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

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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, CO1, 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.

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