alcidae from the Miocene of the Pacific also indicates that additional species richness is present (Smith 2008, 2011). The relative species richness of fossil Pan-Alcidae from numerous localities at different points in geological history (Warheit 2002) and the relatively high species diversity of extant Alcidae ( $n = 23$  species) may reflect a pattern of high species richness through time. Heavy sampling and thorough evaluation of alcid fossil localities continue to result in recognition of new species. However, study of additional alcid-fossil-producing localities from undersampled temporal intervals is needed to determine whether these "snapshots" of alcid species diversity reflect a real trend in alcid population dynamics or whether this apparent trend is the result of sampling bias.

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APPENDIX 1. Measurements of extant alcid species (mm; – = measurements missing because of damage or missing elements; all measurements according to von den Driesch 1976). Abbreviations: gbs = greatest breadth of skull, gls = greatest length of skull, cbls = condylobasal length of skull, ghS = greatest height of skull, gbF = greatest breadth of frontal, glR = greatest length of rostrum, glM = greatest length of mandible, lsM = length of mandibular symphysis, lFa = length from articular to apex of mandible, mlS = maximum length of sternum, dlS = dorsal length of sternum, lcS = length of sternal carina, SBF = smallest breadth between costal rib facets, glC = greatest length of coracoid, mlC = medial length of coracoid, bbC = basal breadth of coracoid, diS = diagonal of proximal scapula, glH = greatest length of humerus, bpH = breadth of proximal humerus, scH = smallest dorsoventral breadth of humeral corpus (shaft), dpH = depth of proximal humerus, bdH = breadth of distal humerus, ddH = distal diagonal of humerus, bdH = breadth of distal humerus, ddH = diagonal of distal humerus, dpH = diagonal of proximal humerus, glR = greatest length of radius, bpR = breadth of proximal radius, scR = greatest width of radial shaft at midpoint, bdr = breadth of distal radius, glU = greatest length of ulna, bpU = breadth of proximal ulna; scU = width of ulnar shaft, bdU = breadth of distal ulna, ddU = diagonal of distal ulna, glC = greatest length of carpometacarpus, lMC1 = length of metacarpal 1, bpC = breadth of proximal carpometacarpus, ddC = diagonal of distal carpometacarpus, glD = greatest length of digit 2 phalanx 1, lD = articular length of digit 2 phalanx 1, glP = greatest length of pelvis, lsP = length to dorsal iliac spine of pelvis, lvP = length of synsacrum, cbP = greatest breadth of ilium, sbP = smallest breadth of ilium, aaP = distance between acetabulae, dA = diameter of acetabulum, bA = breadth across antitrochanters; glF = greatest length of femur, mlF = medial length of femur, bpF = breadth of proximal femur, dpF = depth of proximal femur, scF = breadth of femoral shaft, bdF = breadth of distal femur, ddF = depth of distal femur, glT = greatest length of tibiotarsus, laT = axial length of tibiotarsus, dpT = diagonal of proximal tibiotarsus, scT = breadth of tibial shaft, bdT = breadth of distal tibiotarsus, ddT = depth of distal tibiotarsus, glTm = greatest length of tarsometatarsus, bpTm = breadth of proximal tarsometatarsus, scTm = breadth of tarsal shaft, and bdTm = breadth of distal tarsometatarsus.

Taxon	Catalogue no.	Sex	gbS	glS	cblS	ghS	gbF	glR	ghR	glM	lsM	lFa
<i>Aethia cristatella</i>	USNM 561934	FEMALE	20	50.7	45.8	17.6	4.5	20	5.1	38.4	3.1	9.1
<i>A. cristatella</i>	USNM 223707	?	22.1	52.6	46.7	17.9	4.6	23.2	5.6	42.5	4.2	9.2
<i>A. cristatella</i>	USNM 610941	MALE	21.1	50.3	45.1	17.1	4.9	20.9	6	41.6	3.8	9
<i>A. cristatella</i>	USNM 498282	FEMALE	20.9	50.2	45.1	17.3	4.9	20.5	5.3	40	4.3	11.7
<i>A. cristatella</i>	NCSM 17749	MALE	22	52.8	47.7	17.9	5.1	22.7	6.7	43.2	3.7	9.8
<i>A. psittacula</i>	NCSM 14804	?	20	52.8	48.8	17.5	4.3	23.1	9	42.8	4.2	10.1
<i>A. psittacula</i>	NCSM 18387	?	21.2	55.9	49	19.5	3.7	24.5	9.2	46	4	10.5
<i>A. psittacula</i>	NCSM 14147	MALE	22	–	–	19.6	–	–	–	–	4.3	10.6
<i>A. psittacula</i>	NCSM 20177	?	20.9	56.1	50.1	16.4	4.3	25.2	9.8	46.2	4.3	9.9
<i>A. psittacula</i>	USNM 610513	?	21.3	54.8	49.2	18.5	3.7	23.7	8.3	43.9	4.6	10.4
<i>A. psittacula</i>	USNM 610514	?	20.9	54.3	48.5	18.4	3.8	23.5	7.9	42.4	4	10
<i>A. psittacula</i>	USNM 610937	MALE	21.3	53.6	48.2	18.4	3.7	25	8.4	39.5	3.9	10.3
<i>A. pusilla</i>	NCSM 17737	?	15.5	–	–	15.2	–	–	–	–	2.2	5.9
<i>A. pusilla</i>	NCSM 17736	FEMALE	18.5	–	–	14.7	–	–	–	–	2.5	6.2
<i>A. pusilla</i>	NCSM 17734	FEMALE	15.5	39.3	34.4	15.2	2.5	15.9	3.4	30.7	2.4	6.7
<i>A. pusilla</i>	NCSM 224009	FEMALE	16.4	39.9	34.6	14.5	2.8	15.8	3.2	31		8.3
<i>A. pusilla</i>	USNM 498285	MALE	15.7	39.7	35.4	15	2.8	16.7	3.2	31.7	3.1	6.1
<i>A. pusilla</i>	USNM 224010	MALE	18.8	41.6	36.8	15.2	2.8	17.1	3.6	31.7	2.3	6
<i>A. pygmaea</i>	UMMZ 204592	FEMALE	16.9	42.4	36.4	15.9	2.6	17.1	4	32.2	2.2	6.6
<i>A. pygmaea</i>	UMMZ 224882	MALE	16.8	43.4	37.3	16	2.4	18.5	4.1	32	2.5	8.7
<i>A. pygmaea</i>	UMMZ 224883	FEMALE	16.8	42.6	36.4	16.4	3	18	4.2	32.6	2.2	6.6
<i>A. pygmaea</i>	USNM 344544	?	16	41.1	36	15.5	2.6	17.8	3.4	30.2	2	7.2
<i>Alca torda</i>	USNM 555666	MALE	33.9	95.6	88.6	29.1	6.5	51.2	11.3	82	8.4	25.6
<i>A. torda</i>	USNM 502378	MALE	33.4	94.6	87.5	27.9	5.9	50.4	12.2	78.3	8.6	22.6
<i>A. torda</i>	USNM 502387	MALE	33.6	91.1	85.1	27.7	5.9	47.6	12	80.3	7.1	22.8
<i>A. torda</i>	USNM 502389	FEMALE	31.3	93.9	86.3	28.5	6.2	50.5	11	79	8.6	25.5
<i>A. torda</i>	USNM 18062	FEMALE	35.3	94.7	87.3	27.1	6.8	51.2	12.7	82.6	7.1	23
<i>Alle alle</i>	USNM 560932	MALE	19.8	50.4	45.6	19.3	2.5	22.1	5	41.8	3.4	11.2
<i>A. alle</i>	USNM 560927	MALE	20.2	48.7	43.2	16.3	3.2	23	4.6	41.7	3	10.9
<i>A. alle</i>	USNM 560926	FEMALE	22.1	49.9	43.6	16.3	3.1	23.9	4.9	42.2	3.5	11.2

(continued)

## APPENDIX 1. Continued.

Taxon	Catalogue no.	Sex	gbS	glS	cblS	ghS	gbF	glR	ghR	glM	lsM	lFa	
<i>A. alle</i>	USNM 344748	MALE	19.5	48.8	43.9	18.1	2.9	20.7	4.6	41.1	2.6	11.5	
<i>Alle alle</i>	USNM 502391	FEMALE	18.9	47.7	43.3	18.7	3	22.5	4.7	39.7	2.7	11.2	
<i>Cephus columba</i>	USNM 610936	MALE	24.9	79.4	74.0	22.7	4.3	41.2	6.8	68.7	6.3	16.3	
<i>C. columba</i>	USNM 612989	MALE	24.8	81.3	76.7	22.9	4.1	43.6	6.4	69.6	6.2	17.8	
<i>C. columba</i>	USNM 498423	MALE	25.2	78.3	74.2	22.8	4.4	41.6	6.5	67.8	4.3	17.2	
<i>C. columba</i>	USNM 498422	FEMALE	24.8	80.8	75.5	22.4	4.3	41.4	7.0	69.5	4	15.1	
<i>C. columba</i>	USNM 612988	FEMALE	25.0	80.2	75.7	22.8	3.8	43.1	6.2	71.4	5.3	17.3	
<i>C. grylle</i>	USNM 344753	FEMALE	24.1	69.0	64.0	21.0	3.7	35.6	5.4	59.6	4.5	15	
<i>C. grylle</i>	USNM 344760	MALE	23.5	71.8	66.6	20.4	4.0	36.6	5.7	60.8	5.1	15.9	
<i>C. grylle</i>	USNM 344758	MALE	23.7	71.7	67.2	21.0	3.7	35.5	6.0	61.3	5.7	15.6	
<i>C. grylle</i>	USNM 347071	FEMALE	22.3	72.1	68.1	19.8	3.8	36.2	5.3	62.9	3.3	15.7	
<i>C. grylle</i>	USNM 344754	FEMALE	21.4	73.7	68.3	21.1	3.7	36.3	6.1	61.3	5.5	17.3	
<i>Fratercula arctica</i>	USNM 292346	?	31.6	81.1	72.7	26.3	5.5	46.8	17.2	66.1	5.1	15.6	
<i>F. arctica</i>	USNM225762	?	30.1	76.2	67.0	25.2	5.1	43.1	17.2	63.5	4.1	14.5	
<i>F. arctica</i>	USNM 292344	?	33.7	84.8	75.4	27.7	5.9	47.5	20.1	70.7	5.5	15.8	
<i>F. arctica</i>	USNM 292347	?	30.5	78.8	70.8	25.7	4.9	43.4	17.2	65.1	4.4	15	
<i>F. arctica</i>	USNM 224189	MALE	31.6	79.6	71.6	26.5	5.3	45.4	17.8	64.8	4.2	16.6	
<i>Pinguinus impennis</i>	USNM no #	?	46.5	161.4	155.0	–	8.6	99.2	24.5	142.3	12.7	31.8	
<i>P. impennis</i>	USNM no #	?	46.1	158.1	151.2	–	8.1	100.1	21.6	143.2	11.2	31.6	
<i>P. impennis</i>	USNM no #	?	46.3	160.3	153.7	–	8.9	103.5	23.8	145.9	10.9	37.8	
<i>P. impennis</i>	USNM no #	?	48.0	156.3	149.0	–	7.8	96.2	20.8	139.1	11.8	33.9	
<i>P. impennis</i>	USNM no #	?	44.4	155.5	146.5	–	9.2	94.4	22.7	135.7	13.1	33.1	
<i>Ptychoramphus aleuticus</i>	USNM 557611	MALE	19.1	52.2	46.5	16.5	2.9	27.5	4.6	42.2	3.1	8.1	
<i>P. aleuticus</i>	USNM 491305	MALE	20.9	53.1	46	16.4	3.4	27	4.9	43.2	3.3	9.4	
<i>P. aleuticus</i>	USNM 557607	FEMALE	17.8	48.4	43.7	15.9	2.8	23.9	4.3	38.8	3.7	7.8	
<i>P. aleuticus</i>	USNM 557609	FEMALE	18	49	43.3	16.9	3.1	24.4	4.5	36.6	3.4	8.6	
<i>P. aleuticus</i>	NCSM 18088	FEMALE	18.2	50	44.5	16	2.9	25.2	3.6	41.3	3.1	7.8	
<i>Uria aalge</i>	USNM 502349	MALE	31.8	103.7	98.7	29.3	6.0	55.5	9.2	94.0	9.5	22.6	
<i>U. aalge</i>	USNM 502355	MALE	30.9	104.1	98.1	28.8	6.3	56.9	9.3	90.3	10.7	24.7	
<i>U. aalge</i>	USNM 502348	MALE	31.4	102.6	96.6	28.5	6.0	56.3	8.6	90.3	8.8	25.4	
<i>U. aalge</i>	USNM 557539	FEMALE	30.3	103.3	96.8	28.7	6.8	55.9	8.9	90.6	10	24.1	
<i>U. aalge</i>	USNM 18066	FEMALE	31.1	102.5	97.9	28.0	6.3	57.3	9.1	92.6	9.2	24.2	
<i>U. lomvia</i>	USNM 502358	MALE	32.0	89.1	82.6	26.9	6.3	47.6	8.6	79.0	7.9	21.8	
<i>U. lomvia</i>	USNM 502361	MALE	32.7	92.2	86.3	27.1	5.9	49.4	8.7	82.1	8.7	24.5	
<i>U. lomvia</i>	USNM 502372	FEMALE	32.4	89.1	85.8	27.8	5.8	47.8	8.0	80.2	8.4	23.6	
<i>Uria lomvia</i>	USNM 502369	FEMALE	31.9	92.1	86.2	27.2	6.0	49.1	8.7	81.5	6.5	24.6	
<i>U. lomvia</i>	USNM 502374	FEMALE	30.4	87.5	81.6	26.0	4.9	45.7	8.4	75.5	6	22.4	
Taxon	Catalogue no.	mlS	dlS	lcS	SBF	glC	mlC	bbC	bfC	dlS	glH	bpH	scH
<i>Aethia cristatella</i>	USNM 561934	62.6	57.9	66.9	3.1	28.3	26.2	8.7	7.1	7.9	50.6	11.3	3.8
<i>A. cristatella</i>	USNM 223707	63.5	59.0	69.9	3.5	30.9	28.9	8.7	8.4	8.0	54.3	11.2	4.3
<i>A. cristatella</i>	USNM 610941	61.2	56.9	65.9	3.7	29.2	26.8	8.8	7.7	8.2	51.3	11.2	4.0
<i>A. cristatella</i>	USNM 498282	65.3	61.1	71.0	3.4	30.1	27.7	10.4	8.0	8.6	51.6	11.7	4.1
<i>A. cristatella</i>	NCSM 17749	63.4	59.7	69.1	3.0	29.5	28.6	8.9	8.1	8.5	53.8	12.3	4.2
<i>A. psittacula</i>	NCSM 14804	72.8	65.8	74.9	3.5	27.1	25.6	9.8	7.8	9.1	53.3	12.1	4.1
<i>A. psittacula</i>	NCSM 18387	74.5	70.6	77.7	3.2	27.9	27.1	9.8	8.4	8.2	53.9	11.8	4.0
<i>A. psittacula</i>	NCSM 14147	75.5	71.2	80.4	3.1	28.9	27.8	10.5	8.6	8.8	53.9	12.8	4.4
<i>A. psittacula</i>	NCSM 20177	70.9	64.3	75.3	3.2	27.6	26.9	10.2	7.9	8.1	54.5	11.6	4.1
<i>A. psittacula</i>	USNM 610513	55.0	51.6	57.3	3.0	26.2	25.1	9.9	7.7	8.2	54.6	11.8	4.4
<i>A. psittacula</i>	USNM 610514	56.2	51.8	56.3	2.8	27.9	26.4	10.3	8.5	7.8	55.5	11.9	4.6

(continued)

## APPENDIX 1. Continued.

Taxon	Catalogue no.	mlS	dlS	lcS	SBF	glC	mlC	bbC	bfC	diS	glH	bpH	schH
<i>A. psittacula</i>	USNM 610937	57.8	52.8	58.3	3.5	27.2	24.9	9.4	7.9	8.3	54.2	11.6	4.4
<i>A. pusilla</i>	NCSM 17737	42.9	40.9	38.5	1.4	18.1	17.9	6.4	5.2	5.4	34.0	7.8	2.4
<i>A. pusilla</i>	NCSM 17736	45.0	42.1	39.9	1.9	18.6	17.9	6.1	5.0	5.5	35.3	7.8	2.5
<i>A. pusilla</i>	NCSM 17734	37.0	34.6	39.1	1.7	18.4	18.1	6.0	5.0	5.5	35.2	7.8	2.5
<i>A. pusilla</i>	NCSM 224009	38.3	35.3	40.0	2.3	19.4	17.9	6.9	5.3	5.8	35.6	7.7	2.5
<i>A. pusilla</i>	USNM 498285	35.9	33.1	38.7	2.1	18.6	17.2	6.3	4.9	5.6	33.9	7.5	2.5
<i>A. pusilla</i>	USNM 224010	38.3	35.3	40.0	1.8	18.8	17.5	6.7	5.2	6.0	35.2	7.6	2.5
<i>A. pygmaea</i>	UMMZ 204592	46.9	43.2	47.6	2.9	20.5	18.8	6.7	5.2	6.0	37.8	8.0	2.8
<i>A. pygmaea</i>	UMMZ 224882	44.5	41.2	48.3	2.6	20.8	19.0	6.2	5.3	6.8	38.0	8.4	2.6
<i>A. pygmaea</i>	UMMZ 224883	45.0	42.3	47.0	2.6	19.9	18.5	6.6	5.0	6.2	37.4	8.2	2.7
<i>A. pygmaea</i>	USNM 344544	42.8	40.9	42.0	2.5	20.6	19.5	6.0	5.5	6.1	38.3	7.6	2.9
<i>Alca torda</i>	USNM 555666	104.5	98.0	113.2	4.6	38.8	36.9	19.7	14.7	10.6	79.9	16.7	7.4
<i>A. torda</i>	USNM 502378	99.1	93.9	108.2	5.5	39.0	36.9	19.9	15.0	10.6	76.3	16.8	7.2
<i>A. torda</i>	USNM 502387	98.6	91.6	108.6	4.1	38.5	36.2	19.0	14.7	11.1	77.0	16.3	7.1
<i>A. torda</i>	USNM 502389	92.6	85.1	100.5	4.4	39.1	37.5	19.6	14.4	11.0	82.8	16.9	7.0
<i>A. torda</i>	USNM 18062	96.8	91.1	104.9	5.7	40.6	38.5	19.4	15.0	10.5	77.2	16.2	7.0
<i>Alle alle</i>	USNM 560932	52.4	48.8	54.0	2.4	21.8	18.9	10.4	6.8	7.0	41.6	9.9	3.3
<i>A. alle</i>	USNM 560927	54.0	49.6	54.0	1.8	22.9	19.8	10.3	7.2	6.4	40.3	9.8	3.2
<i>A. alle</i>	USNM 560926	53.4	49.8	56.3	2.0	21.5	19.3	10.1	6.8	6.7	41.1	9.7	3.2
<i>A. alle</i>	USNM 344748	53.0	49.7	55.5	2.1	22.1	20.5	9.6	6.7	6.2	41.2	9.7	3.3
<i>A. alle</i>	USNM 502391	52.4	49.0	56.8	2.0	22.5	19.7	10.9	6.9	6.3	43.4	9.6	3.1
<i>Cepphus columba</i>	USNM 610936	84.2	76.4	90.8	4.0	36.9	33.7	19.3	13.0	9.3	68.8	15.9	5.0
<i>C. columba</i>	USNM 612989	75.8	69.7	84.1	4.0	35.6	31.9	16.4	12.1	8.6	64.6	14.6	4.9
<i>C. columba</i>	USNM 498423	78.3	72.5	79.1	3.4	34.2	31.4	17.2	11.3	9.3	65.9	15.0	5.4
<i>C. columba</i>	USNM 498422	82.2	76.1	86.3	3.2	35.4	32.2	17.7	12.2	8.6	67.1	15.3	5.5
<i>C. columba</i>	USNM 612988	82.5	75.6	88.2	3.1	35.9	32.2	17.6	12.9	9.0	66.5	15.7	4.8
<i>C. grylle</i>	USNM 344753	76.2	69.5	84.0	3.5	31.5	28.2	14.8	11.2	8.6	57.8	13.5	4.1
<i>C. grylle</i>	USNM 344760	76.2	69.5	81.0	3.9	31.1	28.0	15.8	10.9	8.8	59.5	14.0	4.4
<i>C. grylle</i>	USNM 344758	76.6	70.4	82.8	3.5	32.8	29.6	15.5	11.8	9.1	60.4	14.5	4.5
<i>C. grylle</i>	USNM 347071	71.7	71.5	86.3	3.3	32.5	29.8	15.2	11.6	9.5	60.5	14.2	4.5
<i>C. grylle</i>	USNM 344754	76.3	71.1	81.3	3.6	33.9	30.2	16.9	11.8	8.3	61.7	14.2	4.3
<i>Fratercula arctica</i>	USNM 292346	73.3	66.1	85.2	3.7	37.1	35.2	10.5	9.6	8.5	67.2	14.0	4.8
<i>F. arctica</i>	USNM225762	71.9	64.4	80.2	3.4	35.5	33.7	13.3	10.5	9.2	63.3	14.5	4.9
<i>F. arctica</i>	USNM 292344	79.6	76.9	90.0	3.8	38.3	36.1	13.8	10.9	9.6	68.9	15.4	5.7
<i>F. arctica</i>	USNM 292347	71.4	66.6	79.8	3.7	34.8	34.1	13.3	11.0	8.6	61.2	14.5	4.9
<i>F. arctica</i>	USNM 224189	69.5	64.9	78.8	3.4	37.5	34.5	11.9	9.4	9.4	68.2	13.8	4.9
<i>Pinguinus impennis</i>	USNM no #	176.5	165.5	193.5	8.4	66.3	60.5	33.7	24.8	16.7	106.3	24.8	10.5
<i>P. impennis</i>	USNM no #	180.5	167.7	184.0	6.1	63.2	58.6	37.3	26.9	17.6	105.8	24.8	11.0
<i>P. impennis</i>	USNM no #	170.7	161.6	185.9	6.0	62.6	59.1	34.1	26.3	16.1	105.2	24.1	10.0
<i>P. impennis</i>	USNM no #	178.7	166.7	199.2	9.8	61.7	57.6	28.7	24.3	17.1	103.7	24.6	10.2
<i>P. impennis</i>	USNM no #	187.2	177.1	201.5	7.6	65.0	61.0	34.1	28.0	17.9	101.8	24.7	10.8
<i>Ptychoramphus aleuticus</i>	USNM 557611	48.8	45.8	50.2	2.6	23.7	21.5	7.7	6.1	6.7	44.8	9.3	3.4
<i>P. aleuticus</i>	USNM 491305	48.1	46.0	49.9	1.8	24.5	22.7	8.8	6.9	6.7	47.3	9.8	3.4
<i>P. aleuticus</i>	USNM 557607	46.8	43.9	49.5	2.3	23.0	21.6	7.8	6.2	6.3	44.3	9.2	3.5
<i>P. aleuticus</i>	USNM 557609	47.3	44.1	49.0	2.0	23.3	21.4	8.4	6.7	7.0	43.5	9.4	3.2
<i>P. aleuticus</i>	NCSM 18088	49.3	45.4	51.0	1.8	23.4	22.5	8.3	6.5	6.6	45.6	9.4	3.7
<i>Uria aalge</i>	USNM 502349	119.6	110.8	129.0	4.2	40.7	38.3	22.3	16.2	11.8	84.1	17.0	7.2
<i>U. aalge</i>	USNM 502355	125.8	117.1	137.4	4.8	40.1	38.0	21.4	16.3	12.7	85.5	17.5	7.5
<i>U. aalge</i>	USNM 502348	121.1	112.3	133.5	5.1	39.8	38.6	21.6	16.1	12.0	84.9	17.8	7.6
<i>U. aalge</i>	USNM 557539	112.3	102.5	123.4	4.0	39.1	37.1	20.5	14.8	11.1	81.9	16.4	7.5
<i>U. aalge</i>	USNM 18066	126.0	116.9	135.9	5.1	42.5	39.7	23.8	17.1	12.5	89.2	19.0	7.8

(continued)

## APPENDIX 1. Continued.

Taxon	Catalogue no.	mlS	dIS	lcS	SBF	glC	mlC	bbC	bfC	diS	glH	bpH	scH	
<i>U. lomvia</i>	USNM 502358	110.2	102.8	119.8	5.0	41.4	39.0	21.4	16.2	11.5	87.6	17.1	6.8	
<i>U. lomvia</i>	USNM 502361	116.0	108.1	125.3	5.3	41.9	39.4	22.3	16.8	11.8	87.7	17.9	7.6	
<i>U. lomvia</i>	USNM 502372	113.0	104.8	123.3	4.1	44.0	41.0	21.5	16.5	11.9	88.3	17.5	7.3	
<i>U. lomvia</i>	USNM 502369	111.4	103.6	120.4	3.6	40.9	37.8	21.9	17.1	12.0	87.5	18.3	7.2	
<i>U. lomvia</i>	USNM 502374	110.2	102.1	117.6	3.2	39.5	36.6	21.5	16.0	11.9	89.4	17.4	6.9	
Taxon	Catalogue no.	BdH	ddH	dpH	glR	bpR	scR	bdR	glU	bpU	scU	bdU	ddU	glC
<i>Aethia</i>	USNM 561934	8.1	5.6	11.1	41.5	3.3	1.7	3.6	43.9	7.8	6.3	5.7	4.7	29.0
<i>A. cristatella</i>														
<i>A. cristatella</i>	USNM 223707	8.7	6.0	11.5	44.4	3.2	2.2	3.9	46.8	7.8	6.3	6.0	4.8	30.6
<i>A. cristatella</i>	USNM 610941	8.5	5.8	11.5	41.6	3.5	2.2	3.6	52.4	10.6	7.5	7.7	6.1	27.8
<i>A. cristatella</i>	USNM 498282	8.5	6.0	11.1	42.4	3.4	2.1	3.7	44.4	8.5	6.8	6.1	4.5	29.2
<i>A. cristatella</i>	NCSM 17749	8.4	6.0	11.8	—	—	—	—	48.7	9.2	7.3	6.5	5.2	—
<i>A. psittacula</i>	NCSM 14804	8.4	6.3	11.2	46.5	3.5	2.0	3.8	48.5	8.2	6.7	6.2	5.0	30.0
<i>A. psittacula</i>	NCSM 18387	8.9	6.4	11.3	46.6	3.5	2.1	3.7	48.6	8.7	6.9	6.3	5.4	—
<i>A. psittacula</i>	NCSM 14147	9.0	6.6	11.6	46.4	3.9	2.2	3.9	46.9	8.3	6.7	6.1	5.3	—
<i>A. psittacula</i>	NCSM 20177	8.7	6.1	11.3	45.5	3.7	2.0	3.4	47.1	8.8	6.7	6.2	5.1	30.0
<i>A. psittacula</i>	USNM 610513	8.6	6.2	11.3	46.9	3.5	2.2	3.7	49.2	8.4	6.3	6.0	4.9	30.8
<i>A. psittacula</i>	USNM 610514	8.8	6.1	10.9	47.5	3.6	2.3	4.0	49.7	8.6	6.8	6.0	4.3	31.8
<i>A. psittacula</i>	USNM 610937	8.8	6.3	11.5	46.7	3.8	2.3	3.7	49.1	8.5	6.4	6.1	4.8	31.0
<i>A. pusilla</i>	NCSM 17737	5.5	4.1	7.4	27.2	2.2	1.3	2.2	28.8	5.4	4.3	4.0	2.8	—
<i>A. pusilla</i>	NCSM 17736	5.6	4.0	7.1	28.8	2.1	1.4	2.5	30.1	5.6	4.3	4.0	3.2	—
<i>A. pusilla</i>	NCSM 17734	5.4	3.9	7.5	29.2	2.1	1.3	2.6	30.2	5.3	4.3	4.2	3.1	—
<i>A. pusilla</i>	NCSM 224009	5.6	4.1	7.1	29.1	2.2	1.3	2.7	30.5	5.8	4.7	3.5	3.3	20.0
<i>A. pusilla</i>	USNM 498285	5.4	3.9	7.1	27.7	2.2	1.3	2.5	29.2	5.2	4.1	3.9	3.0	19.1
<i>A. pusilla</i>	USNM 224010	5.5	4.1	7.6	28.3	2.3	1.5	2.6	29.8	5.7	4.4	4.2	3.3	19.8
<i>A. pygmaea</i>	UMMZ 204592	5.8	4.3	7.8	30.5	2.5	1.3	2.7	32.2	5.9	4.6	4.4	3.3	21.2
<i>A. pygmaea</i>	UMMZ 224882	6.1	4.4	8.3	30.5	2.5	1.4	2.9	32.2	6.0	4.6	4.5	3.3	20.9
<i>A. pygmaea</i>	UMMZ 224883	5.9	4.2	7.7	30.5	2.5	1.4	2.8	32.0	5.6	4.5	4.3	3.5	20.5
<i>A. pygmaea</i>	USNM 344544	5.8	4.3	7.4	31.3	2.5	1.4	2.7	32.8	5.6	4.4	4.4	3.3	20.8
<i>Alca torda</i>	USNM 555666	11.2	7.9	16.7	61.5	5.1	3.4	5.3	63.6	12.3	7.7	8.5	5.9	42.6
<i>A. torda</i>	USNM 502378	11.2	8.1	15.2	59.4	5.4	3.3	5.4	61.6	12.4	7.8	8.2	6.3	41.0
<i>A. torda</i>	USNM 502387	11.3	8.3	15.6	60.4	5.3	3.4	5.2	62.8	12.1	7.2	8.3	6.0	41.4
<i>A. torda</i>	USNM 502389	11.0	7.8	16.0	62.5	4.9	3.3	5.3	65.1	11.8	7.8	8.6	6.2	41.8
<i>A. torda</i>	USNM 18062	11.1	8.0	16.5	59.5	5.3	3.5	5.7	61.5	12.4	7.8	8.4	7.4	40.8
<i>Alle alle</i>	USNM 560932	6.8	4.8	8.6	31.8	2.7	1.8	2.7	34.1	7.0	4.8	4.8	3.3	21.8
<i>A. alle</i>	USNM 560927	6.4	4.6	8.9	31.9	2.6	1.9	3.2	34.2	7.2	4.3	4.9	3.8	21.9
<i>A. alle</i>	USNM 560926	6.7	4.6	8.6	31.7	2.8	1.7	3.2	33.8	5.8	4.5	5.0	3.3	21.7
<i>A. alle</i>	USNM 344748	6.6	4.6	8.8	31.8	2.9	1.7	3.2	34.2	7.4	4.4	4.9	3.2	22.6
<i>A. alle</i>	USNM 502391	6.5	4.5	9.1	32.5	2.7	1.8	3.1	34.4	6.8	4.4	4.7	3.4	22.2
<i>Cepphus</i>	USNM 610936	10.0	8.0	14.2	55.2	4.5	2.7	5.1	58.2	10.7	7.7	8.0	6.6	39.3
<i>C. columba</i>														
<i>C. columba</i>	USNM 612989	9.5	7.1	13.5	51.7	4.4	2.7	4.7	54.4	10.2	6.3	7.7	6.3	36.2
<i>C. columba</i>	USNM 498423	9.9	7.7	13.7	53.1	4.7	2.9	5.0	56.0	10.7	7.1	7.8	5.9	37.1
<i>C. columba</i>	USNM 498422	9.9	7.7	14.2	54.2	4.5	3.2	4.9	57.1	10.6	7.4	7.7	5.7	38.3
<i>C. columba</i>	USNM 612988	9.3	7.4	14.0	53.6	4.7	2.8	4.6	56.5	10.4	7.6	7.6	5.4	38.2
<i>C. grylle</i>	USNM 344753	8.6	6.4	12.6	47.0	4.2	2.2	4.2	49.4	9.1	6.4	6.7	5.5	33.0
<i>C. grylle</i>	USNM 344760	8.5	6.3	12.5	49.3	3.9	2.6	4.4	52.0	9.2	6.4	6.9	5.5	34.2
<i>C. grylle</i>	USNM 344758	9.0	7.0	13.1	49.3	4.1	2.5	4.6	52.8	9.9	7.2	7.5	6.0	34.2
<i>C. grylle</i>	USNM 347071	9.1	6.9	12.8	49.2	4.1	2.6	4.6	51.4	9.6	6.3	7.0	6.1	33.9
<i>C. grylle</i>	USNM 344754	9.1	7.2	13.4	51.1	4.9	2.8	4.8	53.1	9.7	7.1	7.4	5.7	36.0
<i>Fratercula</i>	USNM 292346	9.8	6.8	13.1	51.2	4.3	2.8	4.3	52.9	9.7	6.5	7.3	4.9	35.5
<i>F. arctica</i>														
<i>F. arctica</i>	USNM225762	9.4	6.5	13.4	48.5	4.0	2.6	4.5	50.8	9.4	6.4	7.1	5.0	33.5

(continued)

APPENDIX 1. Continued.

Taxon	Catalogue no.	BdH	ddH	dpH	glR	bpR	scR	bdR	glU	bpU	scU	bdU	ddU	glC
<i>F. arctica</i>	USNM 292344	10.6	7.2	14.7	51.7	4.5	3.2	5.0	54.0	10.3	6.9	8.1	5.8	37.3
<i>F. arctica</i>	USNM 292347	9.9	6.5	12.7	46.6	4.1	2.9	4.8	48.3	9.2	6.4	7.0	5.3	32.5
<i>F. arctica</i>	USNM 224189	10.0	7.4	13.5	52.3	4.5	3.0	4.9	54.1	9.5	6.9	7.8	6.2	36.3
<i>Pinguinus impennis</i>	USNM no #	16.3	10.7	22.6	58.1	6.7	5.7	6.5	58.1	16.9	10.2	9.7	6.9	43.6
<i>P. impennis</i>	USNM no #	16.5	9.9	22.7	55.2	6.9	5.8	6.5	55.2	16.5	10.8	10.0	7.1	43.0
<i>P. impennis</i>	USNM no #	15.6	10.8	22.5	56.3	6.8	5.9	6.2	56.3	15.8	10.0	10.9	7.2	45.2
<i>P. impennis</i>	USNM no #	15.7	10.8	22.4	56.7	6.4	6.0	6.3	59.7	16.9	10.8	10.3	6.9	41.7
<i>P. impennis</i>	USNM no #	15.4	10.7	23.0	55.9	7.1	6.1	7.1	55.8	16.4	10.3	10.2	6.6	42.7
<i>Ptychoramphus aleuticus</i>	USNM 557611	7.2	4.9	9.1	36.8	2.9	1.9	3.2	38.5	7.1	5.5	5.2	4.2	25.5
<i>P. aleuticus</i>	USNM 491305	7.4	5.2	9.6	38.3	2.8	1.7	3.3	40.1	7.2	5.7	5.2	4.1	25.8
<i>P. aleuticus</i>	USNM 557607	6.6	4.8	8.8	37.1	2.7	1.9	3.0	38.8	6.7	5.4	4.9	3.6	24.5
<i>P. aleuticus</i>	USNM 557609	6.8	4.9	9.6	36.3	2.9	1.7	2.9	38.2	6.8	5.4	5.0	3.8	24.4
<i>P. aleuticus</i>	NCSM 18088	7.1	5.0	9.3	37.5	2.9	2.0	3.0	39.4	6.9	5.4	5.0	3.8	25.5
<i>Uria aalge</i>	USNM 502349	12.1	8.5	15.4	61.4	5.5	3.5	5.6	64.3	13.1	8.3	8.8	6.4	43.6
<i>U. aalge</i>	USNM 502355	12.4	8.6	16.8	62.2	5.8	3.4	5.9	64.0	13.0	8.2	8.9	6.4	43.9
<i>U. aalge</i>	USNM 502348	12.4	8.7	15.9	60.7	5.8	3.7	5.9	62.7	12.9	8.6	9.1	6.5	43.9
<i>U. aalge</i>	USNM 557539	11.9	8.4	16.0	58.6	5.4	3.7	5.6	61.0	12.4	8.0	8.3	6.2	42.4
<i>U. aalge</i>	USNM 18066	12.7	8.8	18.2	65.2	5.9	3.7	6.0	67.8	14.1	8.6	9.6	6.9	44.9
<i>U. lomvia</i>	USNM 502358	12.1	9.3	16.3	66.6	5.7	3.4	5.5	69.4	12.9	9.9	9.4	7.2	44.3
<i>U. lomvia</i>	USNM 502361	12.3	8.9	16.6	65.0	5.4	3.8	5.8	67.7	13.2	8.6	9.3	8.0	44.6
<i>U. lomvia</i>	USNM 502372	11.6	8.3	16.2	65.7	5.0	3.4	5.4	68.5	12.9	9.3	8.9	7.1	45.9
<i>U. lomvia</i>	USNM 502369	12.6	9.1	16.8	65.7	5.7	3.5	5.6	67.8	13.2	8.8	9.3	7.2	44.8
<i>U. lomvia</i>	USNM 502374	12.2	8.6	15.3	65.9	5.5	3.3	5.4	68.1	12.7	8.2		6.5	43.4
Taxon	Catalogue no.	IMC1	bpC	ddC	glD	ID	glP	lsP	lvP	cbP	sbP	aaP	dA	bA
<i>Aethia cristatella</i>	USNM 561934	4.3	4.8	4.4	14.1	13.1	45.1	41.9	35.3	15.7	10.7	14.6	3.1	16.7
<i>A. cristatella</i>	USNM 223707	5.1	4.6	4.5	14.8	13.0	49.5	45.3	37.5	17.0	11.3	16.4	3.0	18.2
<i>A. cristatella</i>	USNM 610941	4.4	4.7	3.0	13.7	12.6	45.3	42.4	40.0	15.6	11.9	16.0	3.4	17.2
<i>A. cristatella</i>	USNM 498282	5.0	4.9	4.3	13.8	12.7	46.8	44.8	36.2	17.9	11.3	16.6	3.5	18.5
<i>A. cristatella</i>	NCSM 17749	–	–	–	–	–	45.4	42.4	32.0	17.2	11.8	15.7	3.3	17.7
<i>A. psittacula</i>	NCSM 14804	4.3	5.2	4.5	14.2	13.2	45.3	41.4	32.4	15.0	12.2	18.0	3.1	20.3
<i>A. psittacula</i>	NCSM 18387	–	–	–	–	–	45.0	41.9	35.2	17.0	13.0	18.0	3.3	20.9
<i>A. psittacula</i>	NCSM 14147	–	–	–	–	–	44.9	41.1	33.5	15.5	12.3	17.8	3.5	21.2
<i>A. psittacula</i>	NCSM 20177	5.1	4.8	3.8	13.7	12.5	46.1	42.2	36.1	16.7	12.0	16.4	3.4	19.9
<i>A. psittacula</i>	USNM 610513	4.3	5.0	3.0	13.3	12.2	–	–	33.1	–	–	–	3.7	–
<i>A. psittacula</i>	USNM 610514	5.3	4.8	4.2	14.1	13.0	–	–	35.3	–	–	–	3.4	–
<i>A. psittacula</i>	USNM 610937	5.1	4.5	4.4	13.8	12.6	47.7	42.6	35.9	15.6	12.7	16.1	3.7	19.9
<i>A. pusilla</i>	NCSM 17737	–	–	–	–	–	26.5	25.0	20.6	10.2	9.1	12.9	1.8	13.3
<i>A. pusilla</i>	NCSM 17736	–	–	–	–	–	28.8	26.4	21.8	11.2	9.7	13.7	2.0	14.1
<i>A. pusilla</i>	NCSM 17734	–	–	–	–	–	28.2	26.4	22.2	11.2	9.2	12.2	2.1	14.0
<i>A. pusilla</i>	NCSM 224009	3.0	3.1	3.0	9.5	8.7	29.4	26.7	22.6	12.2	9.6	13.2	2.1	14.6
<i>A. pusilla</i>	USNM 498285	3.1	3.1	3.2	9.4	8.6	28.4	27.3	22.5	11.5	10.3	13.9	1.8	15.0
<i>A. pusilla</i>	USNM 224010	3.3	3.3	2.9	9.3	8.3	29.4	27.6	22.9	12.5	9.8	13.8	2.1	14.6
<i>A. pygmaea</i>	UMMZ 204592	3.3	3.5	3.2	10.1	9.3	33.2	30.3	27.5	13.1	9.2	13.1	2.5	15.0
<i>A. pygmaea</i>	UMMZ 224882	3.5	3.3	3.3	10.4	9.6	35.2	31.7	26.0	13.9	9.4	13.3	2.6	15.0
<i>A. pygmaea</i>	UMMZ 224883	3.1	3.5	3.3	9.6	8.8	31.8	29.2	27.8	11.9	9.2	12.5	2.5	13.9
<i>A. pygmaea</i>	USNM 344544	3.8	3.2	2.4	10.6	9.7	31.6	28.7	25.6	11.8	9.0	12.3	2.2	13.4
<i>Alca torda</i>	USNM 555666	7.9	10.7	7.0	21.1	18.8	76.6	66.3	54.4	24.2	16.7	20.4	4.8	23.7
<i>A. torda</i>	USNM 502378	7.1	10.7	6.7	20.6	18.4	72.4	66.6	56.6	22.5	15.6	19.5	4.8	21.6
<i>A. torda</i>	USNM 502387	7.2	10.8	6.8	20.8	19.3	73.3	64.3	53.7	21.2	15.0	18.7	4.6	21.8
<i>A. torda</i>	USNM 502389	7.2	10.4	7.1	20.9	18.8	79.7	64.6	52.2	23.5	17.1	18.1	4.7	23.7
<i>A. torda</i>	USNM 18062	7.7	10.2	7.1	21.0	18.9	74.0	66.7	54.7	23.0	16.0	18.5	4.6	22.0

(continued)

## APPENDIX 1. Continued.

Taxon	Catalogue no.	lmc1	bpC	ddC	glD	ID	glP	lsP	lvP	cbP	sbP	aaP	dA	bA
<i>Alle alle</i>	USNM 560932	3.6	6.1	3.8	10.6	10.2	40.2	33.7	27.8	13.8	12.4	15.1	2.1	17.1
<i>A. alle</i>	USNM 560927	3.7	6.3	4.3	11.1	9.8	41.7	31.9	27.1	14.9	11.9	14.3	2.2	16.3
<i>A. alle</i>	USNM 560926	2.7	6.3	4.1	10.7	9.9	40.4	31.3	25.0	14.5	12.8	15.5	2.1	16.4
<i>A. alle</i>	USNM 344748	4.0	6.3	4.4	11.7	10.6	39.1	32.9	28.8	14.4	12.1	15.3	2.2	17.1
<i>Alle alle</i>	USNM 502391	3.8	6.0	4.3	11.3	10.3	41.3	32.4	28.4	13.7	11.7	14.2	2.2	15.7
<i>Cepphus columba</i>	USNM 610936	6.0	9.8	6.3	17.4	15.6	72.8	56.2	54.5	22.9	16.3	21.8	4.3	24.0
<i>C. columba</i>	USNM 612989	5.1	9.3	6.2	15.9	14.2	67.8	51.5	46.7	21.5	16.3	19.4	3.9	23.0
<i>C. columba</i>	USNM 498423	6.1	9.5	6.3	16.5	14.5	69.4	54.0	47.1	19.3	15.6	21.3	3.8	24.2
<i>C. columba</i>	USNM 498422	6.6	9.4	6.3	17.9	15.9	66.7	51.3	49.7	20.8	16.7	21.9	4.6	24.1
<i>C. columba</i>	USNM 612988	6.7	9.3	6.1	18.3	16.4	71.6	52.9	48.3	23.7	17.8	22.5	4.3	24.9
<i>C. grylle</i>	USNM 344753	5.0	7.9	5.3	14.7	13.1	61	45.1	41.2	17.9	14.2	17.3	3.4	21.0
<i>C. grylle</i>	USNM 344760	5.3	7.8	5.5	16.1	14.2	60.7	46.8	38.9	17.3	14.0	17.9	3.2	20.8
<i>C. grylle</i>	USNM 344758	5.1	8.7	5.7	16.4	15.1	59.1	48.3	43.8	20.7	14.0	18.6	3.4	20.8
<i>C. grylle</i>	USNM 347071	5.5	8.4	5.8	16.0	14	62.1	49.2	38.8	21.6	15.0	18.8	3.5	21.6
<i>C. grylle</i>	USNM 344754	5.7	8.6	6.2	16.2	14.8	67	49.3	41.3	20.0	15.1	19.2	3.9	23.0
<i>Fratercula arctica</i>	USNM 292346	6.2	8.3	5.1	18.2	16.1	66.6	53.3	38.0	18.2	13.6	19.2	4.1	22.8
<i>F. arctica</i>	USNM225762	6.0	8.4	5.7	16.3	14.9	61.7	48.8	40.5	16.6	14.8	20.4	3.6	24.3
<i>F. arctica</i>	USNM 292344	6.8	9.0	6.3	18.3	15.8	71.3	55.4	43.6	18.1	14.9	20.7	4.3	26.0
<i>F. arctica</i>	USNM 292347	5.6	8.4	5.7	16.5	14.7	66.2	52.7	44.4	17.9	16.2	21.8	4.0	26.2
<i>F. arctica</i>	USNM 224189	6.4	9.1	6.2	18.5	16.8	68.9	53.9	45.2	15.9	14.3	21.3	4.4	24.3
<i>Pinguinus impennis</i>	USNM no #	12.5	12.6	9.2	22.5	21.9	-	-	98.8	-	-	-	9.1	-
<i>P. impennis</i>	USNM no #	12.5	13.3	9.4	23.0	21.4	-	-	100.7	-	-	-	9.0	-
<i>P. impennis</i>	USNM no #	12.4	12.9	8.6	22.4	20.8	-	-	95.3	-	-	-	9.3	-
<i>P. impennis</i>	USNM no #	11.5	12.8	9.2	21.2	20.6	-	-	94.2	-	-	-	9.1	-
<i>P. impennis</i>	USNM no #	11.5	13.2	8.5	22.0	20.5	-	-	94.1	-	-	-	9.4	-
<i>Ptychoramphus aleuticus</i>	USNM 557611	4.0	3.8	4.2	11.7	10.9	36.0	32.5	26.1	11.7	10.1	13.8	2.3	15.8
<i>P. aleuticus</i>	USNM 491305	4.2	4.5	4.5	12.5	11.5	38.5	36.1	28.5	-	-	-	2.8	-
<i>P. aleuticus</i>	USNM 557607	4.0	3.7	3.5	11.4	10.5	37.1	33.4	26.8	14.8	10.6	13.7	2.1	15.2
<i>P. aleuticus</i>	USNM 557609	4.1	3.8	3.9	11.4	10.8	36.8	34.7	28.2	12.9	10.1	13.8	2.5	16.1
<i>P. aleuticus</i>	NCSM 18088	4.0	4.0	3.1	12.2	11.6	38.4	25.4	30.4	14.2	10.6	14.3	2.6	16.0
<i>Uria aalge</i>	USNM 502349	8.0	10.6	7.1	21.1	19.4	88.2	72.9	62.1	22.9	17.2	22.0	5.2	22.5
<i>U. aalge</i>	USNM 502355	8.6	10.7	8.0	20.3	18.6	86.7	75.5	57.9	26.4	16.5	21.6	4.6	22.9
<i>U. aalge</i>	USNM 502348	8.9	10.4	7.8	21.2	19.3	90	73.6	55.5	27.2	17.4	22.1	5.0	23.4
<i>U. aalge</i>	USNM 557539	7.6	9.6	6.9	19.4	18.2	84.8	70.8	62.2	23.3	15.9	19.5	4.9	22.0
<i>U. aalge</i>	USNM 18066	8.5	10.6	7.9	21.7	19.7	91.4	78.8	60.8	25.9	18.0	22.4	5.7	24.7
<i>U. lomvia</i>	USNM 502358	7.6	10.5	7.6	20.5	19.2	81.3	68.6	54.1	26.0	16.6	20.3	4.6	22.7
<i>U. lomvia</i>	USNM 502361	9.0	10.5	7.5	21.5	19.7	82.6	68.7	54.5	23.3	16.9	20.1	5.1	21.2
<i>U. lomvia</i>	USNM 502372	8.6	10.4	7.6	22.2	20.1	84.5	71.1	59.4	28.2	18.2	22.3	4.9	23.8
<i>U. lomvia</i>	USNM 502369	8.5	10.8	7.7	21.0	19.1	82.7	67.3	53.1	24.6	17.8	22.7	5.1	23.0
<i>U. lomvia</i>	USNM 502374	7.2	10.3	7.2	20.6	19.4	78.1	65.6	54.2	23.0	15.5	20.4	4.3	21.7
Taxon	Catalogue no.	glF	mlF	bpF	dpF	scF	bdF	ddf	glT	laT	dpT	scT	bdT	ddT
<i>Aethia cristatella</i>	USNM 561934	34.8	33.0	6.1	4.0	2.8	5.5	5.2	58.4	54.3	6.7	2.6	4.9	4.7
<i>A. cristatella</i>	USNM 223707	36.9	35.3	6.5	4.0	3.0	5.9	5.4	63.8	59.6	7.7	2.8	4.8	5.2
<i>A. cristatella</i>	USNM 610941	33.8	32.1	6.5	4.2	2.8	5.5	5.3	58.7	55.1	7.0	2.8	5.1	5.0
<i>A. cristatella</i>	USNM 498282	34.7	33.6	6.3	4.4	3.2	6.1	5.4	61.4	56.9	7.0	2.8	5.3	5.0
<i>A. cristatella</i>	NCSM 17749	36.0	34.2	6.8	4.3	2.9	5.8	5.8	63.7	59.7	7.2	2.7	5.5	5.1
<i>A. psittacula</i>	NCSM 14804	32.5	31.9	6.6	4.9	3.0	5.9	5.5	58.1	53.6	7.7	2.4	5.4	5.2
<i>A. psittacula</i>	NCSM 18387	34.7	33.0	6.6	4.5	3.0	6.3	5.9	60.2	55.4	7.8	2.9	4.8	5.4
<i>A. psittacula</i>	NCSM 14147	34.0	32.8	6.6	4.5	2.8	6.5	5.9	60.6	55.9	7.1	3.0	5.9	5.7
<i>A. psittacula</i>	NCSM 20177	35.1	33.3	6.9	4.5	2.7	6.0	5.6	59.0	54.9	7.4	2.8	5.7	5.5

(continued)

## APPENDIX 1. Continued.

Taxon	Catalogue no.	glF	mlF	bpF	dpF	scF	bdF	ddF	glT	laT	dpT	scT	bdT	ddT
<i>A. psittacula</i>	USNM 610513	34.8	33.4	6.8	4.4	3.2	6.0	5.5	59.4	55.8	7.5	2.8	5.2	5.2
<i>A. psittacula</i>	USNM 610514	34.1	32.5	6.2	4.9	3.2	5.8	5.8	59.3	54.0	7.2	2.9	5.4	5.4
<i>A. psittacula</i>	USNM 610937	33.9	32.7	6.3	4.7	2.9	5.9	5.9	58.8	54.3	7.2	3.0	5.7	5.5
<i>A. pusilla</i>	NCSM 17737	21.9	21.0	3.9	2.6	2.0	3.8	3.4	36.8	35.6	4.8	1.7	2.8	3.3
<i>A. pusilla</i>	NCSM 17736	23.0	22.1	4.3	2.8	1.9	4.1	3.5	40.1	37.3	4.8	1.8	3.3	3.3
<i>A. pusilla</i>	NCSM 17734	22.7	21.8	4.0	2.6	1.9	3.9	3.4	39.9	37.2	4.9	1.7	3.4	3.4
<i>A. pusilla</i>	NCSM 224009	22.4	21.4	4.1	3.1	2.1	3.9	3.5	41.1	38.2	4.9	1.6	3.4	3.3
<i>A. pusilla</i>	USNM 498285	22.7	21.7	3.8	2.9	2.0	3.8	3.7	40.1	37.2	4.5	1.8	3.2	3.3
<i>A. pusilla</i>	USNM 224010	23.0	21.9	4.5	3.0	2.0	3.9	3.7	40.9	37.4	5.0	1.8	3.4	3.5
<i>A. pygmaea</i>	UMMZ 204592	26.9	25.6	5.2	3.0	2.3	4.1	4.1	45.3	42.4	4.9	1.8	3.6	3.6
<i>A. pygmaea</i>	UMMZ 224882	25.6	24.5	4.7	2.8	2.1	4.3	3.7	43.8	41.4	5.0	1.8	3.6	3.6
<i>A. pygmaea</i>	UMMZ 224883	24.4	23.4	4.2	3.1	2.0	4.1	3.8	43.7	41.2	4.8	2.0	3.8	3.4
<i>A. pygmaea</i>	USNM 344544	25.6	24.4	4.9	2.9	2.3	4.0	4.0	45.6	43.1	4.4	1.7	3.7	3.3
<i>Alca torda</i>	USNM 555666	43.0	41.4	9.1	6.7	4.0	8.0	7.4	79.8	73.8	9.6	4.0	6.7	6.8
<i>A. torda</i>	USNM 502378	42.9	41.1	8.0	6.5	3.9	8.0	7.4	76.1	71.0	10.6	3.6	6.8	6.1
<i>A. torda</i>	USNM 502387	41.9	40.8	8.1	6.4	4.1	7.7	6.8	76.1	71.4	9.5	3.7	6.3	6.1
<i>Alca torda</i>	USNM 502389	45.5	44.0	8.6	7.1	3.8	7.6	7.1	81.6	76.5	9.5	3.6	6.6	6.4
<i>A.a torda</i>	USNM 18062	41.7	40.6	8.8	6.9	3.9	7.9	7.2	78.4	72.7	9.4	4.0	6.7	6.3
<i>Alle alle</i>	USNM 560932	26.8	26.1	4.8	3.3	2.4	4.5	3.5	47.5	44.0	5.6	2.0	4.0	4.0
<i>A. alle</i>	USNM 560927	26.9	25.8	4.8	3.3	2.1	4.3	4.1	46.9	43.4	5.7	1.8	3.9	4.2
<i>A. alle</i>	USNM 560926	25.9	24.8	4.5	3.6	2.1	4.5	4.1	45.9	42.5	5.2	2.0	4.1	4.1
<i>A. alle</i>	USNM 344748	27.4	26.5	5.1	3.4	2.1	4.7	3.9	46.9	43.6	5.3	1.9	4.2	3.8
<i>A. alle</i>	USNM 502391	26.1	25.2	4.6	3.1	2.0	4.4	3.7	45.9	42.7	5.3	1.8	3.8	3.6
<i>Cephus columba</i>	USNM 610936	40.4	38.6	8.2	5.9	3.8	8.3	6.8	75.6	69.2	9.4	4.0	6.3	6.5
<i>C. columba</i>	USNM 612989	38.7	37.2	7.5	5.6	3.7	7.4	6.7	73.9	68.0	8.8	3.8	5.9	6.0
<i>C. columba</i>	USNM 498423	39.8	37.5	7.7	5.8	3.8	7.8	6.8	72.6	66.4	9.5	4.7	6.2	6.2
<i>C. columba</i>	USNM 498422	39.3	37.6	7.3	5.7	3.9	7.6	6.9	74.8	68.8	9.0	4.1	6.6	6.2
<i>C. columba</i>	USNM 612988	39.8	38.3	7.6	5.6	3.5	7.5	6.1	74.9	68.7	9.3	4.0	6.2	6.2
<i>C. grylle</i>	USNM 344753	35.0	32.8	6.7	5.0	2.9	6.1	5.7	62.8	58.0	7.1	2.8	5.4	5.2
<i>C. grylle</i>	USNM 344760	35.7	34.2	6.4	4.4	3.3	6.4	5.7	62.7	58.1	7.9	3.0	5.6	5.3
<i>C. grylle</i>	USNM 344758	36.5	34.5	7.0	5.2	3.2	6.7	6.0	65.2	60.3	8.4	2.9	6.1	5.6
<i>C. grylle</i>	USNM 347071	35.3	33.8	6.8	4.8	3.6	6.4	6.2	62.9	58.3	8.2	3.1	5.7	5.3
<i>C. grylle</i>	USNM 344754	37.6	35.9	7.2	5.6	3.3	7.1	6.5	66.6	61.4	8.8	3.1	6.4	5.8
<i>Fratercula arctica</i>	USNM 292346	40.3	38.9	7.1	5.3	3.3	6.8	6.3	67.9	63.4	8.3	3.4	6.4	6.4
<i>F. arctica</i>	USNM 225762	37.7	36.5	7.5	5.7	3.1	7.2	6.2	66.5	62.3	8.2	3.5	5.6	6.1
<i>F. arctica</i>	USNM 292344	42.3	41.1	8.8	5.2	3.5	7.8	6.4	73.3	68.8	9.3	3.6	6.4	6.5
<i>F. arctica</i>	USNM 292347	38.1	36.8	7.2	5.5	3.1	7.1	6.1	63.0	59.3	9.0	3.7	5.9	6.2
<i>F. arctica</i>	USNM 224189	41.5	40.2	7.7	5.4	3.2	7.4	7.3	70.4	66.6	9.1	3.6	6.4	6.7
<i>Pinguinus impennis</i>	USNM no #	76.6	73.4	16.2	11.2	9.4	14.6	13.8	133.6	124.6	15.6	7.3	12.6	12.3
<i>P. impennis</i>	USNM no #	72.4	69.8	14.0	10.0	7.8	13.3	12.6	131.3	122.1	16.7	7.1	12.8	12.3
<i>P. impennis</i>	USNM no #	71.0	68.3	14.6	10.5	7.3	12.9	12.0	133.5	125.8	16.2	7.1	11.4	11.4
<i>P. impennis</i>	USNM no #	74.6	72.4	16.2	11.6	9.2	14.8	13.1	129.7	120.8	16.6	7.0	12.1	10.8
<i>P. impennis</i>	USNM no #	76.5	74.2	15.6	11.0	8.2	14.4	13.5	129.9	121.6	16.1	7.3	12.9	12.8
<i>Ptychoramphus aleuticus</i>	USNM 557611	27.9	26.6	4.8	3.4	2.5	4.7	4.7	50.6	46.5	6.1	2.3	4.3	4.3
<i>P. aleuticus</i>	USNM 491305	29.6	28.2	5.2	3.5	2.3	5.0	4.9	51.6	47.2	5.0	2.3	4.4	4.3
<i>P. aleuticus</i>	USNM 557607	26.7	25.7	4.7	3.0	2.5	4.3	4.4	47.8	43.5	5.6	2.3	4.3	4.0
<i>P. aleuticus</i>	USNM 557609	26.0	25.0	4.7	3.7	2.4	4.5	4.5	47.7	43.9	5.8	2.1	4.2	4.1
<i>P. aleuticus</i>	NCSM 18088	28.1	26.8	5.0	3.7	2.7	4.8	4.5	51.0	46.9	5.8	2.5	4.4	4.3
<i>Uria aalge</i>	USNM 502349	48.2	46.1	9.2	7.4	5.0	8.4	8.0	97.0	90.5	10.1	4.7	8.1	7.7
<i>U. aalge</i>	USNM 502355	48.4	46.1	9.0	7.6	4.8	8.6	7.9	94.0	87.4	9.9	4.6	7.8	7.3

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## APPENDIX 1. Continued.

Taxon	Catalogue no.	glF	mlF	bpF	dpF	scF	bdF	ddF	glT	laT	dpT	scT	bdT	ddT
<i>U. aalge</i>	USNM 502348	47.7	45.5	9.1	7.3	5.1	8.5	8.5	94.2	87.2	10.1	5.0	8	7.8
<i>U. aalge</i>	USNM 557539	45.0	43.4	8.9	7.4	4.8	7.8	7.2	88.4	82.4	9.6	4.5	7.6	7.0
<i>U. aalge</i>	USNM 18066	47.1	45.3	9.0	7.3	5.0	8.2	7.8	92.4	85.9	9.4	4.2	7.4	7.4
<i>U. lomvia</i>	USNM 502358	45.7	43.6	8.3	6.9	4.6	8.0	7.8	86.8	80.9	9.6	3.7	7.3	7.0
<i>U. lomvia</i>	USNM 502361	45.9	44.1	8.6	7.2	5.0	7.8	7.5	88.2	82.4	9.8	3.9	7.5	6.8
<i>U. lomvia</i>	USNM 502372	47.8	45.5	8.3	7.1	4.7	7.8	7.6	87.7	82.1	9.1	3.7	7.3	6.9
<i>U. lomvia</i>	USNM 502369	46.2	43.8	8.6	6.9	4.5	7.9	7.2	86.8	80.6	8.9	3.7	7.1	6.6
<i>U. lomvia</i>	USNM 502374	44.9	43.8	7.7	6.4	4.2	7.2	7.0	83.8	78.6	8.3	3.5	6.8	6.1

Taxon	Catalogue no.	glTm	bpTm	scTm	bdTm
<i>Aethia cristatella</i>	USNM 561934	26.7	5.3	2.3	4.9
<i>A. cristatella</i>	USNM 223707	30.7	5.2	2.4	5.0
<i>A. cristatella</i>	USNM 610941	25.5	5.3	2.0	5.0
<i>A. cristatella</i>	USNM 498282	27.6	5.4	2.2	5.3
<i>A. cristatella</i>	NCSM 17749	29.0	5.9	2.3	5.4
<i>A. psittacula</i>	NCSM 14804	28.1	6.1	2.8	5.4
<i>A. psittacula</i>	NCSM 18387	29.6	6.0	2.5	5.5
<i>A. psittacula</i>	NCSM 14147	29.2	6.8	2.7	6.1
<i>A. psittacula</i>	NCSM 20177	29.4	6.2	2.8	5.3
<i>A. psittacula</i>	USNM 610513	29.2	5.7	2.6	5.3
<i>A. psittacula</i>	USNM 610514	29.9	6.0	3.1	5.4
<i>A. psittacula</i>	USNM 610937	29.1	6.1	2.6	5.7
<i>A. pusilla</i>	NCSM 17737	18.5	3.3	1.4	3.3
<i>A. pusilla</i>	NCSM 17736	18.7	3.5	1.5	3.4
<i>A. pusilla</i>	NCSM 17734	19.1	3.6	1.4	3.5
<i>A. pusilla</i>	NCSM 224009	19.8	3.6	1.5	3.8
<i>A. pusilla</i>	USNM 498285	19.1	3.6	1.4	3.2
<i>A. pusilla</i>	USNM 224010	19.1	3.7	1.5	3.6
<i>A. pygmaea</i>	UMMZ 204592	21.8	3.5	1.5	3.0
<i>A. pygmaea</i>	UMMZ 224882	20.8	4.1	1.7	3.7
<i>A. pygmaea</i>	UMMZ 224883	19.8	4.0	1.9	3.8
<i>A. pygmaea</i>	USNM 344544	20.5	3.6	1.7	3.5
<i>Alca torda</i>	USNM 555666	36.0	7.3	3.2	7.2
<i>A. torda</i>	USNM 502378	33.8	7.5	3.2	7.2
<i>A. torda</i>	USNM 502387	33.5	6.8	3.7	7.2
<i>A. torda</i>	USNM 502389	34.9	7.4	3.5	7.3
<i>A. torda</i>	USNM 18062	34.8	7.3	3.6	7.8
<i>Alle alle</i>	USNM 560932	20.4	4.2	2.2	4.6
<i>A. alle</i>	USNM 560927	19.7	4.3	2.0	4.5
<i>A. alle</i>	USNM 560926	20.0	4.4	2.2	3.3
<i>A. alle</i>	USNM 344748	20.1	4.6	1.9	4.5
<i>A. alle</i>	USNM 502391	19.6	4.0	1.9	4.0
<i>Cephus columba</i>	USNM 610936	38.3	7.2	2.9	6.8
<i>C. columba</i>	USNM 612989	35.0	6.5	2.6	6.2
<i>C. columba</i>	USNM 498423	35.6	7.2	3.2	6.5
<i>C. columba</i>	USNM 498422	35.8	7.4	2.7	6.8
<i>C. columba</i>	USNM 612988	35.4	6.9	3.1	6.1
<i>C. grylle</i>	USNM 344753	30.0	6.0	2.1	5.3
<i>C. grylle</i>	USNM 344760	29.8	5.9	2.3	5.6
<i>C. grylle</i>	USNM 344758	31.3	6.9	2.5	6.1
<i>C. grylle</i>	USNM 347071	29.9	6.0	2.3	5.6
<i>C. grylle</i>	USNM 344754	1.7	6.6	2.5	6.1

(continued)

## APPENDIX 1. Continued.

Taxon	Catalogue no.	glTm	bpTm	scTm	bdTm
<i>Fratercula arctica</i>	USNM 292346	28.7	6.8	3.2	7.1
<i>F. arctica</i>	USNM225762	26.9	6.3	3.3	6.6
<i>F. arctica</i>	USNM 292344	30.7	6.8	4.1	7.7
<i>F. arctica</i>	USNM 292347	27.0	6.3	3.7	6.7
<i>F. arctica</i>	USNM 224189	30.2	6.8	3.2	7.1
<i>Pinguinus impennis</i>	USNM no #	50.3	13.4	7.5	14.8
<i>P. impennis</i>	USNM no #	55.6	14.4	7.9	15.1
<i>P. impennis</i>	USNM no #	53.0	14.5	7.4	14.7
<i>P. impennis</i>	USNM no #	54.1	13.6	7.1	14.4
<i>P. impennis</i>	USNM no #	52.8	14.9	7.3	14.2
<i>Ptychoramphus aleuticus</i>	USNM 557611	25.6	4.8	1.8	4.1
<i>P. aleuticus</i>	USNM 491305	25.5	4.9	2.3	4.4
<i>P. aleuticus</i>	USNM 557607	24.3	4.6	1.8	4.0
<i>P. aleuticus</i>	USNM 557609	24.6	4.7	2.5	4.0
<i>P. aleuticus</i>	NCSM 18088	25.9	5.0	2.1	4.1
<i>Uria aalge</i>	USNM 502349	40.5	8.9	3.8	7.8
<i>U. aalge</i>	USNM 502355	38.1	9.0	4.0	8.0
<i>U. aalge</i>	USNM 502348	40.5	8.5	3.9	8.3
<i>U. aalge</i>	USNM 557539	36.6	8.2	3.9	7.4
<i>U. aalge</i>	USNM 18066	37.8	8.3	3.7	7.6
<i>U. lomvia</i>	USNM 502358	36.6	8.3	3.1	7.0
<i>U. lomvia</i>	USNM 502361	37.8	8.2	3.2	7.2
<i>U. lomvia</i>	USNM 502372	37.1	7.8	3.1	7.1
<i>U. lomvia</i>	USNM 502369	34.8	7.7	3.0	7.1
<i>U. lomvia</i>	USNM 502374	33.8	7.7	2.8	6.5

APPENDIX 2. Measurements (mm) and species referrals for humeri used in the final morphometric analysis (– = measurements missing because of damage; all measurements according to von den Driesch 1976). Abbreviations: glH = greatest length of humerus, bpH = breadth of proximal humerus, dpH = depth of proximal humerus, scH = smallest dorsoventral breadth of humeral corpus (shaft), bdH = breadth of distal humerus, and ddH = distal diagonal of humerus.

Specimen	glH	bpH	dpH	scH	bdH	ddH	Specimen referral to species
ANSP 13357	96.2	19.7	18.8	8.2	13.9	9.4	<i>Alca grandis</i> (holotype)
NHMUK 7052	111.2	22.8	21.8	8.9	15.5	12.1	<i>A. stewarti</i> (paratype)
NHMUK 7055	–	–	–	9.0	13.9	10.4	<i>A. grandis</i>
NHMUK 7054	–	–	–	7.8	14.1	11.3	<i>A. carolinensis-olsoni</i>
GCVP 5691	99.6	20.0	19.5	8.5	14.8	10.4	<i>A. grandis</i>
GCVP 5690	–	–	–	–	13.7	10.0	<i>Alcini incertae sedis</i>
IGF 14875	–	–	–	7.5	12.4	9.1	<i>A. ausonia</i> (holotype)
NCMNS 13734	102.4	20.8	21.0	9.2	14.9	10.4	<i>A. carolinensis</i> (holotype)
NCMNS 13001	–	–	–	7.2	12.5	9.0	<i>A. ausonia</i>
NCMNS 14116	–	–	–	8.1	12.8	9.2	<i>A. ausonia</i>
NCMNS 15064	97.8	8.5	–	14.4	10.2	19.5	<i>A. grandis</i>
NCSM 24366	104.3	23.2	23.0	8.8	16.2	11.6	<i>A. carolinensis-olsoni</i>
UF 61953	–	17.0	16.3	6.6	–	–	<i>A. torda</i>
UF 61539	–	17.6	16.9	7.0	–	–	<i>A. torda</i>
UF 61531	–	18.2	16.1	7.7	–	–	<i>A. torda</i>
UF 21031	–	16.3	15.0	7.2	–	–	<i>A. torda</i>
UF 61995	–	–	–	7.0	12.0	8.1	<i>A. ausonia</i>
UF 58456	–	–	–	6.7	11.8	8.3	<i>A. ausonia</i>
UF 61542	–	–	–	6.6	11.2	8.2	<i>A. torda</i>
UF 61541	–	–	–	7.2	11.7	8.2	<i>A. ausonia</i>
UF 61537	–	16.1	15.4	5.7	–	–	<i>A. torda</i>
UF 57254	–	–	–	5.9	11.2	7.8	<i>A. torda</i>
UF 12473	–	15.8	15.2	6.3	–	–	<i>A. torda</i>
UF 12474	–	15.8	14.3	7.1	–	–	<i>A. torda</i>
UF 21069	–	16.0	14.9	6.8	–	–	<i>A. torda</i>
UF 21074	–	16.0	14.8	7.2	–	–	<i>A. torda</i>
UF 61533	–	–	–	9.0	14.4	10.0	<i>A. grandis</i>
UF 67956	–	–	–	8.8	13.8	9.6	<i>A. grandis</i>
UF 12477	–	–	–	7.5	13.7	9.5	<i>A. grandis</i>
UF 21191	–	16.5	15.0	6.9	–	–	<i>A. torda</i>
UF 21032	–	–	–	5.9	11.0	7.8	<i>A. torda</i>
UF 21038	–	–	–	6.7	11.5	7.9	<i>A. torda</i>
UF 21078	–	–	–	7.0	12.2	8.8	<i>A. ausonia</i>
UF 21114	–	–	–	7.7	13.3	8.6	<i>A. ausonia</i>
UF 208612	–	16.6	16.0	7.1	–	–	<i>A. torda</i>
UF 95473	–	14.9	14.9	6.7	–	–	<i>A. torda</i>
UF 125027	–	–	–	6.5	10.8	7.7	<i>A. torda</i>
UF 123805	–	–	–	7.1	11.9	8.8	<i>A. ausonia</i>
UF 117423	–	–	–	6.5	10.5	7.4	<i>A. torda</i>
UF 49094	–	–	–	8.4	13.7	9.4	<i>A. grandis</i>
UF 49095	–	15.7	14.6	6.2	–	–	<i>A. torda</i>
UF 117492	–	16.9	15.5	6.6	–	–	<i>A. torda</i>
UF 211946	–	–	–	6.3	10.7	8.0	<i>A. torda</i>
UF 208384	–	–	–	8.6	13.7	9.9	<i>A. grandis</i>
UF 21145	–	–	–	6.5	11.6	7.9	<i>A. torda</i>
UF 61954	–	–	–	6.3	11.3	8.0	<i>A. torda</i>
UF 21107	–	15.7	14.7	6.7	–	–	<i>A. torda</i>
UF/PB 7948	–	–	–	6.5	11.9	8.3	<i>A. ausonia</i>
UF/PB 7949	–	–	–	6.6	10.9	7.7	<i>A. torda</i>
UF/PB 7989	–	–	–	6.5	11.3	7.8	<i>A. torda</i>

(continued)

## APPENDIX 2. Continued.

Specimen	glH	bpH	dpH	scH	bdH	ddH	Specimen referral to species
UF/PB 7942	–	15.3	15.2	6.9	–	–	<i>A. torda</i>
UF/PB 7945	–	–	–	7.3	13.1	9.0	<i>A. ausonia</i>
UF/PB 7947	–	–	–	6.0	11.1	7.8	<i>A. torda</i>
UF/PB 7752	–	19.3	18.7	8.2	–	–	<i>A. grandis</i>
UF/PB 91	–	–	–	6.5	11.7	8.3	<i>A. ausonia</i>
UF/PB 304	–	–	–	6.2	11.4	8.1	<i>A. torda</i>
UF/PB 305	–	–	–	7.0	11.6	7.9	<i>A. ausonia</i>
USNM 192101	–	21.6	21.0	8.9	–	–	<i>A. carolinensis-olsoni</i>
USNM 419708	–	20.8	20.1	8.6	–	–	<i>A. grandis</i>
USNM 460786	–	16.7	15.5	7.0	–	–	<i>A. torda</i>
USNM 178221	–	21.1	20.0	8.6	–	–	<i>A. grandis</i>
USNM 236802	95.8	20.7	19.7	8.8	14.0	10.1	<i>A. grandis</i>
USNM 236802	95.9	–	–	8.6	14.0	10.1	<i>A. grandis</i>
USNM 495613	103.4	21.9	–	8.9	15.1	11.0	<i>A. carolinensis-olsoni</i>
USNM 242238	111.4	24.1	23.7	10.4	17.0	12.1	<i>A. stewarti</i>
USNM 177981	94.6	–	–	8.2	13.8	10.2	<i>A. grandis</i>
USNM 179285	98.9	21.1	–	8.7	14.2	9.8	<i>A. grandis</i>
USNM 181086	93.6	19.1	18.6	8.0	13.8	10.0	<i>A. ausonia</i>
USNM 192840	96.9	20.4	19.6	8.6	13.8	10.0	<i>A. grandis</i>
USNM 206301	104.9	22.2	21.0	9.7	15.0	10.7	<i>A. carolinensis-olsoni</i>
USNM 242288	95.9	19.6	–	8.5	14.0	9.8	<i>A. ausonia</i>
USNM 302324	63.7	13.8	–	5.7	–	–	<i>A. minor</i> (holotype)
USNM 192879	–	13.2	–	–	–	–	<i>A. minor</i>
USNM 495600	–	–	–	5.8	9.1	7.0	<i>A. minor</i>
USNM 275787	94.3	20.1	19.1	8.0	13.6	9.6	<i>A. ausonia</i>
USNM 302358	94.6	19.9	17.9	8.4	–	–	<i>A. ausonia</i>
USNM 367013	106.4	22.2	21.0	9.2	15.5	10.5	<i>A. carolinensis-olsoni</i>
USNM 446649	102.9	–	–	8.9	14.8	10.8	<i>A. carolinensis-olsoni</i>
USNM 446652	105.8	22.7	21.9	9.6	15.7	11.1	<i>A. carolinensis-olsoni</i>
USNM 446654	89.7	19.0	18.4	7.9	13.2	9.2	<i>A. ausonia</i>
USNM 446662	92.7	19.5	19.5	8.8	14.0	9.7	<i>A. ausonia</i>
USNM 446663	97.7	21.4	20.3	8.9	14.4	10.1	<i>A. grandis</i>
USNM 446664	96.5	20.8	19.9	8.6	13.6	9.3	<i>A. grandis</i>
USNM 446666	102.0	21.5	21.0	8.8	14.1	9.9	<i>A. carolinensis-olsoni</i>
USNM 446668	104.7	22.3	21.7	9.2	14.3	10.8	<i>A. carolinensis-olsoni</i>
USNM 192014	92.3	20.2	19.4	8.5	13.1	8.8	<i>A. ausonia</i>
USNM 215795	91.0	20.4	19.5	8.3	13.6	9.8	<i>A. ausonia</i>
USNM 275846	103.1	20.8	–	8.8	14.8	10.4	<i>A. carolinensis-olsoni</i>
USNM 302320	101.8	21.9	20.3	8.8	14.8	10.4	<i>A. carolinensis-olsoni</i>
USNM 321235	103.9	20.6	–	8.6	14.2	10.3	<i>A. carolinensis-olsoni</i>
USNM 366793	100.3	22.4	–	8.8	15.1	10.6	<i>A. carolinensis-olsoni</i>
USNM 446671	92.0	19.7	19.0	8.2	14.1	10.1	<i>A. ausonia</i>
USNM 446673	102.1	22.0	20.9	8.8	15.1	11.3	<i>A. carolinensis-olsoni</i>
USNM 446674	106.5	22.3	–	9.7	14.9	10.6	<i>A. carolinensis-olsoni</i>
USNM 446675	104.3	21.5	21.2	9.1	15.0	10.2	<i>A. carolinensis-olsoni</i>
USNM 446676	101.8	21.6	21.3	9.0	15.2	10.8	<i>A. carolinensis-olsoni</i>
USNM 446677	99.0	21.5	20.7	8.6	14.0	10.6	<i>A. grandis</i>
USNM 446680	99.3	21.5	21.0	8.9	14.8	10.7	<i>A. grandis</i>
USNM 446681	104.3	21.6	20.9	9.6	15.0	10.2	<i>A. carolinensis-olsoni</i>
USNM 446682	102.8	22.2	20.4	9.5	14.7	11.4	<i>A. carolinensis-olsoni</i>
USNM 446683	98.8	20.7	20.4	9.0	13.8	9.5	<i>A. grandis</i>
USNM 446687	99.6	20.4	19.3	8.9	–	9.6	<i>A. grandis</i>
USNM 446688	98.1	20.9	20.3	8.8	13.6	9.9	<i>A. grandis</i>
USNM 446692	91.0	19.4	18.7	7.7	12.5	8.9	<i>A. ausonia</i>

(continued)

## APPENDIX 2. Continued.

Specimen	gH	bpH	dpH	scH	bdH	ddH	Specimen referral to species
USNM 446690	93.9	19.6	19.1	8.4	13.5	9.8	<i>A. ausonia</i>
USNM 446694	105.9	21.4	21.1	8.8	15.4	10.7	<i>A. carolinensis-olsoni</i>
USNM 446695	97.7	20.5	20.0	8.5	14.3	10.6	<i>A. grandis</i>
USNM 446696	101.1	21.2	21.0	9.3	15.2	10.1	<i>A. carolinensis-olsoni</i>
USNM 446697	101.9	21.7	21.1	9.0	–	10.3	<i>A. carolinensis-olsoni</i>
USNM 495673	101.0	21.8	21.6	9.3	15.0	11.4	<i>A. carolinensis-olsoni</i>
USNM 446684	101.7	22.4	21.2	9.2	15.5	10.7	<i>A. carolinensis-olsoni</i>
USNM 446699	106.8	22.1	21.7	9.6	15.8	11.0	<i>A. carolinensis-olsoni</i>
USNM 532685	–	21.4	21.6	9.6	–	–	<i>A. carolinensis-olsoni</i>
USNM 532686	–	20.7	20.2	9.3	–	–	<i>A. grandis</i>
USNM 532689	90.9	19.4	18.8	8.2	13.9	9.5	<i>A. ausonia</i>
USNM 532715	–	19.0	18.3	8.4	–	–	<i>A. ausonia</i>
USNM 532738	–	22.5	22.2	8.8	–	–	<i>A. grandis</i>
USNM 532741	–	20.4	20.1	9.0	–	–	<i>A. grandis</i>
USNM 532742	–	16.7	16.0	6.7	–	–	<i>A. torda</i>
USNM 532858	–	16.3	15.4	6.6	–	–	<i>A. torda</i>
USNM 532859	–	19.5	18.2	7.9	–	–	<i>A. grandis</i>
USNM 532860	–	16.5	15.3	6.9	–	–	<i>A. torda</i>
USNM 532861	–	13.9	13.2	5.6	–	–	<i>A. minor</i>
USNM 275856	–	18.8	17.8	7.7	–	–	<i>A. grandis</i>
USNM 366257	–	19.3	19.1	7.8	–	–	<i>A. ausonia</i>
USNM 366258	–	21.5	20.8	8.8	–	–	<i>A. carolinensis-olsoni</i>
USNM 181098	–	19.4	18.3	8.3	–	–	<i>A. ausonia</i>
USNM 368484	–	21.6	20.3	8.5	–	–	<i>A. grandis</i>
USNM 368485	–	21.0	20.4	8.8	–	–	<i>A. grandis</i>
USNM 532869	–	21.2	20.4	8.6	–	–	<i>A. grandis</i>
USNM 532870	–	20.4	19.7	8.3	–	–	<i>A. carolinensis-olsoni</i>
USNM 532871	–	18.1	17.2	7.3	–	–	<i>A. torda</i>
USNM 532874	–	17.0	16.6	7.4	–	–	<i>A. torda</i>
USNM 532878	–	22.1	21.4	8.5	–	–	<i>A. grandis</i>
USNM 532880	–	21.7	20.6	9.0	–	–	<i>A. carolinensis-olsoni</i>
USNM 532884	–	21.3	20.6	8.3	–	–	<i>A. carolinensis-olsoni</i>
USNM 532885	–	21.5	21.3	9.4	–	–	<i>A. carolinensis-olsoni</i>
USNM 532886	–	21.4	20.2	8.5	–	–	<i>A. grandis</i>
USNM 532887	–	21.9	21.1	8.9	–	–	<i>A. carolinensis-olsoni</i>
USNM 532890	–	20.6	19.9	8.6	–	–	<i>A. grandis</i>
USNM 532896	–	20.7	20.3	8.8	–	–	<i>A. grandis</i>
USNM 532897	–	21.8	21.5	9.4	–	–	<i>A. carolinensis-olsoni</i>
USNM 532900	–	17.3	17.1	7.0	–	–	<i>A. torda</i>
USNM 532908	–	16.6	16.2	6.5	–	–	<i>A. torda</i>
USNM 275852	–	18.6	18.1	7.6	–	–	<i>A. ausonia</i>
USNM 533145	–	18.8	19.0	7.4	–	–	<i>A. grandis</i>
USNM 366558	102.4	20.9	–	8.3	14.7	10.5	<i>A. carolinensis-olsoni</i>
USNM 446656	83.5	16.8	16.2	6.9	12.0	8.7	<i>A. torda</i>
USNM 533036	99.4	22.0	20.8	9.1	15.1	10.8	<i>A. grandis</i>
USNM 533037	96.9	20.6	19.6	8.1	14.6	10.5	<i>A. grandis</i>
USNM 533038	101.1	21.8	21.0	8.7	15.4	10.7	<i>A. carolinensis-olsoni</i>
USNM 533039	100.0	21.7	–	8.5	15.0	10.7	<i>A. grandis</i>
USNM 533040	86.7	19.3	18.4	7.5	13.3	8.8	<i>A. ausonia</i>
USNM 533041	74.5	16.0	15.6	6.9	10.9	8.0	<i>A. torda</i>
USNM 533042	71.2	14.7	14.2	6.4	9.8	7.8	<i>A. torda</i>
USNM 533171	–	–	–	7.1	13.2	9.0	<i>A. ausonia</i>
USNM 533172	–	–	–	9.2	15.2	10.8	<i>A. carolinensis-olsoni</i>
USNM 215443	88.8	19.1	18.8	8.4	14.0	9.8	<i>A. ausonia</i>

(continued)

## APPENDIX 2. Continued.

Specimen	glH	bpH	dpH	scH	bdH	ddH	Specimen referral to species
USNM 368479	82.7	17.1	16.2	7.3	12.3	8.7	<i>A. torda</i>
USNM 179220	84.4	19.1	17.9	7.9	12.4	9.1	<i>A. torda</i>
USNM 275870	78.7	16.2	15.3	6.6	11.5	8.4	<i>A. torda</i>
USNM 366571	86.4	–	–	7.3	11.9	9.2	<i>A. ausonia</i>
USNM 181038	82.2	17.7	15.4	6.7	12.1	8.6	<i>A. torda</i>
USNM 495672	85.3	–	–	7.8	13.0	8.8	<i>A. ausonia</i>
USNM 366584	81.7	–	–	7.5	12.8	8.9	<i>A. torda</i>
USNM 183425	87.8	19.9	18.5	8.0	13.9	9.8	<i>A. ausonia</i>
USNM 368480	87.5	18.2	17.1	7.1	12.9	9.4	<i>A. ausonia</i>
USNM 495671	89.7	19.5	19.3	8.3	13.8	9.9	<i>A. ausonia</i>
USNM 446685	86.0	19.7	18.4	7.7	13.0	9.6	<i>A. ausonia</i>
USNM 446661	82.2	18.9	–	6.8	12.7	9.2	<i>A. torda</i>
USNM 446670	78.6	17.3	16.6	7.2	12.0	8.3	<i>A. torda</i>
USNM 495670	81.2	17.3	16.7	7.0	11.4	8.4	<i>A. torda</i>
USNM 256354	–	–	–	7.0	11.1	8.3	<i>A. torda</i>
USNM 256361	–	–	–	9.1	13.6	10.5	<i>A. grandis</i>
USNM 256355	–	15.2	14.9	6.5	–	–	<i>A. torda</i>
USNM 256358	–	15.6	14.9	6.0	–	–	<i>A. torda</i>
USNM 447052	–	16.2	15.7	6.8	–	–	<i>A. torda</i>
USNM 447054	–	16.1	15.7	6.5	–	–	<i>A. torda</i>
USNM 532557	–	–	–	7.0	11.8	8.6	<i>A. ausonia</i>
USNM 532559	–	–	–	7.5	13.6	9.7	<i>A. grandis</i>
USNM 495616	97.9	20.4	–	8.8	14.3	10.3	<i>A. grandis</i>
USNM 495614	–	20.5	20.8	8.8	–	–	<i>A. grandis</i>
USNM 459609	–	–	–	8.5	15.0	10.3	<i>A. carolinensis-olsoni</i>
USNM 454590	104.0	22.8	21.7	8.8	15.4	11.0	<i>A. olsoni</i> (holotype)
USNM 336379	–	8.8	–	8.8	14.1	10.3	<i>A. grandis</i>
USNM 215454	–	–	–	8.4	13.9	9.7	<i>A. grandis</i>
USNM 495613	103.4	21.9	–	8.9	15.1	11.0	<i>A. carolinensis-olsoni</i>
USNM 495612	–	21.4	20.9	8.6	14.2	10.2	<i>A. carolinensis-olsoni</i>
USNM 183510	–	19.8	18.6	9.0	–	–	<i>A. grandis</i>
USNM 237248	–	22.1	20.1	9.1	–	–	<i>A. carolinensis-olsoni</i>
USNM 237264	–	16.9	15.0	6.2	–	–	<i>A. torda</i>
USNM 446650	112.0	24.2	22.4	10.0	16.8	12.2	<i>A. stewarti</i>
USNM 299637	–	–	–	10.6	16.7	11.7	<i>A. stewarti</i>
USNM 460811	–	–	–	9.9	16.3	11.6	<i>A. stewarti</i>
USNM 210532	–	–	–	6.0	10.5	7.5	<i>A. torda</i>
USNM 321314	76.0	16.0	–	6.7	11.2	8.2	<i>A. torda</i>
USNM 446657	74.0	15.2	14.2	6.2	10.6	7.6	<i>A. torda</i>
USNM 446686	75.7	15.6	14.1	7.3	11.5	8.0	<i>A. torda</i>
USNM 446691	76.9	16.0	15.5	6.7	11.1	8.0	<i>A. torda</i>
USNM 495589	79.0	17.2	13.6	7.3	–	–	<i>A. torda</i>
USNM 257519	77.6	–	–	6.7	10.0	7.2	<i>A. torda</i>
USNM 495592	65.4	–	–	5.8	8.8	6.6	<i>A. minor</i>
USNM 250772	–	–	–	5.7	9.6	6.7	<i>A. torda</i>
USNM 495591	–	–	–	5.8	9.1	6.4	<i>A. minor</i>

## APPENDIX 3. Morphological Character List

1. **Premaxilla, anterior tip in lateral view:** (0) slightly decurved; (1) hooked.
2. **Premaxilla in lateral view, dorsal enlargement** (modified from Chandler 1990, character 17): (0) absent; (1) present.
3. **Maxilla in ventral view, fenestra adjacent to junction of maxilla and palatine:** (0) absent; (1) present.
4. **Maxilla, maxillopalatine process, orientation** (Chu 1998, character 45): (0) dorsally tilted; (1) ventral, flat lying.
5. **Palatine, anteromedial margin of the ventral palatal crest in ventral view** (crista ventralis; Baumel and Witmer 1993; modified from Chandler 1990, character 3): (0) angular; (1) rounded.
6. **Palatine, posterior margin of the ventral palatal crest in ventral view** (crista ventralis; Baumel and Witmer, 1993; modified from Chandler 1990, character 3); (0) angular (1) rounded.
7. **Palatine, lateral margin anterior to contact with the pterygoid** (angulus caudolateralis; Baumel and Witmer 1993; Chandler 1990, character 2): (0) widens posteriorly; (1) narrows posteriorly.
8. **Vomer, curvature of anterior tip in ventral view** (Chandler 1990, character 1): (0) straight; (1) sloped.
9. **Vomer, anterior tip shape:** (0) pointed; (1) bifurcated.
10. **Lamina dorsalis, size:** (0) large (mesethmoid margin interrupted only by suture between it and the lamina dorsalis); (1) small (lamina dorsalis not continuous with margin of mesethmoid, appears to be a separate accessory structure).
11. **Frontal, supraorbital rims** (lateral to fossa glandulae nasalis; Baumel and Witmer 1993; modified from Strauch 1985, character 5; Chandler 1990, character 11): (0) absent; (1) present.
12. **Mesethmoid, fenestra in nasal capsule anterior to nasofrontal hinge:** (0) fenestrated; (1) not fenestrated.
13. **Fonticulus orbitocranialis** (Chu 1998, character 33): (0) not enclosed; (1) enclosed
14. **Lacrimal, position in lateral view:** (0) posteroventrally directed; (1) ventrally directed.
15. **Lacrimal, supraorbital process** (Chu 1998, character 30): (0) absent; (1) present.
16. **Squamosal, temporal fossa** (Chandler 1990, character 19): (0) shallow (not bordered anteriorly and posteriorly by a distinct lip or crest); (1) deep (bordered anteriorly and posteriorly by a distinct lip or crest).
17. **Squamosal, temporal fossa, medial extent:** (0) not medially extended; (1) separated by a thin flat space; (2) separated only by a thin crest. Ordered.
18. **Squamosal, temporal fossa, shape of medial margin:** (0) narrow; (1) broad. In species that possess medially expanded temporal fossae (see character 32) the medial–most extent of these temporal fossae varies in alcids from a broad, relatively “U-shaped” curve (e.g., *Alca torda*) to a more pointed, medially narrowing groove (e.g., *Uria aalge*).
19. **Supraoccipital, paired fontanelles** (foramen venae occipitalis externae, fonticulus occipitalis; Beddard 1898; Strauch, 1978; Baumel and Witmer 1993; Strauch 1985, character 6; Chandler 1990, character 14): (0) absent; (1) present.
20. **Foramen magnum, dorsal margin shape** (modified from Strauch 1978, character 19): (0) rounded; (1) pointed.
21. **Mandible, symphysis length** (modified from Chandler 1990, character 22): (0) short (i.e., <15% of the total length of the mandible; e.g., *A. torda*); (1) long (i.e., >15% of the total length of the mandible; e.g., *U. aalge*).
22. **Mandible, ventral margin in lateral view:** (0) straight; (1) ventrally expanded.
23. **Mandible, curvature of rami in dorsal view:** (0) laterally concave; (1) laterally convex.
24. **Prearticular, anterior margin in medial view** (modified from Chandler 1990, character 21): (0) forked; (1) not forked.
25. **Articular, medial articular process foramen** (foramen pneumaticum articulare medialis; Baumel and Witmer 1993; Chandler 1990, character 20): (0) absent; (1) present.
26. **Articular, medial articular process shape in dorsal view:** (0) anteroposteriorly compressed; (1) dorsoventrally compressed.
27. **Articular, retroarticular process length** (modified from Chandler 1990, character 23): (0) short; (1) long (i.e., as long or longer than the dorsoventral height from the articular facet to the ventral margin of the mandible in lateral view).
28. **Atlas, flange on the lateral margins of the arcus atlanticus in dorsal view:** (0) posteriorly directed; (1) posterolaterally angled.
29. **Axis, dorsal extension of neural spine:** (0) short (i.e., less than half of the length of the neural spine extends above the level of the anapophyses); (1) long (i.e., more than half of the length of the neural spine extends above the level of the anapophyses).

## APPENDIX 3. Continued.

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30. **Thoracic vertebrae, number of hypapophyses** (crista [processus] ventralis corporis; Baumel and Witmer 1993; modified from Strauch 1985, character 14): (0) well developed on all thoracic vertebrae; (1) well developed on all but last vertebra; (2) well developed on all but last three vertebrae. Ordered.
31. **Sternum, costal processes, quantity** (Strauch 1985, character 12; Chandler 1990, character 41): (0) seven; (1) six.
32. **Sternum, posterior width in dorsal view** (modified from Chandler 1990, character 39): (0) narrow posteriorly; (1) broad posteriorly.
33. **Sternum, length of area between distal extent of medial fenestra and posterior margin of sternum** (modified from Chandler 1990, character 43): (0) short (i.e., wider than long); (1) long (i.e., nearly as long or longer than it is wide).
34. **Furcula, anterior surface of rami** (Strauch 1978, character 41): (0) smooth; (1) grooved.
35. **Furcula, cristae on anterior surface of rami**: (0) absent; (1) present.
36. **Furcula, tubercle on anterior apophysis**: (0) absent; (1) present.
37. **Furcular, tubercle on posterior apophysis**: (0) absent; (1) present.
38. **Scapula, width of distal extremity in lateral view**: (0) tapering; (1) dorsoventrally expanded.
39. **Coracoid, shape of furcular facet** (modified from Chandler 1990, character 28): (0) oval; (1) rounded.
40. **Coracoid, ventral margin of furcular facet**: (0) rounded; (1) notched.
41. **Coracoid, supracoracoidal sulcus**: (0) shallowly excavated; (1) deeply excavated.
42. **Coracoid, brachial tuberosity, shape in medial view**: (0) approximately straight; (1) distinctly curved.
43. **Coracoid, acroracoid process in dorsal view** (Chandler 1990, character 29): (0) short (i.e., roughly as wide as it is long); (1) long (i.e., longer than wide).
44. **Coracoid, m. supracoracoideus scar**: (0) a distinct ridge; (1) ridge reduced or absent.
45. **Coracoid, n. supracoracoideus foramen** (Strauch 1985, character 13; Chandler 1990, character 25): (0) absent; (1) present.
46. **Coracoid, position of n. supracoracoideus foramen**: (0) positioned near the midpoint of the procoracoid process; (1) positioned on the extreme sternal edge of the procoracoid process leaving only a very thin strut of bone which forms the ventral margin of the procoracoid process.
47. **Coracoid, lateral sternocoracoidal ligament scar extension**: (0) extends to sternal articulation; (1) bordered sternally by crest.
48. **Coracoid, crest along sternal edge of lateral process**: (0) absent; (1) present.
49. **Coracoid, anterolateral surface extending from the sternal facet to the glenoid facet**: (0) smooth; (1) grooved.
50. **Coracoid, procoracoid process, shape of sternal edge**: (0) concave; (1) convex.
51. **Coracoid, dorsal margin of medial sternal process**: (0) smooth; (1) notched.
52. **Coracoid, medial angle of sternal facet in sternal view** (Chandler 1990, character 26): (0) angled  $\sim 135^\circ$ ; (1) angled  $\sim 90^\circ$ .
53. **Humerus, distal margin of head in posterior view**: (0) convex curve; (1) triangular point.
54. **Humerus, dorsal caput, shape of posterior side in proximal view** (modified from Chandler, 1990; character 49): (0) rounded; (1) notched.
55. **Humerus, distal extent of deltopectoral crest**, (modified from Chandler 1990, character 53): (0) does not extend past midpoint of shaft; (1) extends distally past the midway point of shaft.
56. **Humerus, deltopectoral crest, transition to shaft**: (0) smooth; (1) abrupt.
57. **Humerus, dorsal surface of humeral head in dorsal view, curvature**: (0) concave; (1) flat.
58. **Humerus, m. coracobrachialis impression depth** (Chandler 1990, character 60): (0) shallow (i.e., less deep than wide); (1) deep (i.e., as deep as wide).
59. **Humerus, distal edge of bicipital crest, angle with respect to long axis of shaft in anterior view**: (0) not perpendicular; (1) nearly perpendicular.
60. **Humerus, bicipital crest, transition to shaft**: (0) smooth; (1) notched.
61. **Humerus, m. coracobrachialis sulcus conformation**: (0) open sulcus; (1) closed duct.



## APPENDIX 3. Continued.

62. **Humerus, m. coracobrachialis sulcus curvature:** (0) dorsal; (1) ventral. The distal most point of the bicipital surface, as defined by the curvature of the coracobrachial sulcus, which curves or angles dorsal to the bicipital crest on the anterior surface of the humerus in some alcids (e.g., *Pinguinus impennis*), while in other alcids (e.g., *Alle alle*) the coracobrachial sulcus and the distal edge of the bicipital surface extend ventrally to terminate where the bicipital crest contacts the ventral surface of the humeral shaft.
63. **Humerus, shape of m. supracoracoideus attachment scar** (crista m. supracoracoidei; Baumel and Witmer 1993): (0) long, does not broaden proximally; (1) long, proximally broadening.
64. **Humerus, m. supracoracoideus scar, transition to the secondary pneumotricipital fossa** (modified from Chandler 1990, character 58): (0) secondary pneumotricipital fossa borders scar; (1) scar separated from the secondary pneumotricipital fossa.
65. **Humerus, medial crest between pneumotricipital fossae, extension relative to the bicipital crest** (modified from Chandler 1990, character 51): (0) ends proximal to distal-most extension of bicipital crest; (1) crest extends to distal extant bicipital crest.
66. **Humerus, primary pneumotricipital fossa, depth** (fossa pneumotricipitalis ventralis; Baumel and Witmer 1993): (0) shallow (i.e., less deep than wide); (1) moderately deep (i.e., ~ as deep as wide).
67. **Humerus, primary pneumotricipital fossa, shape:** (0) round; (1) oval.
68. **Humerus, attachment of m. subcoracoideus, position:** (0) dorsal; (1) ventral.
69. **Humerus, m. subcoracoideus, attachment scar depth:** (0) flat or slightly concave; (1) a deep pit.
70. **Humerus, primary pneumotricipital fossa, shape of distal edge in posterior view:** (0) concave; (1) straight.
71. **Humerus, secondary pneumotricipital fossa** (fossa pneumotricipitalis dorsalis; Baumel and Witmer 1993; modified from Strauch 1985, character 17; Chandler 1990, character 50): (0) shallow or flat; (1) pneumatized.
72. **Humerus, secondary pneumotricipital fossa, depth;** modified from Strauch 1985, character 17): (0) deep; (1) shallow.
73. **Humerus, secondary pneumotricipital fossa:** (0) dorsoventrally continuous; (1) divided by a bony crest.
74. **Humerus, shape of ventral tubercle in ventral view:** (0) long and thin; (1) short and thick.
75. **Humerus, ventral tubercle, shape of posterior tip in posterior view:** (0) rounded or oval; (1) elongate.
76. **Humerus, ventral tubercle, orientation of posterior tip in posterior view:** (0) posteriorly oriented; (1) ventrally down-turned.
77. **Humerus, m. latissimus dorsi scar curvature in posterodorsal view:** (0) straight; (1) curves dorsally.
78. **Humerus, cross-sectional shape of shaft:** (0) dorsoventrally compressed; (1) semi-rounded.
79. **Humerus, shaft thickness:** (0) robust (i.e., width of shaft in anterior view greater than or equal to half the width of the humeral head; e.g., *P. impennis*); (1) gracile (i.e., width of shaft in anterior view less than or equal to half the width of the humeral head; e.g., *Alle alle*).
80. **Humerus, shape of dorsal supracondylar process in posterior view:** (0) smoothly transitioning (i.e., angle with shaft  $>90^\circ$ ); (1) small dorsally pointing projection.
81. **Humerus, ventral epicondyle, position relative to ventral condyle in anterior view** (Chandler 1990, character 62): (0) does not extend distal to ventral condyle; (1) extends distal to ventral condyle.
82. **Humerus, tricipital sulci, width in distal view:** (0) scapulotricipital sulcus narrower than humerotricipital sulcus; (1) sulci of equal width; (2) scapulotricipital sulcus broader than humerotricipital sulcus.
83. **Humerus, humerotricipital sulcus, shape in distal view:** (0) flattened; (1) U-shaped or curved.
84. **Humerus, ventral condyle in distal view, posterodorsally oriented projection** (0) absent; (1) present.
85. **Humerus, tubercle dorsal to scapulotricipital groove:** (0) absent; (1) present.
86. **Humerus, shape of ventral supracondylar tubercle (anterior ligament scar):** (0) triangular; (1) rounded.
87. **Humerus, m. pronator sublimis scar associated with ventral supracondylar tubercle:** (0) absent; (1) present.
88. **Humerus, position of pit adjacent to ventral supracondylar tubercle:** (0) proximal; (1) ventral.
89. **Radius, bicipital tubercle:** (0) reduced; (1) distinct.
90. **Radius, position of bicipital tubercle:** (0) anterior; (1) distal; (2) posterior.
91. **Radius, distal end, sulcus tendinosus** (Chu 1998, character 102): (0) not divided lengthwise (i.e., proximodistally) by a crest; (1) divided by a crest.
92. **Radius, distal end in distal view:** (0) rounded; (1) notched.

## APPENDIX 3. Continued.

93. **Ulna, length of olecranon:** (0) long (i.e., projects well past the medial extent of the ventral cotyla); (1) short (i.e., does not extend past the medial extent of the ventral cotyla).
94. **Ulna, olecranon curvature in ventral view:** (0) flares posteriorly; (1) curves anteriorly.
95. **Ulna, ventral collateral ligament tubercle shape:** (0) triangular; (1) rounded.
96. **Ulna, crest extending from the ventral cotyla to the posterior margin of the ventral collateral ligament tubercle:** (0) absent; (1) present.
97. **Ulna, dorsal cotylar process, anterior margin shape in dorsal view:** (0) rounded; (1) straight.
98. **Ulna, brachial impression, development:** (0) in line with shaft of ulna; (1) anteriorly expanded.
99. **Ulna, brachial impression, anteroposterior breadth:** (0) thin (i.e., does not comprise more than half the width of the ulnar shaft); (1) broad (i.e., comprises more than half of the width of this proximal portion of the ulna).
100. **Ulna, intramuscular line:** (0) nondistinct; (1) distinct, raised ridge.
101. **Ulna, shaft compression:** (0) dorsoventrally compressed; (1) semi-flattened.
102. **Ulna, posterior margin of dorsal condyle, shape in dorsal view:** (0) rounded; (1) angular.
103. **Ulna, carpal tubercle, shape in anterior view:** (0) flat or angled distally; (1) concave.
104. **Ulna, sulcus intercondylaris:** (0) depressed; (1) flat.
105. **Carpometacarpus, extensor process of metacarpal 1, anterior margin shape** (modified from Strauch 1985, character 18; Chandler 1990, character 69): (0) rounded knob; (1) flattened.
106. **Carpometacarpus, proximal intermetacarpal spatium, position relative to the distal extent of metacarpal 1** (modified from Chandler 1990, character 71): (0) symphysis proximal to the first metacarpal; (1) symphysis level with the first metacarpal.
107. **Carpometacarpus, posterior extension of ventral trochlear margin, relative to metacarpal III in dorsal view** (modified from Chandler 1990, character 70): (0) ventral trochlear margin of carpometacarpus extends posteriorly to metacarpal III; (1) ventral trochlear margin and metacarpal III extend an equal distance posteriorly.
108. **Carpometacarpus, distal end, tendinal groove** (i.e., sulcus interosseous; Baumel and Witmer 1993): (0) open-ended sulcus; (1) a bony canal.
109. **Carpometacarpus, metacarpal II articulation with digit II, phalanx 1, dorsal surface in distal view:** (0) flat; (1) anteriorly expanded.
110. **Carpometacarpus, distal extension of metacarpal II relative to metacarpal III:** (0) metacarpal II level with metacarpal III; (1) metacarpal III proximal to metacarpal II.
111. **Carpometacarpus, digit II phalanx 1, shape of process on dorsal surface of the distal end in dorsal view:** (0) rounded; (1) rectangular.
112. **Carpometacarpus, length of digit II, phalanx 1:** (0)  $<1/2$  length of carpometacarpus; (1)  $>1/2$  length of carpometacarpus.
113. **Ilium, pre-acetabular ilium, lateral expansion in dorsal view:** (0) not expanded, narrow; (1) expanded laterally, spatulate.
114. **Pelvis, synsacral strut extending to acetabulum** (Strauch 1985, character 15; Chandler 1990, character 47): (0) absent; (1) present.
115. **Pelvis, shape of renal depression in ventral view** (Chandler 1990, character 44): (0) broad; (1) narrows posteriorly.
116. **Pelvis, antitrochanteral sulcus, distal extension:** (0) terminates at antitrochanter; (1) extends distal to antitrochanter.
117. **Pelvis, iliosynsacral suture:** (0) fused; (1) perforated.
118. **Ilium, post acetabular dorsal iliac crest in dorsal view:** (0) broadens; (1) narrows.
119. **Ilium, dorsolateral iliac spine, orientation:** (0) dorsal; (1) dorsolateral.
120. **Femur, trochanteric ridge in lateral view, shape:** (0) convex; (1) straight.
121. **Tibiotarsus, cnemial crests, shape in proximal view:** (0) T-shaped; (1) L-shaped.
122. **Tibiotarsus, cnemial crests, distal extent** (Chandler 1990, character 74): (0) anterior crest extends further distally than lateral cnemial crest; (1) both extend distally about equal.

## APPENDIX 3. Continued.

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123. **Tibiotarsus, lateral margin of medial condyle** (Chandler 1990, character 75): (0) rounded; (1) notched.
  124. **Tibiotarsus, lateral projection of crest lateral to the groove for peroneus profundus tendon, posterior view**: (0) a distinct projection; (1) not visible in dorsal view.
  125. **Tibiotarsus, supratendinal bridge**: (0) not fully ossified; (1) fully ossified.
  126. **Tarsometatarsus, tendinal canal 1 of hypotarsus** (modified from Strauch 1978, character 64; Chandler 1990, character 82): (0) deep channel; (1) bony canal.
  127. **Tarsometatarsus, position of tendinal canal 2 of hypotarsus** (modified from Strauch 1978, character 65): (0) posterior to tendinal canal 1; (1) confluent with tendinal canal 1.
  128. **Tarsometatarsus, tendinal canal 3 of hypotarsus** (modified from Strauch 1978, character 66): (0) open groove; (1) mostly or completely enclosed bony channel.
  129. **Tarsometatarsus, anterior groove of tarsometatarsus, depth** (Chandler 1990, character 79): (0) deep groove; (1) shallow groove.
  130. **Tarsometatarsus, cross-sectional shape**: (0) square; (1) rectangular.
  131. **Tarsometatarsus, proximal vascular foramen**: (0) does not penetrate medial calcaneal ridge; (1) penetrates medial calcaneal ridge.

APPENDIX 4. Morphological character matrix (A = 0 and 1; i.e., polymorphism).

	10	20	30
<i>Alca ausonia</i>	????????????????????????????????		
<i>A. carolinensis</i>	????????????????????????????????00		
<i>A. stewarti</i>	????????????????????????????????		
<i>A. minor</i>	????????????????????????????????		
<i>A. torda</i>	111010010011101111110110011011000		
<i>A. olsoni</i>	????????????????????????????????		
<i>A. grandis</i>	????????????????????????????????		
<i>Pinguinus alfrednewtoni</i>	????????????????????????????????10??????		
<i>P. impennis</i>	11101001001111112110010011010?00		
<i>Alle alle</i>	10110101011000100-11001101101201		
<i>Miocepphus mergulellus</i>	??????????????????????????????????		
<i>M. blowi</i>	011????00011?00110?0000?010??????		
<i>M. bohaski</i>	??????????????????????????????????		
<i>M. mcclungi</i>	??????????????????????????????????		
<i>Uria aalge</i>	00111011001100111000100101000000		
<i>U. lomvia</i>	00111001001100111000100101000000		
<i>U. brodkorbi</i>	00?????????1?0?11?0?0?0?0?0?1?0?11		
<i>Cepphus columba</i>	00000100100000111100100010000101		

	40	50	60
<i>Alca ausonia</i>	????????????????????????????110010001000		
<i>A. carolinensis</i>	00111100011010000010110010001100		
<i>A. stewarti</i>	??????0001101000010000000000?100		
<i>A. minor</i>	?????????????????????????01001000?100		
<i>A. torda</i>	00110000011010000111010010001100		
<i>A. olsoni</i>	?0?00?001110100??101110010001100		
<i>A. grandis</i>	??????000110100??111110010001000		
<i>Pinguinus alfrednewtoni</i>	??????01110010??111111010101000		
<i>P. impennis</i>	00100101100010000111011010101000		
<i>Alle alle</i>	0000011000100-001112110110110100		
<i>M. mergulellus</i>	?????????????????????????100110110100		
<i>M. blowi</i>	?????????????????????????0010110000		
<i>M. bohaski</i>	?00????00001010011010?01??????????		
<i>M. mcclungi</i>	?????????????????????????00110??0000		
<i>Uria aalge</i>	00100101101010010011100010000000		
<i>U. lomvia</i>	00100101101010010011100010000000		
<i>U. brodkorbi</i>	??????????0?10??1?1?1?????????00		
<i>Cepphus columba</i>	1100000001111100110100111010111		

	70	80	90
<i>Alca ausonia</i>	0011000-1100000111101110??????????		
<i>A. carolinensis</i>	0011010-110000011110111011100000		
<i>A. stewarti</i>	0001010-?10100011110111010??0100		
<i>A. minor</i>	1001000-11?0000111101110??????????		
<i>A. torda</i>	1001010-110000011110111010100100		
<i>A. olsoni</i>	0011010-110000011110111012100000		
<i>A. grandis</i>	0011010-110000011111110????0000		
<i>Pinguinus alfrednewtoni</i>	0001110-010000001A11110-0-111000		
<i>P. impennis</i>	0001010-110000001111110-0-101000		
<i>Alle alle</i>	1110010-110000110200100-1-000001		

(continued)

## APPENDIX 4. Continued.

	70	80	90
<i>Miocepphus mergulellus</i>	0110110-000000010010?10-????????		
<i>M. blowi</i>	0001000-0100000101101110?????11		
<i>M. bohaski</i>	?????????????0?11110?1110-000111		
<i>M. mcclungi</i>	0?????0-0????0?101101110???????		
<i>Uria aalge</i>	0111010-11000001010110-0-110011		
<i>U. lomvia</i>	0111010-110000001010110-0-110011		
<i>U. brodkorbi</i>	??1????-01000000101?1?????1100??		
<i>Cepphus columba</i>	111011110110111010100001012100010		
	100	110	120
<i>Alca ausonia</i>	????????????????????????????????		
<i>A. carolinensis</i>	0001010111?100???????????????????		
<i>A. stewarti</i>	10110100?????????????????????????		
<i>A. minor</i>	???????????????????????????????????		
<i>A. torda</i>	0011010011000010101111110001010		
<i>A. olsoni</i>	11010000???????????????????????????		
<i>A. grandis</i>	001100?0????0001?0?1??110???????		
<i>Pinguinus alfrednewtoni</i>	00000001????????????????????1010?00??		
<i>P. impennis</i>	00100001100001111011111101110010		
<i>Alle alle</i>	00100000110100000110111011001101		
<i>Miocepphus mergulellus</i>	???????????????????????????????????		
<i>M. blowi</i>	00010100110100?????????????????????		
<i>M. bohaski</i>	10010000???????????????????????????		
<i>M. mcclungi</i>	???????????????????????????????????		
<i>Uria aalge</i>	00000100110001101111101111011010		
<i>U. lomvia</i>	00100100110001101111101111011010		
<i>U. brodkorbi</i>	0???01??11101110???????????????????		
<i>Cepphus columba</i>	00101010010100101101000010101101		
	130		
<i>Alca ausonia</i>	???		
<i>A. carolinensis</i>	???		
<i>A. stewarti</i>	???		
<i>A. minor</i>	???		
<i>A. torda</i>	111		
<i>A. olsoni</i>	???		
<i>A. grandis</i>	???		
<i>Pinguinus alfrednewtoni</i>	01?		
<i>P. impennis</i>	110		
<i>Alle alle</i>	111		
<i>M. mergulellus</i>	???		
<i>M. blowi</i>	???		
<i>M. bohaski</i>	???		
<i>M. mcclungi</i>	???		
<i>Uria aalge</i>	110		
<i>U. lomvia</i>	110		
<i>U. brodkorbi</i>	???		
<i>Cepphus columba</i>	101		

APPENDIX 5. GenBank accession numbers and authorship of molecular sequences used in this analysis. Key to lowercase letters in parentheses following accession numbers that denote authorship of sequences: a = Baker et al. 2007, b = Pereira and Baker 2008, c = Moum et al. 2002, d = Moum et al. 1994, e = Friesen et al. 1996, f = Fain and Houde 2007, and g = Paton et al. 2003.

Taxon	ND2		ND5		ND6		CO1	
<i>Alca torda</i>	EF373220	(a)	AJ242683	(c)	X73916	(d)	EF380318	(b)
<i>Alle alle</i>	EF373221	(a)	AJ242684	(c)	X73915	(d)	EF380319	(b)
<i>Cephalus columba</i>	EF373229	(a)	–		X73918	(d)	EF380325	(b)
<i>Pinguinus impennis</i>	–		AJ242685	(c)	AJ242685	(c)	–	
<i>Uria aalge</i>	EF380348	(b)	AJ242686	(c)	X73913	(d)	EF380334	(b)
<i>U. lomvia</i>	EF373273	(a)	AJ242687	(c)	X73914	(d)	EF380336	(b)
Taxon	cyt <i>b</i>		12S rDNA		16S rDNA		RAG-1	
<i>Alca torda</i>	U37288	(e)	EF373065	(a)	EF380281	(b)	AY228788	(g)
<i>Alle alle</i>	U37287	(e)	AJ242684	(c)	EF380282	(b)	EF373166	(a)
<i>Cephalus columba</i>	U37293	(e)	X76349	(d)	DQ674610	(f)	EF373173	(a)
<i>Pinguinus impennis</i>	AJ242685	(c)	AJ242685	(c)	–		–	
<i>Uria aalge</i>	U37307	(e)	DQ485794	(f)	DQ485832	(f)	EF380276	(b)
<i>U. lomvia</i>	U37308	(e)	AJ242687	(c)	EF380299	(b)	EF373216	(a)