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Two species of *Uria* (Aves: Alcidae) from the Pleistocene of Shiriya, northeast Japan, with description and body mass estimation of a new species

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Abstract：The genus *Uria* includes volant wing-propelled diving birds widely distributed in the Arctic and boreal waters in the Northern Hemisphere. It includes two Recent species, *U. lomvia* and *U. aalge*, which represent the largest living members of Alcidae, all of which are volant. Compared to other parts of its current distribution, the fossil record of the genus is scarce in the western North Pacific. In this report, two species of *Uria*, extant *U. lomvia* and extinct *U. onoi*, sp. nov., are reported from the middle–upper Pleistocene of Shiriya, northeast Japan. *U. onoi* is represented by several isolated fossil bones including nearly complete humeri, whose length and stoutness greatly exceed those of Recent species. Body mass estimation based on a scaling relationship of body mass and humerus length in volant alcids resulted in an estimate of ~1.5 kg for the body mass of *U. onoi*. This value, as well as those previously estimated for several extinct *Alca* spp. from the Atlantic, exceeds a commonly supposed "upper limit" of body mass attainable by volant wing-propelled diving birds, ~1 kg. These examples indicate that independent evolutions and extinctions of large-bodied species took place in two different lineages of Alcidae and in two major oceans, *Alca* in the Atlantic and *Uria* in the Pacific, and demonstrate the importance of incorporating extinct taxa in analyses of evolutionary patterns and morphological diversities.

Key words: Pleistocene, Alcidae, *Uria*, biogeography, body mass estimation

INTRODUCTION

The family Alcidae includes 23 (or 24) living species of wing-propelled diving seabirds which play major roles as predators in the Arctic and boreal marine ecosystems in the Northern Hemisphere (Bédard, 1985; Gaston and Jones, 1998). Its evolutionary history is relatively well documented, with many fossil records from the Neogene and Quaternary marine deposits throughout the world (e.g., Olson, 1985; Olson and Rasmussen 2001; Wijnker and Olson, 2009; Smith 2011, 2014; Smith and Clarke 2011, 2015). The genus *Uria* (murres or guillemots) includes two Recent species, *U. lomvia* and *U. aalge*, each of which has a Holoarctic (northern circumpolar) distribution and represents one of largest Recent volant members of the family. Traditionally, *Uria* has been considered to be allied with Atlantic genera *Alca* and *Pinguinus* (e.g., Storer, 1945, 1960), and most recent phylogenetic analyses based on morphological (Strauch, 1985) or molecular (Moum *et al*., 1994; Friesen *et al*., 1996a) data recovered a clade consisting of these three genera and another Atlantic genus *Alle* as a monophyletic one. Most recently, combined analyses of Smith and Clarke (2011, 2015) recovered *Uria* as most closely related to a clade consisting of *Alle* and an extinct paraphyletic genus *Miocepphus*.

Each of the two Recent species of *Uria* has a broad distribution in along North Pacific, North Atlantic, and Arctic oceans, with *U. lomvia* occupying more northern waters than *U. aalge* with some overlaps (e.g., Tuck, 1960; Fig. 1). Several subspecies are recognized for each species, based on geographic variations in the plumage and external morphometric characters (Storer, 1952; Tuck, 1960; Bédard, 1985; Gaston and Jones, 1998). In both species, birds from the Pacific are known to be generally larger than those from the Atlantic (Storer, 1952; Gaston and Jones, 1998). Sexual dimorphisms in morphometric characters are rather slight, and differences in external (Storer, 1952) and osteological (Stewart, 1993) dimensions were found to be not statistically significant except for those on the bill or

cranium. There is some evidence of hybridization between the two species (Taylor *et al*., 2012).

Several recent studies on the population genetic structures of these species (Birt-Friesen *et al*., 1992; Friesen *et al*., 1996b; Morris-Pocock *et al*., 2008; Tigano *et al*., 2015) showed that Pacific and Atlantic populations of each Recent species of *Uria* are genetically well differentiated from each other. Divergence times between Pacific and Atlantic populations have been estimated as 56,000–226,000 years ago for *U. aalge* (according to Morris-Pocock *et al*., 2008), and ~99,000 years ago for *U. lomvia* (according to Tigano *et al*., 2015); i.e., they are likely to have taken place in the middle–late Pleistocene (although it should be noted these estimates are based on different estimation methods). In both species, little genetic structure was found among colonies within the Pacific and Atlantic except for *U. aalge* colonies in the Atlantic where significant structuring was found (Friesen *et al*., 1996b; Morris-Pocock *et al*., 2008; Tigano *et al*., 2015). It is likely that the Pacific population of each of these species once underwent a range constriction in the late Pleistocene glaciations and a subsequent rapid expansion (Morris-Pocock *et al*., 2008; Tigano *et al*., 2015).

A few fossil species of *Uria* have been described so far (Table 1, Fig. 1), but most of them are not well established. *U. brodkorbi* Howard, 1981, described from impressions of a partial skeleton on diatomite from the upper Miocene of California (Howard, 1981), marks the oldest definite record of the genus (Olson, 1985; Smith and Clarke, 2011, 2015). *U. paleohesperis* Howard, 1982 was described from an associated elements from the upper Miocene of California (Howard, 1982). Howard (1978) reported the occurrence of a proximal humerus from the Miocene of California and treated it as ?*Uria* sp., which was later considered by Howard (1982) as possibly conspecific as *U. paleohesperis*. In a taxonomic review mainly concerning *Alca*, Smith and Clarke (2011) pointed out that *U. paleohesperis* lacks any apomorphies that would allow the referral to *Uria*, and that it is also not clearly separable from *U. brodkorbi*, but left the
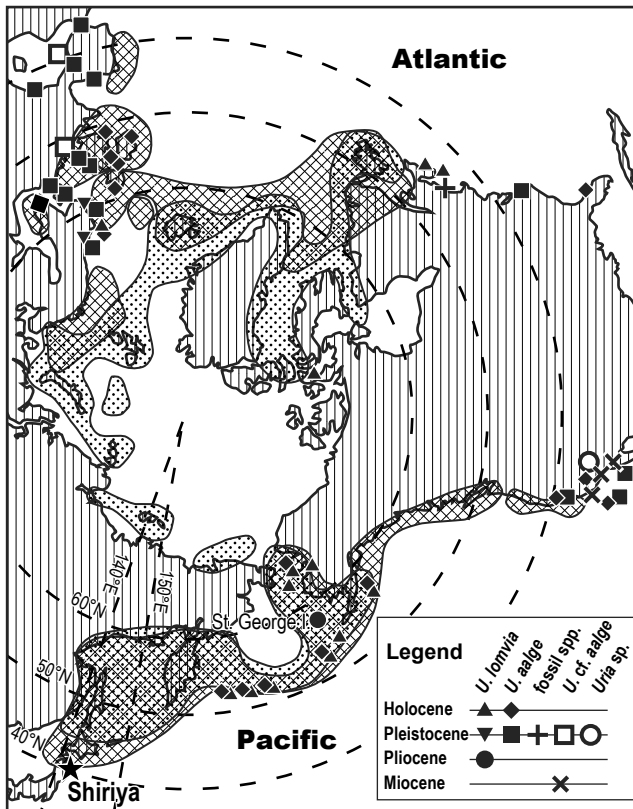
Figure 1. Summary of geographic and temporal distributions of *Uria*. Approximate Recent breeding distributions of *U. aalge* (cross hatched) and *U. lomvia* (stippled) are shown after Tuck (1960). For clarity, not all localities are indicated for Britain, Denmark, Gibraltar, and Nova Scotia, where too many localities of same ages are concentrated. Compiled after Marsh (1872), Lydekker (1891), Winge (1903), Bell (1915), Garrod *et al.* (1928), Howard (1929, 1936, 1978, 1981, 1982), Howard and Dodson (1933), Friedman (1934a, b, 1937), Miller and Peabody (1941), Brodkorb (1967), Ray *et al.* (1968), Rick (1980), Harrison (1980, 1987), Guthrie (1980, 1992), Lie (1986, 1989), Becker (1987), Larsen *et al.* (1987), Fisher (1997), Lefèvre *et al.* (1997), Tyrberg (1998, 2008), Savinetsky *et al.* (2004), Seward *et al.* (2006), van Geel *et al.* (2006), and Olson (2013).

problem open until further materials are available. *Uria affinis* (Marsh, 1872) from the upper Pleistocene of Maine is similar to Recent *U. lomvia arra* in its size and might be referable to one of the Recent species (Olson, 1985; Smith and Clarke, 2011). The species formerly known as "*Uria*" *antiqua* (Marsh, 1870) is removed to *Alca* by Olson and Rasmussen (2001), and currently known as *Alca grandis* (Brodkorb, 1955) because of the preoccupation of the name (Olson, 2007; Smith and Clarke, 2011). Similarly, "*Uria*" *ausonia* Portis, 1888 is now placed in *Alca* (Olson and Rasmussen, 2001; Dyke and Walker, 2005; Smith and Clarke, 2011).

Notably, no fossils referable to *Uria* are known from deposits older than the Pleistocene in the North Atlantic, including the Miocene–Pliocene rocks of the PCS Phosphate mine (Lee Creek Mine) where numerous fossils of alcids and other seabirds have been recovered (Olson and Rasmussen, 2001; Smith *et al.*, 2007; Wijnker and Olson, 2009; Smith and Clarke, 2011), leading to the presumption that *Uria* was practically absent from the Atlantic until the Pleistocene (Olson, 1985; Wijnker and Olson, 2009). This pattern and the occurrence of *U. brodkorbi* from the upper Miocene of Pacific strongly suggest that *Uria* was originated in the Pacific by ~10 Ma (Wijnker and Olson, 2009). A partial skeleton referable to *U. lomvia* from the upper Pliocene of St. George Island, Pribilof Islands, is the oldest record of either extant species (Olson, 2013). Fossils of the two Recent species have been recorded from various Pleistocene and Holocene localities in the Northern Hemisphere, and *U. aalge* is even known from a Holocene midden in Florida, well outside of current range of the species (Brodkorb, 1960). The temporal and geographic distributions of the genus are summarized in Fig. 1. Note that this summary is not attempted to be complete (especially for the Holocene archaeological records) and that no critical evaluation of previous identifications was attempted (which was often impossible because in most works little or no justification for identification was given).

In this work, two species of *Uria*, one of which is a new species, is reported as members of the Shiriya local fauna, which is known from the Pleistocene fissure-filling deposits in the Shiriya area, northeast Japan (Hasegawa *et al.*, 1988). The occurrence of vertebrate remains from this area was first reported by Nakajima and Kuwano (1957) and Nakajima (1958). Hasegawa *et al.* (1988) gave a synopsis for the vertebrate remains, listed 15 non-passeriform birds and mentioned the presence of at least four species of passeriforms. However, mainly because of the lack of sufficient comparative material, the treatment of avian material remained provisional. This report is a part of the ongoing revision of seabird fossils by the authors (Watanabe and Matsuoka, 2015, in prep.).

Geological setting

The fossils described in this study came from fissure-filling deposits in the Shiriya area, northeastern Japan. Basic geological background of the localities has been reviewed by Hasegawa *et al.* (1988) and Watanabe and Matsuoka (2015), and only a brief summary is given here.

The Shiriya area is located at the northeastern tip of Honshu Island, Japan (Fig. 2). The oldest geological unit exposed in this area is a pre-Tertiary tectonic complex (Kamada 2000), which is unconformably overlain by Neogene sedimentary rocks (Tsushima and Takizawa, 1977). On these basement rocks, a well-developed set of middle–late Pleistocene marine terraces is distributed, each of whose age is correlated to a Marine Isotope Stage (MIS) based on dated volcanic ash layers interbedded in terrace deposits and relative altitudes of terrace surfaces (Koike and Machida, 2001).
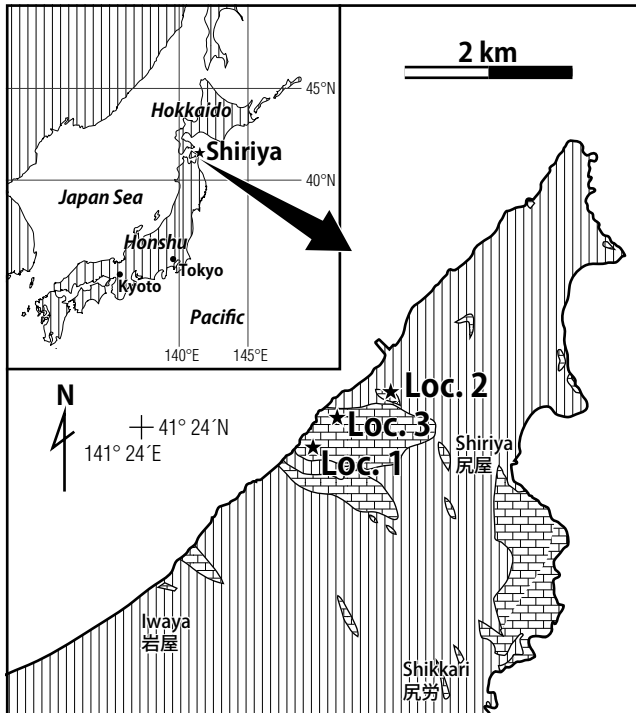
Table 1. Summary of geographic and temporal distributions of *Uria* spp.

Species	Geography	Age	Note
Uria aalge (Pontoppidan, 1763)		Pleistocene–Recent	
Uria lomvia (Linnaeus, 1758)		Late Pliocene–Recent	
Uria affinis (Marsh, 1872)	Maine, U.S.A.	Late Pleistocene	Olson (1985) and Smith and Clarke (2011) considered indistinguishable from Recent species
Uria brodkorbi Howard, 1981	California, U.S.A.	Late Miocene	
Uria paleohesperis Howard, 1982	California, U.S.A.	Late Miocene	Validity and affinity doubted by Smith and Clarke (2011)
?*Uria* sp.; Howard, 1978	California, U.S.A.	Late Miocene	Howard (1982) considered perhaps conspecific with *U. paleohesperis*

Figure 2. Geographical locations of Shiriya localities. Locations of major localities are indicated by stars (Hasegawa *et al.*, 1988). Distribution of limestone/limestone breccia bodies are shown with brick pattern (after Tsushima and Takizawa, 1977).

Vertebrate fossils described here came from mostly unconsolidated sediments that fill fissures or caves developed in limestone and limestone breccia bodies in the tectonic complex. Occurrences of vertebrate remains from these deposits were first reported by Nakajima and Kuwano (1957) and Nakajima (1958). Hasegawa *et al.* (1988) reported results of extensive excavations of these deposits. According to Hasegawa *et al.* (1988), there are four major vertebrate localities (Fig. 2): the "Locality A" in Nakajima and Kuwano (1957) (Loc. 1); the Shiriya Second Quarry (Loc. 2); the Shiriya Tunnel (Loc. 3); and an unnamed tunnel near Shikkari (Loc. 4). Avian remains are known from Locs. 1–3.

No direct dating is available for the fossil localities, but the occurrences of marine vertebrates and the inclusion of marine-originated sediments indicate that the fossil-bearing layers had been deposited near the past sea level (Nakajima and Kuwano, 1957; Hasegawa *et al.*, 1988). Therefore, the localities can be roughly correlated to certain marine terrace surfaces; Loc. 2 (70–80 m above sea level) can be correlated to the Toei surface (65–80 m) of Koike and Machida (2001), and both Loc. 1 (~45 m above sea level) and Loc. 3 (~35 m) to the Tonamigaoka surface (35–45 m) of Koike and Machida (2001). Thus, the age of Loc. 2 would be MIS 9 (~320 ka), and those of Locs. 1 and 3 would be MIS 5e (~120 ka; ages of terraces according to Koike and Machida, 2001). These age estimates are roughly consistent with the occurrence of land mammals typical of the Pleistocene of Japan (Hasegawa, 1972).

Material and methods

Institutional abbreviations
AMB: Abiko Museum of Birds, Abiko, Japan; **CAS:** Ornithology Collection, California Academy of Sciences, San Francisco, California, USA; **EP:** Masaki Eda Collection, Hokkaido University Museum, Sapporo, Japan; **HUNHM:** Botanic Garden and Museum, Field Science Center for Northern Biosphere, Hokkaido University, Sapporo, Japan; **ICM:** Iida City Museum, Iida, Japan; **KUGM:** Department of Geology and Mineralogy, Kyoto University, Kyoto, Japan; **LACM-O:** Ornithology Department, Natural History Museum of Los Angeles County, Los Angeles, California, USA; **LACM-VP:** Vertebrate Paleontology Department, Natural History Museum of Los Angeles County, Los Angeles, California, USA; **MVZ:** Museum of Vertebrate Zoology, University of California, Berkeley, California, USA; **NSMT-AS:** Avian Skeleton Collection, Department of Zoology, National Museum of Nature and Science, Tsukuba, Japan; **NSMT-PV:** Vertebrate Paleontology Collection, Department of Geology and Paleontology, National Museum of Nature and Science, Tsukuba, Japan; **USNM:** Division of Birds, Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA; **UWBM:** Ornithology Collection, Burke Museum of Natural History and Culture, University of Washington, Seattle, Washington, USA; **YIO:** Yamashina Institute for Ornithology, Abiko, Japan.

Fossil and comparative materials
The fossil specimens reported in this study, along with other avian fossils from Shiriya, had originally been collected at Loc. 1 by Z. Nakajima in the 1950's, or at Locs. 2 and 3 by Y. Hasegawa and others in 1960's and 1987. They were temporarily stored in ICM, KUGM, and NSMT-PV, and are currently stored in NSMT-PV. All fossil limb bones examined had a rather smooth surface texture and completely ossified epiphyses, indicating that they are osteologically mature (Tumarkin-Deratzian *et al.*, 2006; Watanabe and Matsuoka, 2013).

Osteological descriptions were based on comparison with skeletal specimens of every living species of Alcidae. Skeletal collection of MVZ were the primary basis of comparison, which was supplemented with collections in AMB, CAS, EP, HUNHM, KUGM, LACM-O, NSMT-AS, UWBM, USNM, and YIO. The two Recent species of *Uria* are known to show geographic variation in plumage and external dimensions and divided into several subspecies for each (Storer, 1952; Tuck, 1960), but it is not clear whether they show any variations in osteological characters. Comparative specimens were not available for some of the recognized subspecies, and comparisons were mainly based on Recent birds from the Pacific (from geography, 6 *U. aalge inornata*, ~50 *U. a. californica*, 5 *U. a. aalge*, and ~30 *U. lomvia arra*). A cast of the holotype specimen of *Uria brodkorbi*, LACM-VP 121967, whose original specimen is an impression of partial skeleton from the upper Miocene Sisquoc Formation, was also examined.

List of primary comparative specimens is as follows (f, female; m, male; u, unsexed)—*Aethia cristatella*: California, CAS 84952 (f), Aleutian/Bering Sea, LACM-O 110616–110618, 110671, and YIO 62864 (3 m, 1 f, 1 u). *A. pygmaea*: Bering Sea, LACM-O 110691, 110841, 110842, and MVZ 60629 (2 m, 2 f). *A. psittacula*: California, MVZ 89469 and 119099 (1 f, 1 u); Bering Sea, LACM-O 107192 (f); Arctic, MVZ 140831 and 142738 (1 m, 1 u). *A. pusilla*: Bering Sea, LACM-O 110833, MVZ 60612 and 134083 (1 m, 2 f). *Ptychoramphus aleuticus*: California, MVZ 19040, 49390, 54001, 68344, and 118981 (1 m, 1 f, 3 u). *Cerorhinca monocerata*: California, MVZ 49331–49335, 49337, 49338, 49397, 54409, 54410, 72299, 151844–151846, 156800, and 158762 (5 m, 11 u); Japan, HUNHM 60455 and 60456 (2 m). *Fratercula arctica*: YIO 60957, 60958, 62491, and 64404 (all are captive birds, 2 m, 2 u). *F. corniculata*: California, MVZ 30713 and 30714 (2 u); Alaska, MVZ 28957, 60637, 68413–68417, 134084, and 160699 (4 m, 4 f, 1 u). *F. cirrhata*: Alaska, MVZ 68419, 125348, 126818, and 159161 (2 m, 1 f, 1 u). *Alca torda*: Netherlands (ssp. *islandica*), USNM 555666 (m); New York (ssp. *torda*), UWBM 37177 (u). *Alle alle*: Greenland, MVZ 84652 (m); Maine, UWBM 38109 (f). *Uria lomvia arra*: Alaska, MVZ 60576–60578, 68408–68412, 129408, 133577, 133578, 142054, 142055, 142737, and 156028 (11 m, 3 f, 1 u); Japan, EP 116–118, 120–124, 158, NSMT-AS 1055, and YIO 60951 (all u). *U. aalge aalge*: YIO 60952, 60953, 62450, 64421, 64505 (all are captive birds, originally from Iceland, 1 m, 3 f, 1 u). *U. aalge californica*: California, MVZ

19046–19048, 41121, 46806, 49341–49394, 53825, 53826, 54413, 54416, 54417, 68070, 70631–70635, 77238, 151839–151843, 170863–170869, 176038, 176039, and 183432 (15 m, 9 f, 32 u). *U. aalge inornata*: Alaska, MVZ 60554 (m); Japan, HUNHM 60410–60413 and MVZ 124097 (5 f). *Cepphus carbo*: Japan, HUNHM 60457 and MVZ 119013 (2 u). *C. columba*: California, MVZ 68343 (u); Alaska, MVZ 160710 (m). *C. grylle*: Alaska, UWBM 78969 (f). *Synthliboramphus hypoleucus*: Mexico (ssp. *hypoleucus*), MVZ 134046 and 134054 (1 m, 1 f); California (ssp. *scrippsi*), MVZ 46844 (u). *S. craveri*: Mexico, MVZ 54725 and 54742 (2 m). *S. antiquus*: California, MVZ 19044, 19045, 62755, 66972, 70638, 70639, 71104, 89695 (2 m, 4 f, 2 u); Washington, UWBM 38779 (f) and 39594 (m); Russia, UWBM 43338 and 43339 (2 f); Japan, MVZ 123166–123168, 126464, 128734 (1 m, 4 f). *S. wumizusume*: North Pacific, UWBM 55587 and 55695–55698 (4 m, 1 f). *Brachyramphus marmoratus*: California, MVZ 1942, 19043, 41126, 41127, 51384, 70637, 124875 (2 m, 2 f, 3 u). *B. brevirostris*: Alaska, MVZ 152792 (f).

Terminology and measurement

Osteological terminology mainly follows Baumel and Witmer (1993), but those of Howard (1929) and Livezey and Zusi (2006) are also used when appropriate. Measurements were taken with a digital caliper (Mitutoyo, Kawasaki, Japan) to 0.01 mm, and values rounded to the nearest 0.1 mm are reported. Definition of measurements is as follows: coracoid—shaft width, mediolateral width of shaft at foramen n. supracoracoidei with medial side of shaft flat on a caliper leg; shaft depth, dorsoventral depth at the same point with dorsal side flat on a caliper leg; humerus—length, greatest length from caput humeri to condylus dorsalis (not processus flexorius); proximal width, greatest dorsoventral width from the ventral tip of crista bicipitale to the dorsal surface of bone which is laid flat on a caliper leg; width at midshaft, dorsoventral width (minimum diameter) of shaft around midpoint; depth at midshaft, craniocaudal depth (maximum diameter) of shaft at the same point; distal width, dorsoventral width of distal end measured across both epicondyles with the ventral surface flat on a caliper leg; distal depth, craniocaudal depth of distal end with condyles flat on a caliper leg; greatest distal breadth, as in Bd of von den Driesch (1976); ulna—proximal width, dorsoventral width of proximal end with the ventral margin of cotyla ventralis flat on a caliper leg; width and depth at midshaft, as in humerus; radius—proximal width, dorsoventral width of proximal end with the ventral margins of cotyla humeralis and tuberculum bicipitale radii flat on a caliper leg; width at midshaft, dorsoventral width of shaft at midpoint with the ventral surface flat on a caliper leg; depth at midshaft, craniocaudal depth at the same point with the caudal surface of shaft flat on a caliper leg; carpometacarpus—width at midshaft, as in radius; depth at midshaft, craniocaudal depth at the same point with the cranial surface flat on a caliper leg; distal width, dorsoventral width of distal end with the ventral margin flat on a caliper leg; femur—width at midshaft, mediolateral width (minimum diameter) of shaft at midpoint; depth at midshaft, craniocaudal depth at the same point; distal width, mediolateral width of the distal end with the medial surface flat on a caliper leg; distal depth, craniocaudal depth of the distal end with the caudal tips of condyles flat on a caliper leg.

Osteological dimensions were compared and visually assessed with bivariate plots of dimensions. When more than three dimensions were available for a single element, bivariate plots of principal component (PC) scores were also utilized, which are basically summarizations of distribution of multiple variables with appropriate centering and rotation of axes (e.g., Reyment, 1991). For each element, PCs were extracted from the pooled variance-covariance matrix of log-transformed variables in Recent comparative specimens, and PC scores for fossil specimens were calculated and plotted a posteriori. Results of analyses are presented for the purpose of reproducibility.

Body mass estimation

To estimate body mass of fossil species, a linear bivariate regression analysis was performed. The scaling relationship of body mass and humerus length (both log-transformed) was utilized, which was found by Smith (2016) as the best osteological predictor of body mass in volant alcids (in terms of strong correlation of variables and little phylogenetic signal in residuals).

The humerus length was measured with a modification from Smith's (2016) "greatest length of humerus (glH)," which was stated to be measured following von den Driesch (1976). However, the definition of von den Driesch's (1976) greatest length of humerus is quite ambiguous and not suitable for interspecific comparison, since a greatest length of an avian humerus may be either the distance between caput humeri and condylus ventralis (i.e., distance between articular surfaces) or the one between caput humeri and processus flexorius (see also von den Driesch, 1976: fig. 54a–c). Such an ambiguity may lead to reduced repeatability or even nonsense comparison between non-homologous measurements. These problems apply to this particular case, because it varies interspecifically and even intraspecifically which of the two distances described above is the greatest length of humerus in Alcidae (JW, personal observation). In this study, the former of the two distances was employed as a measurement of humeral length as stated above, because the species means of it showed slightly smaller variance and higher correlation with body mass than those of the other.

Body mass data for Recent species were taken from Dunning (2008), and the average of male and female means is used for each species. For *Cepphus carbo*, for which the value given in Dunning (2008) was rather questionable (too small), the mean of original measurements of dead animals collected near Haboro (Hokkaido, Japan), which had been provided by Hokkaido Seabird Center, Haboro, was used (average of male [$n = 7$] and female [$n = 2$] means 706 g, including birds from both breeding and wintering seasons). For *Alle alle* and *Uria aalge*, where values for more than one subspecies are given by Dunning (2008), that for subspecies mainly sampled in this study is used (*A. alle alle* and *U. aalge californica*, respectively). For *Synthliboramphus antiquus* and *Fratercula arctica*, where values from two localities are given by Dunning (2008), the average of the two values were taken. Osteological measurements were taken from 359 individuals representing 22 species of Recent volant alcids (all species except *Brachyramphus perdix* where no specimens were available). These species mean data were natural log-transformed before the analysis, and back-transformed values are presented as results. The scaling parameters were estimated with the ordinary least squares (model I) fitting, since the purpose of analysis was a prediction for a new observation rather than the estimation of symmetrical relationship (see Warton *et al.*, 2006; Smith, 2009). As in standard regression procedures, a confidence interval of dependent variable (log-body mass) was calculated for an expected value of that variable, given a certain value of independent variable (log-humerus length) (i.e., incorporating only the variance of sample regression coefficients), and a prediction interval was obtained by further incorporating the variance of residual from the expectation. Confidence and prediction intervals for body mass in the original scale were obtained by back-transforming the corresponding intervals in the log scale. The correction for antilog-transformation "bias" (Smith, 1993; Hayes and Shonkwiler, 2006) was not attempted, in order to facilitate comparison with a previous work (Smith, 2016) and also because such corrections might cause another bias in the prediction in the original scale (Hui *et al.*, 2010). The statistical analysis was performed on the statistical software package R version 3.2.0 (R Core Team, 2015).

Figure 3. Humeri of *Uria* spp. from Shiriya compared with Recent species. A–D, J–M, Q, *Uria onoi*, sp. nov., from Shiriya: A, J, holotype right humerus (NSMT-PV 23722); B, K, Q, right humerus (NSMT-PV 23731); C, L, paratype right humerus (NSMT-PV 23723); D, M, right humerus (NSMT-PV 23732). E–G, N–P, *U. lomvia* from Shiriya: E, N, left humerus (NSMT-PV 23737); F, O, right humerus (NSMT-PV 23736); G, P, R, right humerus (NSMT-PV 23735). H, Recent *U. lomvia arra* (MVZ 133578), right humerus. I, Recent *U. aalge inornata* (MVZ 60554), right humerus. Caudal (A–I), cranial (J–P), and craniodorsal (Q, R) views. Fossils coated with ammonium chloride. Scale bar equals 5 cm. Abbreviations: cb, (distal extent of) crista bicipitalis; df, dorsal part of fossa tricipitalis; psd, processus supracondylaris dorsalis; r, ridge between distal margin of caput humeri and impressio m. supracoracoideus; sc, sulcus n. coracobrachialis; sh, sulcus humerotricipitalis; ss, sulcus scapulotricipitalis; st, sulcus transversus; vf, ventral part of fossa tricipitalis.

Systematic paleontology

Order Charadriiformes Huxley, 1867
Family Alcidae Leach, 1820
Genus *Uria* Brisson, 1760

Remarks. More than ten humeri from the Shiriya localities are referable to this genus. In Alcidae, the humerus bears numbers of taxonomically useful characters, serving for bases of many fossil taxa described to date (e.g., Chandler, 1990; Wijnker and Olson, 2009; Smith, 2011, 2014; Smith and Clarke, 2011). Among alcids, the humerus of this genus can be characterized by the following osteological features: overall slender proportion; distally extending impressio m. supracoracoideus (Livezey and Zusi, 2006) which is widened distally; dorsal part of fossa pneumotricipitalis relatively shallow (in contrast to, e.g., *Aethia*, *Fratercula*, and *Cerorhinca*); crus dorsale fossae not directed proximodistally (in contrast to *Cepphus*); tip of crista deltopectoralis only slightly deflected ventrally (strongly deflected in *Cepphus*, virtually not deflected in, e.g., *Fratercula*); crista deltopectoralis extending distally over the proximal one-third of the shaft as a rugose ridge on the cranial margin (unlike e.g., *Fratercula*, but not as distally as in *Pinguinus* and Mancallinae); sulcus n. coracobrachialis not enclosed by a bone wall (in contrast to *Alca*, see Wijnker and Olson, 2009; Smith and Clarke, 2011); pit for the attachment of m. pronator superficialis virtually absent, sometimes observable as a indistinct pit merged to the ventral margin of tuberculum supracondylare ventrale (distinct pit present proximal to the tubercle in *Alca* and *Cepphus* and ventral to it in e.g., *Fratercula*); sulcus humerotricipitale distinctively wider than sulcus scapulotricipitalis (roughly equal width in *Alca* and the former narrower in *Alle*; see also Smith and Clarke, 2011).

Other osteological features of the genus include: sternum, medial extent of sulcus articularis coracoideus, moderately pointed (strongly pointed in Mancallinae, rounded in, e.g., *Aethia*, *Fratercula*, and *Cerorhinca*); furcula, the ridge on the ventral margin is lying cranially (as in *Alle*); coracoid, processus acrocoracoideus strongly produced ventromedially; the medial part of facies articularis sternalis narrowing gently and pointed; processus procoracoideus broad and pointed; foramen n. supracoracoideus present; femur, cranial margin of distal shaft strongly convex; two distinct scars present on the lateral surface of shaft proximal to trochlea lateralis (in, e.g., *Fratercula*, the proximal one lies more cranially); distal end craniocaudally deep; and prominent ridge present on caudomedial margin of distal shaft and forms the medial margin of fossa poplitea.

Two discrete size classes, which differ from each other by about 10% in linear dimensions, are recognized for humeri, even within specimens from a single locality (Loc. 3). Given the small magnitudes of sexual dimorphism and intrapopulational variation of linear dimensions in the Recent representatives of this genus (Table 2; Storer, 1952), it is reasonable to assume these size classes represent two distinct species. Humeri of the smaller of the two size classes have a size and proportion comparable to Recent *Uria lomvia*, and those of the larger one clearly exceed the size range of Recent species, and seem to represent a previously undescribed species as detailed below. Specific identifications of other elements than the humerus should be regarded as tentative for the absence of associated skeletons, the scarcity of other elements, and the undiagnostic nature of postcranial bones other than the humerus in the specific level in Alcidae.

The following specimens probably represent species of *Uria*, but could not be identified to the specific level. Loc. 1: shaft of
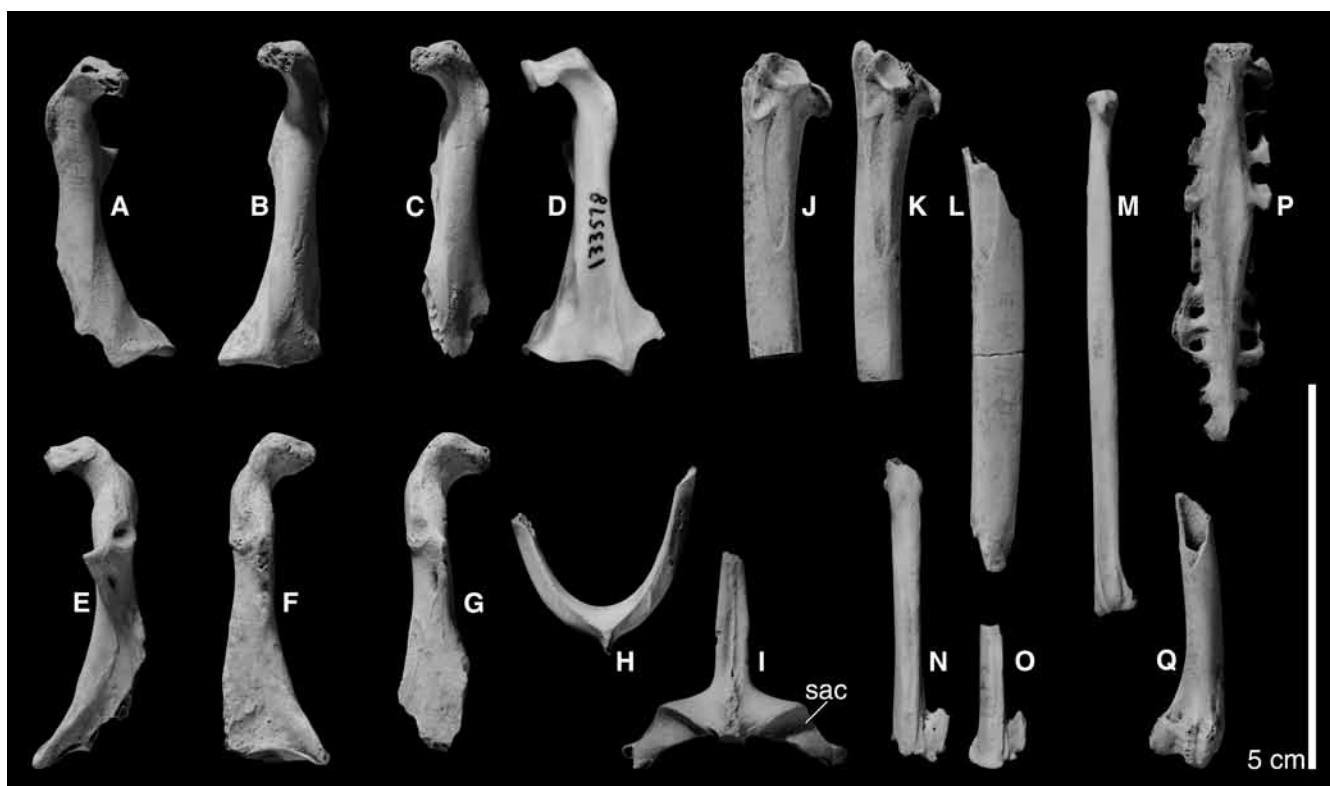

Figure 4. *Uria* spp. from Shiriya compared with Recent species. B, C, F, G, J, K, N, *Uria onoi*, sp. nov., from Shiriya: B, C, left coracoids (NSMT-PV 23725 and 23726, respectively), ventral view; F, G, same, dorsal view; J, K, left ulnae (NSMT-PV 23729 and 23730, respectively), ventral view; N, left carpometacarpus (NSMT-PV 23734), dorsal view. M, O, *U. lomvia* from Shiriya: M, left radius (NSMT-PV 23738), cranial view; O, left carpometacarpus (NSMT-PV 23739), dorsal view. D, Recent *U. lomvia arra* (MVZ 133578), left coracoid, ventral view. A, E, H, I, L, P, Q, *Uria* specimens from Shiriya not identified to specific level: A, right coracoid (NSMT-PV 23746), ventral view; E, same, dorsal view; H, furcula (NSMT-PV 23745), dorsal view; I, sternum (NSMT-PV 23743), cranial view; L, right ulna (NSMT-PV 23740), ventral view; P, synsacrum (NSMT-PV 23751), ventral view; Q, right femur (NSMT-PV 23741), caudolateral view. Fossils coated with ammonium chloride. Scale bar equals 5 cm. Abbreviation: sac, sulcus articularis coracoideus.

TABLE 2. Measurements (mm) of *Uria* spp. from Shiriya compared with Recent taxa.
Abbreviations: D, depth perpendicular to width; GDB, greatest distal breadth; W, lateromedial or dorsoventral width. (*n* = number of individuals.)

Elements	*U. lomvia* (Shiriya)	*U. onoi*, sp. nov. (Shiriya)			*Uria* sp. indet. (Shiriya)	*U. aalge* sspp. (Recent)			*U. lomvia arra* (Recent)		
		n	Range	Mean		*n*	Range	Mean	*n*	Range	Mean
Coracoid											
Medial length	—	1	c. 42.7, —	—	c. 41.7, —	64	37.3–43.1	40.3	24	39.4–46.1	41.7
Shaft W	—	2	5.5, 5.6	—	5.2, 5.1	66	4.2–6.0	4.7	26	4.0–5.4	4.7
Shaft D	—	2	5.3, 5.4	—	5.1, 4.8	66	4.0–5.1	4.5	26	4.3–5.5	4.7
Humerus											
Length	—, —, —	2	101.0, 101.9	—	—	62	81.2–91.6	87.3	31	84.2–96.4	90.5
Proximal W	18.3, 18.9, —	2	19.4, 20.8	—	—	63	15.8–17.7	17.0	31	16.1–19.4	18.0
W midshaft	4.2, 4.2, 4.1	7	4.6–5.1	5.0	4.6	63	3.6–4.4	3.9	31	3.8–4.6	4.2
D midshaft	7.3, 8.4, 8.3	7	8.2–9.4	8.7	8.0	63	6.7–9.2	7.7	31	6.9–9.1	7.7
Distal W	—, —, 9.0	5	9.9–10.6	10.2	—	63	8.2–9.5	8.9	31	8.7–10.6	9.5
Distal D	—, —, 9.8	3	10.1–10.4	10.3	—	63	8.9–9.9	9.5	31	8.9–10.3	9.8
GDB	—, —, 12.7	3	13.2–13.6	13.4	—	63	11.7–12.8	12.2	31	11.7–13.4	12.7
Ulna											
Proximal W	—	2	9.8, 9.3	—	—	62	7.7–9.0	8.4	30	8.1–9.8	8.9
W midshaft	—	2	4.6, 4.7	—	4.3	62	3.6–4.3	3.9	30	3.6–4.7	4.1
D midshaft	—	2	6.4, 7.0	—	6.8	62	5.5–6.8	6.1	30	5.8–7.1	6.2
Radius											
Length	68.8	—	—	—	—	61	59.4–67.1	63.7	29	59.8–72.1	67.3
Proximal W	4.2	—	—	—	—	61	3.7–4.5	4.1	29	3.9–4.8	4.3
W midshaft	2.8	—	—	—	—	61	2.4–2.9	2.7	29	2.4–3.0	2.7
D midshaft	3.8	—	—	—	—	61	2.9–4.0	3.6	29	3.0–4.5	3.7
Distal W	5.4	—	—	—	—	61	4.8–6.0	5.3	29	4.8–6.1	5.6
Carpometacarpus											
W midshaft	—	1	4.8	—	—	61	3.4–4.3	3.9	29	3.4–4.6	4.1
D midshaft	—	1	3.5	—	—	61	2.7–3.4	3.0	29	2.8–3.5	3.1
Distal W	4.4	—	—	—	—	61	4.0–4.8	4.4	29	4.3–5.0	4.7
Femur											
W midshaft	—	—	—	—	4.1	65	3.5–4.5	4.0	32	3.4–4.1	3.8
D midshaft	—	—	—	—	5.5	65	4.3–5.5	4.8	32	4.4–5.3	4.9
Distal W	—	—	—	—	9.3	63	8.1–9.6	8.8	27	8.1–9.3	8.5
Distal D	—	—	—	—	8.5	63	7.2–9.1	8.3	27	7.5–8.6	8.1

right ulna, NSMT-PV 23740. Loc. 2: distal right femur, NSMT-PV 23741; and fragmentary synsacrum, NSMT-PV 23742. Loc. 3: fragmentary sternum preserving the manubrial area, NSMT-PV 23743; sternal fragment preserving left processus craniolateralis, NSMT-PV 23744; fragmentary furcula preserving symphysis, NSMT-PV 23745; right coracoid lacking lateral part of sternal end, NSMT-PV 23746; shaft of left coracoid, NSMT-PV 23747; shaft of left humerus, NSMT-PV 23748; fragmentary proximal ends of right humeri, NSMT-PV 23749 and 23750; and worn synsacrum, NSMT-PV 23751.

Uria lomvia (Linnaeus, 1758)
(Figs. 3E–G, N–P, R, 4M, O)

Referred specimens. Loc. 3: right humeri lacking distal end, NSMT-PV 23735 and 23736; left distal humerus, NSMT-PV 23737; left complete radius, NSMT-PV 23738; and distal end of left carpometacarpus, NSMT-PV 23739.

Measurement. See Table 2 and Fig. 5.
Description and comparison. Three *Uria* humeri are referred to this species (Fig. 3E–G, N–P, R). Overall size is smaller than the species described below, and comparable to the humeri of two Recent species which are morphologically rather similar to each other. The humerus of *U. lomvia* tends to have a broader proximal end and crista bicipitalis which is sloping more steeply from the shaft than that of *U. aalge* (Fig. 3H, I). Also, as noted by Brodkorb (1960), the two Recent species tend to differ in the profile of overhanging ridge between distal margin of caput humeri and impressio m. supracoracoideus; in *U. aalge*, the ridge is more strongly concave in caudal view than in *U. lomvia*. In these features the referred humeri agree with *U. lomvia*.

One complete radius is referred to this species (Fig. 4M). Both dorsal and ventral margins of sulcus tendinosus are prominent, with the ventral one nearly reaching the distal end (unlike *Cepphus*) and the dorsal one being separated from the dorsal margin of shaft (unlike, e.g., *Fratercula*). Length of the referred
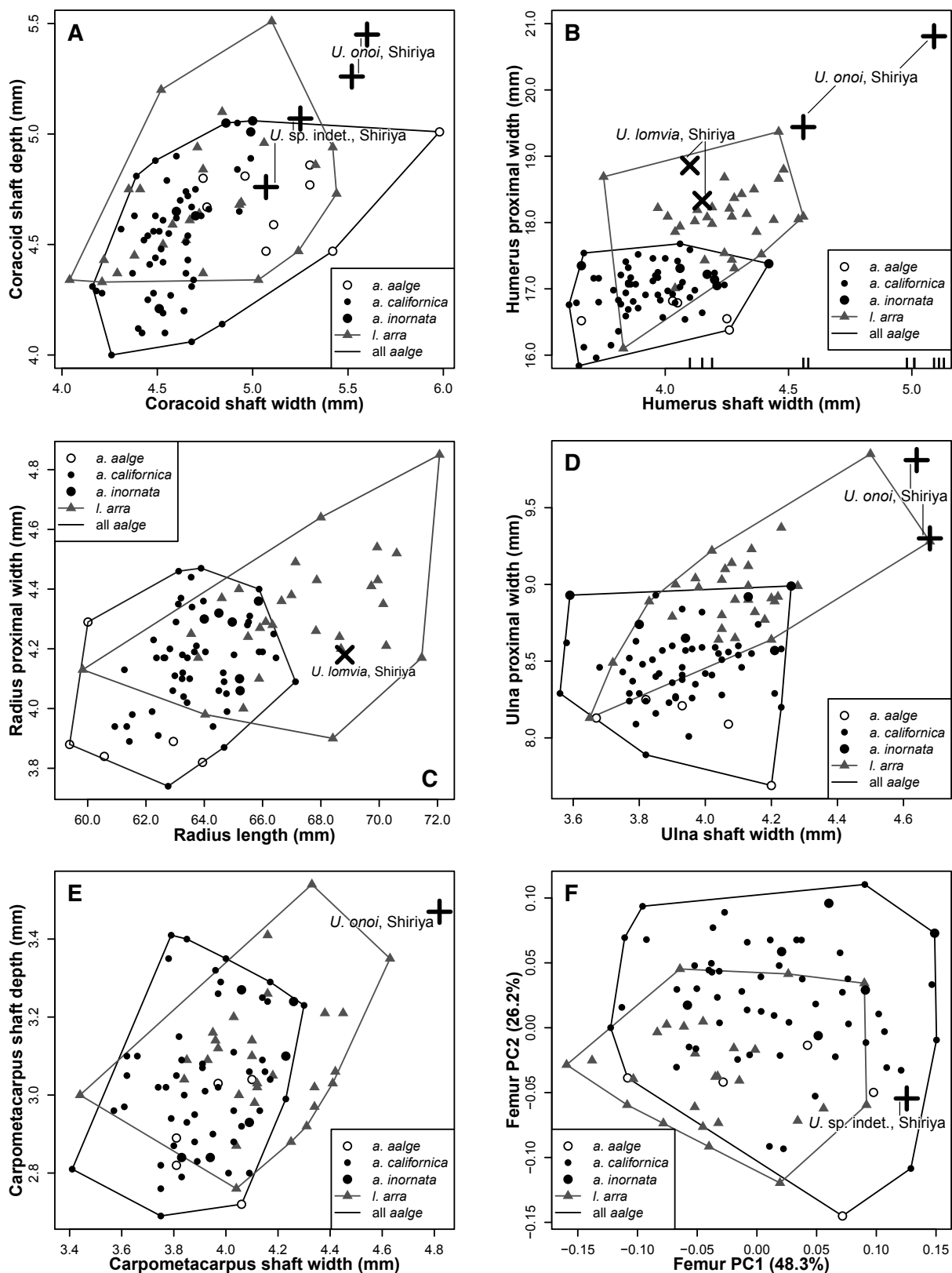
Figure 5. Bivariate scatter plots of individual measurements and principal component (PC) for *Uria*. A, coracoidal shaft measurements, points for fossils represent, from top to bottom, NSMT-PV 23726, 23725, 23746, and 23747; B, humeral measurements, points for fossils represent, from top to bottom, NSMT-PV 23722, 23732, 23736, and 23735; C, radial measurements, point for fossil represents NSMT-PV 23738; D, ulnar measurements, points for fossils represent, from top to bottom, NSMT-PV 23729 and 23730; E, carpometacarpal shaft measurements, point for fossil represents NSMT-PV 23734; F, PC scores based on four femoral measurements, point for fossil represents NSMT-PV 23741. In B, distribution of humerus shaft width for Shiriya fossils are also shown as vertical bars on bottom. See Tables 3 for details of analyses. Legend: open circle, Recent *U. aalge aalge*, captive individuals originally from Iceland; small filled circle, Recent *U. aalge californica* from California; large filled circle, Recent *U. aalge inornata* from Alaska, Japan, and northern North Pacific; triangle, Recent *U. lomvia arra* from Alaska, Japan, and northern North Pacific; cross, *U. lomvia* from Shiriya; plus sign, *Uria onoi*, sp. nov., from Shiriya, or *Uria* specimens from Shiriya not identified to specific level.

TABLE 3. Summary of principal component (PC) analysis for *Uria*, based on four measurements of femur (Fig. 3F).
Analysis was based on covariance matrix of natural log-transformed variables. Eigenvectors, corresponding eigenvalues and proportion of variance explained (PVE), total mean vector (Mean) of variables, and PC loadings are shown. Sample includes 5 individuals of *U. aalge aalge*, 52 *U. aalge californica*, 6 *U. aalge inornata*, and 26 *U. lomvia arra* (total n = 89).

Variable	Eigenvectors				Mean	PC Loadings			
	PC1	PC2	PC3	PC4		PC1	PC2	PC3	PC4
W midshaft	0.8041	0.1500	−0.5566	−0.1454	1.3623	0.9130	0.1255	−0.3824	−0.0662
D midshaft	0.4633	−0.7643	0.4384	0.0953	1.5653	0.5962	−0.7250	0.3413	0.0492
Distal W	0.2709	0.4359	0.2987	0.8046	2.1633	0.4839	0.5739	0.3227	0.5764
Distal D	0.2558	0.4510	0.6393	−0.5678	2.1060	0.4165	0.5411	0.6295	−0.3707
Eigenvalue	0.0716	0.0527	0.0433	0.0287					
PVE	48.3%	26.2%	17.7%	7.8%					

radius exceeds the size range of Recent *Uria aalge* but falls within that of *U. lomvia*. One distal end of carpometacarpus, which conforms well with Recent *Uria* species in size and morphological details, is tentatively referred to this species (Fig. 4O).

Remarks. This species has more northern distribution than the other Recent species (Tuck, 1960), and in Japan it occurs as a winter visitor in Hokkaido, or as an irregular visitor in northern Honshu. The oldest known fossil record of this species is from the upper Pliocene of St. George Island, Pribilof Islands (Olson, 2013). Pleistocene fossils are known from several localities in Norway and Sweden (Brodkorb, 1967; Lie, 1986; Larsen, 1987).

Uria onoi, sp. nov.
(Figs. 3A–D, J–M, Q, 4B, C, F, G, J, K, N)

Holotype. Right humerus with worn ends, NSMT-PV 23722, stored in vertebrate paleontology collection at the National Museum of Nature and Science, Tsukuba, Japan. Shaft is broken but glued with no substantial loss. Collected by Yoshikazu Hasegawa and colleagues. Exact collection date unknown, but probably in 1987.

Type locality. The fissure-fill deposit of the Shiriya second quarry (Loc. 2 of Hasegawa *et al.*, 1988), northeast of Iwaya, Higashidori, Aomori Prefecture, northeast Japan. 41°24'N, 141°26'E. Possibly middle Pleistocene (Marine Isotope Stage [MIS] 9) in age, based on correlation with marine terraces.

Occurrence. Other than the type locality, known from two geographically nearby localities: the fissure-fill sediments at "Locality A" (Loc. 1 of Hasegawa *et al.*, 1988), and the Shiriya tunnel (Loc. 3 of Hasegawa *et al.*, 1988). Both are possibly late Pleistocene (MIS 5e) in age, based on correlation with marine terraces and co-occurring terrestrial mammal fauna.

Measurement of holotype (mm). Length, 101.0; proximal width, 20.8; width at midpoint, 5.1; depth at midpoint, 9.4; distal width, c. 10.6. See also Table 2.

Paratype. Right and left humeri lacking proximal ends, NSMT-PV 23723 and 23724, respectively, from the type locality (Loc. 2).

Measurement of paratypes (mm). Width at midpoint, 5.1, 5.1; depth at midpoint, 8.3, 8.2; distal width, c. 9.9, c. 9.9; distal depth, —, c. 10.3; greatest distal breadth, c. 13.2, c. 13.4. See also Table 2.

Referred specimens. Loc. 1: left coracoids with broken sternal end, NSMT-PV 23725 and 23726; fragmentary right proximal humeri, NSMT-PV 23727 and 23728. Loc. 2: Proximal left ulnae, NSMT-PV 23729 and 23730. Loc. 3: right humerus lacking ventral part of proximal end, NSMT-PV 23731; proximal right humerus, NSMT-PV 23732; worn distal end of left humerus, NSMT-PV 23733; and shaft of left carpometacarpus, NSMT-PV 23734.

Etymology. The species epithet, *onoi*, is taken after Mr. Keiichi Ono, one of the earliest Japanese avian paleontologists. It is

dedicated to him in recognition of his contributions to the early works on Japanese avian fossils, including a previous report of Shiriya paleoavifauna (Hasegawa *et al.*, 1988). It is genitive.

Diagnosis. Large species of *Uria*, exceeding other species of the genus in overall length of the humerus and many other dimensions. Further characterized by the following osteological features: humerus—fossa tricipitalis, part dorsal to crus fossae dorsale extremely wide dorsoventrally and shallowly depressed, part ventral to crus fossae dorsale relatively narrow, sulcus transversus deeply incised, corpus humeri extremely stout and thick dorsoventrally, processus supracondylaris dorsalis lying relatively distally; ulna—prominent ridge present between olecranon and caudal tip of cotyla dorsalis.

Measurement. See Table 2 and Fig. 5.

Description and comparison. Eight humeri, including nearly complete ones, are referred to this species (Fig. 3A–D, J–M, Q). They are referable to *Uria* from the osteological features described above, but exceeds humeri of Recent species in their length. They are also much more robust than those of two Recent species and *U. lomvia* from Shiriya (Fig. 3Q, R), although the smallest specimen (t2) falls on the upper margin of the range of Recent *U. lomvia*. The proximal end is relatively wide dorsoventrally and crista bicipitalis is sloping rather steeply from the shaft as in *U. lomvia* and unlike *U. aalge*. In some humeri including the holotype (NSMT-PV 23722), but not others (e.g., NSMT-PV 23731), a clear ridge is present on the caudal margin of proximal shaft, extending from the midpoint of the distal margin of caput humeri to the distal end of impressio m. supracoracoideus of Livezey and Zusi (2006) (Fig. 3A, D). The dorsal part of fossa tricipitalis (the part dorsal to crus dorsale fossae) is rather wide, only shallowly depressed, and not strongly excavating the area below caput humeri, compared to the Recent species. Compared to the dorsal part, the ventral part of the fossa (ventral to crus dorsale fossae) is relatively narrow dorsoventrally. Where observable, sulcus transversus is deeply incised, and in ventrodistal view its margins are forming nearly a right angle, rather than obtuse angle in Recent species. Tuberculum supracondylare dorsale is lying relatively distally for its size. Fossa m. brachialis is relatively small, and tends to be separated from condylus dorsalis with a wide space. Both condylus dorsalis et ventralis are well developed and bulbous. The proximocaudal margin of tuberculum supracondylare ventrale is well developed and elevated from the shaft.

Two coracoids which lack the tip of processus acrocoracoideus and the lateral part of sternal end are referred to this species (Fig. 4B, C, F, G). In the referred coracoids, processus acrocoracoideus is directed rather sternally, agreeing with that of *Uria lomvia* and differing from that of *U. aalge* (see also Spring, 1971). Although the overall length is within the ranges of Recent *Uria* species, the shaft is disproportionately stouter than them.

Two proximal ulnae are referred to this species (Fig. 4J, K). The referred ulnae are much more stout than ulnae of Recent species. Cotyla dorsalis is relatively shallow and wide

dorsoventrally. Olecranon is well developed proximally and bulbous. On the caudodorsal part of proximal end, a prominent ridge is present between olecranon and the caudal tip of cotyla dorsalis (the tip also forms the ventral margin of impressio m. scapulotricipitis), unlike Recent species of *Uria*. Tuberculum lig. collateralis ventralis is dorsally rimmed by a distinct ridge which is leading to the ventrocaudal tip of cotyla ventralis (the margin is not markedly rimmed in *Alle* and *Cepphus*, and the ridge is less prominent in other alcids), only slightly elevated from the shaft (more elevated in *Cepphus*, *Cerorhinca*, *Fratercula*), and separated from the ventral rim of cotyla ventralis by a depression. One shaft of carpometacarpus is tentatively referred to this species (Fig. 4N). It is much more robust than carpometacarpi of Recent *Uria* species.

Remarks. The humerus of this species is characterized by its large size, extremely stout shaft (Figs. 3, 4), and several unique qualitative characters, allowing to treat some humeri from the Shiriya locality as a distinct species. The most readily recognizable character is its stoutness of the humeral shaft (Fig. 3D), although there seems to be a slight overlap with Recent species in a single dimension (Fig. 5B). Dimensions of some *Uria* specimens from the Shiriya localities, including coracoids, ulnae, and a carpometacarpus, exceed the ranges of corresponding elements of Recent species, thus they are also referred to this species. The ulnae are also distinct from Recent species in qualitative characters. Other specimens from Shiriya are relatively large but fall within the variation of Recent species, thus could not be referred to this species with confidence. In a few features of the coracoid and humerus, *U. onoi* is similar to *U. lomvia* rather than *U. aalge* as described above.

Although the comparative material examined here represents only a limited part of the presumed morphological diversity of Recent *Uria* (only three and one subspecies are sampled, respectively, for *U. aalge* and *U. lomvia*), birds from the Pacific (*U. a. californica*, *U. a. inornata*, and *U. l. arra*), which consist of the primary part of the material, are known to be generally larger than their conspecifics in the Atlantic (Storer, 1952; Gaston and Jones, 1998). Therefore, it is reasonable to conclude that *U. onoi* is larger than Recent *U. aalge* and *U. lomvia* in general.

Uria onoi seems distinct from previously described fossil species of the genus. A cast of holotype of *U. brodkorbi*, LACM 121967, impressions of a partial skeleton from the Miocene

of California, was examined for comparison. The state of preservation precludes a satisfactory examination of qualitative and quantitative characters, but its humerus is only as large as those of Recent species (estimated length: ~85 mm). It also differs from *U. onoi* in linea m. latissimi dorsi that is extending distocaudally on the dorsal surface of the shaft, as described by Howard (1981). According to Howard (1981), ?*Uria* sp. of Howard (1978), later considered possibly conspecific with *U. paleohesperis* by Howard (1982), is still smaller and also differ from *U. onoi* in the same feature of linea m. latissimi dorsi mentioned above. Although the humerus is not known for *U. paleohesperis* from the Miocene of California, known elements of the species are, according to published measurements (Howard, 1982), considerably smaller than referred specimens of *U. onoi*. (Also note that Smith and Clarke [2011] suggested the possible synonymy of *U. brodkorbi* and *U. paleohesperis*.) *U. affinis* known from a humerus from the upper Pleistocene of Maine is, according to Olson (1985) and Smith and Clarke (2011), similar to Recent *U. lomvia arra* in size and might be referable to one of the Recent species. Thus it would be, if recognized as a valid species, smaller than *U. onoi*.

It is worth noting that *Uria onoi* does not possess osteological features of humerus that are observed in flightless *Pinguinus* and Mancallinae, including the lack of sigmoidal curvature of the shaft and extreme thickns of bone walls (see Smith, 2011; Smith and Clarke, 2014). It is probable that *U. onoi* retained the ability of aerial flight despite its large size, as in the large species of *Alca* from the Pliocene of Atlantic (Smith and Clarke, 2011).

Discussion

Notes on biogeography

In their synopsis of the Shiriya local fauna, Hasegawa *et al*. (1988: table 1) mentioned the occurrence of *Uria aalge* from Loc. 3, but did not give designation, description, or illustration of their material. Consequently, the correspondence of their and our materials is not clear. However, the absence of specimens clearly referable to *U. aalge* would be a good reason for the exclusion of the Shiriya local fauna from the fossil record of *U. aalge*, although, of course, the possibility of the presence of *U. aalge* in this area in the Pleistocene cannot be excluded. In contrast, each of the two species reported herein, *U. lomvia* and *U. onoi*, is represented by at least two diagnostic specimens, suggesting for the regular presence of these species in the area at the time of deposition.

Uria onoi is a unique component of the Shiriya paleoavifauna, not having been reported from other regions including eastern North Pacific where Pleistocene records of the genus is by far more extensive (e.g., Howard 1936; Miller and Peabody, 1941; Guthrie, 1992). It is easy to speculate that *U. onoi* was originated from an isolated population of either of the Recent species during the Pleistocene glacial-interglacial cycles, but at present virtually no evidence is available for discussions on its origin. Nevertheless, it is notable that fossils referable to this species have been recovered from both horizons of the Shiriya localities, MIS 9 (Loc. 2) and MIS 5e (Locs. 1 and 3). If these age assignments are correct, this suggests the persistence of the species for at least ~200,000 years.

The occurrence of *U. lomvia* from the Shiriya localities seems to be the first example of this species from the Pleistocene of the Pacific. Although the oldest fossil of the species is known from the upper Pliocene of Pribilof Islands, Bering Sea (3.0–2.6 Ma; Olson, 2013), the previous Pleistocene records have been restricted to those from Norway and Sweden (Brodkorb, 1967; Lie, 1986; Larsen, 1987). In Shiriya, fossils confidently referable to this species are known only from the MIS 5e horizon (Loc. 3) and absent from the MIS 9 horizon (Loc. 2). But a relatively small number of identifiable avian fossils from Loc. 2 (Watanabe and Matsuoka, personal observation) precludes the assertion that *U. lomvia* was absent in the area in MIS 9. It is notable that this species occurs in Recent Honshu only as an irregular visitor (The
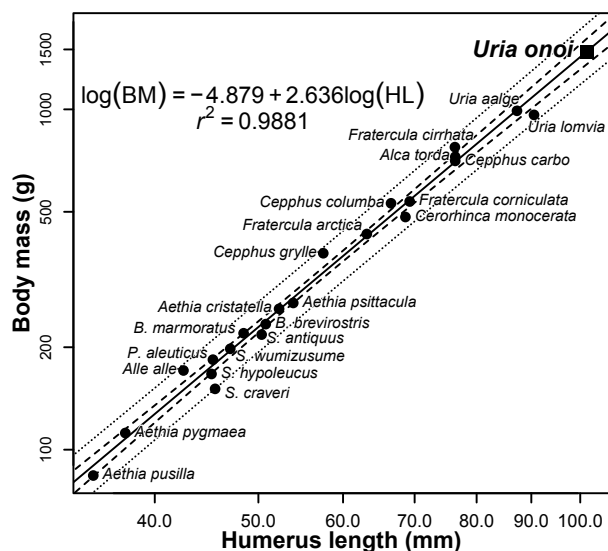

Figure 6. Bivariate scatter plot for body mass estimation in volant Alcidae. Species mean values of humerus length (HL) and body mass (BM) are plotted in log scale, and ordinary least squares regression line is shown. 95% confidence and prediction intervals are also shown with broken and dotted lines, respectively. The predicted body mass for *Uria onoi* is shown with a solid square.

$$\log(BM) = -4.879 + 2.636\log(HL)$$
$$r^2 = 0.9881$$

Ornithological Society of Japan, 2012).

The late Pleistocene age (~MIS 5e) of *Uria lomvia* from Shiriya roughly coincides with or slightly predates an estimate of divergence time between Pacific and Atlantic populations of the species by Tigano *et al.* (2015), ~99,000 years ago (90% highest probability density 70,659–137,685 years ago). According to Tigano *et al.* (2015), each of Pacific and Atlantic populations of this species underwent a range contraction after the divergence. Fossils of this age might be of potential importance in testing such hypotheses on the evolutionary history of the species, or in addressing how and when the geographic variations observed among birds from various localities were formed. The apparent agreement in size of the material of *U. affinis*, a possible synonym of either Recent species (Olson, 1985; Smith and Clarke, 2011), from the upper Pleistocene on the Atlantic coast of North America to the Recent Pacific race *U. lomvia arra* (see Olson, 1985) might be indicative of relatively recent origin of the geographic variation of body size in the Recent species. Unfortunately, however, the scarcity of the fossil record and the difficulty of tracing temporal variation practically preclude inferences on those problems and sometimes even rigorous identifications, the issue credited as "taxonomic ambiguity" by Stewart (2002). Ideally, with sufficient fossil materials and age resolution, temporal variation could be traced (Ericson, 1987). Even when large numbers of fossils are available, the importance of information on the nature of intraspecific variation in the modern world cannot be overemphasized (Olson, 2005).

Body mass estimation

Body mass of *Uria onoi* was estimated from the scaling relationship of body mass and humerus length in volant alcids, with a dataset of 22 Recent species (all living volant alcids except *Brachyramphus perdix*). The dataset is shown in Table 4. Log-transformed variables are highly and significantly correlated ($r = 0.994$, $p < 0.001$; Fig. 6). A preliminary analysis with phylogenetic generalized least squares using Pagel's (1999) λ statistic (Freckleton *et al.*, 2002), with hypermetric tree of Smith and Clarke (2015), resulted in a maximum likelihood estimate of $\lambda = 0.00$, confirming the result of Smith (2016). This result suggests the presence of little phylogenetic structure in residuals, and justifies the use of ordinary least squares regression with this dataset instead of phylogenetic generalized least squares, since the two models yield equivalent parameter estimates when $\lambda = 0$ (Freckleton *et al.*, 2002). The ordinary least squares regression of body mass (BM, g) and humerus length (HL, mm) resulted in: $\log(BM) = -4.8786 + 2.6364 \log(HL)$, with standard errors for intercept and slope being 0.2615 and 0.0647, respectively (Fig. 6). This model, with mean HL of 101.4 mm, yielded 1479 g as a prediction of the body mass of *U. onoi* (95% prediction interval: 1226–1783 g). This value exceeds the mean body mass of largest Recent volant alcids, *U. aalge* and *U. lomvia* (991 and 964 g, respectively) as expected. For comparison, body mass estimation of fossil species of *Alca* from the Pliocene of Atlantic (see Smith and Clarke, 2011) is attempted with the current model and the humerus length data given by Smith (2016), although it should be noted that measurement methods might not be comparable (see above). The prediction ranged from 434 g for *A. minor* to 1904 g for *A. stewarti* (Table 5). For all species considered, the current model yielded lower estimates of body mass than those of Smith (2016), with the upper limits of confidence intervals of the former being smaller the values given in that study. This is probably because of minor differences in datasets resulting from different taxonomic compositions (including/excluding *B. perdix*), differing treatments of body mass data (for body mass of *Cepphus carbo*, where the value in Dunning (2008) was unreliable, Smith (2016) took data from Gaston and Jones (1998), whereas in this study original data were used), sampling errors within species, or difference in measurement methods. This example illustrates the importance of standardizing data sets in estimating body mass or other traits of extinct organisms. It is important to clarify the definition of measurements used

TABLE 4. Summary of data used for body mass estimation. Body mass data shown are average values of male and female means given by Dunning (2008), except for *Cepphus carbo* which is taken from unpublished data by JW. See text for details of body mass data. Humerus length data are means for each species, sexes and localities pooled. *n*: number of individuals.

Species	Body mass	Humerus length Mean	*n*
Aethia cristatella	259.5	52.3	10
Aethia pygmaea	112.0	37.5	5
Aethia psittacula	270.0	53.9	9
Aethia pusilla	84.0	35.0	8
Ptychoramphus aleuticus	184.0	45.3	8
Cerorhinca monocerata	483.0	68.6	36
Fratercula arctica	430.5	63.2	6
Fratercula corniculata	536.5	69.3	20
Fratercula cirrhata	775.0	76.3	45
Alca torda	726.0	76.4	5
Alle alle	171.0	42.6	2
Uria aalge	991.0	87.3	63
Uria lomvia	964.0	90.5	31
Cepphus carbo	706.0	76.4	2
Cepphus columba	530.0	66.5	3
Cepphus grylle	378.0	57.5	1
Synthliboramphus hypoleucus	167.0	45.2	2
Synthliboramphus craveri	151.0	45.6	2
Synthliboramphus antiquus	218.0	50.4	29
Synthliboramphus wumizusume	198.0	47.1	64
Brachyramphus marmoratus	220.0	48.4	6
Brachyramphus brevirostris	234.0	50.8	1

in estimation so that later workers can reproduce comparable measurements (see above). Several studies, including this one, built scaling models to estimate body mass of extinct birds (e.g., Field *et al.*, 2013; Jones *et al.*, 2013; Smith, 2016), relying on body mass datasets comiled by Dunning (2008) or by other workers, but it should be noted that avian body mass may substantially vary ontogenetically, sexually, geographically, seasonally, or depending on trophic conditions of individuals measured. It is therefore important to critically evaluate such compiled data sets (e.g., the case of *Cepphus carbo* noted above). Some of these problems may be avoided or corrected by explicitly describing the treatment of data as done in this study. Despite apparent discrepancy of the predicted values, the result of this study supports Smith's (2016) conclusion that some extinct species of *Alca* were over 1 kg in body mass, and adds another example of a large species in *Uria*.

This large size of a fossil alcid deserves discussion, because there seems to be a common belief that the largest body mass attainable by a volant wing-propelled diving bird is about 1 kg, or near the size of Recent species of *Uria* or *Alca* (Storer, 1960; Elliot *et al.*, 2013). A similar idea had been proposed by Meunier (1951; also cited in Guillemette and Ouellet, 2005), who claimed that Recent *U. [aalge] albionis* is close to flightless condition because of its high wing loading (~2.0 g/cm^2) and that the likely "critical" upper limit of wing loading for a volant bird is 2.5 g/cm^2. Although it is theoretically conceivable that as an bird increases size while retaining the same proportion the minimal power required for sustained flight increases to eventually reach the maximal power available, it is not clear at which point this takes place (Pennycuick, 1987). Later empirical studies (Humphrey and Livezey, 1982; Livezey and Humphrey, 1986) confirmed that the upper limit of wing loading of 2.5 g/cm^2

TABLE 5. Results of body mass estimation of fossil *Uria* and *Alca* from the length. Predicted value and corresponding 95% confidence (C.I.) and prediction (P.I.) intervals is shown for each species. Predictions were based on the model presented in text, and for *Alca* spp., humerus length data given by Smith (2016) were used. Estimates given for *Alca* spp. by Smith (2016) are shown for comparison.

Species	Estimate	C.I.	P.I.	Smith (2016)
Uria onoi	1479	1356–1612	1226–1783	—
A. ausonia	1638	1465–1794	1355–1979	1799
A. carolinensis	1498	1373–1634	1242–1807	1640
A. grandis	1144	1062–1233	954–1373	1239
A. minor	434	418–451	366–515	453
A. olsoni	1581	1445–1729	1309–1909	1734
A. stewarti	1904	1725–2101	1570–2309	2104

applies for steamer ducks *Tachyeres*, but this value might not be applicable to every bird species as shown by Guillemette and Ouellet (2005). In any way, the upper limit of body mass of 1 kg for a volant wing-propelled diving bird has no empirical or theoretical supports. The upper limit of body mass extrapolated simply by the absence of Recent volant alcid weighing more than 1 kg is not sustained when paleontological data are taken into account (Olson, 1985; Smith, 2016). Smith (2016) took a comprehensive analysis of body mass evolution in Alcidae and its relatives using both modern and fossil representatives. In the Pliocene Atlantic, six fossil species of *Alca* have been recorded (Olson and Rasmussen, 2001; Smith and Clarke, 2011), most of which are larger than Recent *A. torda* and one species (*A. stewarti*) was estimated to had weighed as much as 2104 g (Smith, 2016). Importantly, these large species does not possess osteological features associated with flightlessness which appear in two distinct lineages of flightless alcids, *Pinguinus* and Mancallinae (Smith, 2011), in a convergent manner (Olson, 1985; Smith and Clarke, 2011), nor does *U. onoi* from Shiriya. Therefore, there is no positive evidence suggestive of flightlessness for those species, and their retention of flight ability would be a more parsimonious scenario. In summary, *U. onoi* from the Pleistocene North Pacific represents an upper part of the body mass spectrum currently not occupied by Recent volant alcids, so do large *Alca* spp. from the Pliocene North Atlantic, showing an interesting parallel pattern in these two lineages in different ocean basins and geological ages. Biological consequences of large size in those alcids would deserve further study.

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青森県尻屋地域の更新統より産出した2種のウミガラス類（鳥綱：ウミスズメ科）および1新種の記載と体重推定

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要旨：ウミガラス属*Uria*はウミスズメ科に属する翼推進性潜水鳥類の一群で，北半球の高緯度海域に分布する2種の現生種を含む．本論では青森県北東部尻屋地域の中部–上部更新統より産出した2種のウミガラス類，現生種*U. lomvia*および絶滅種*U. onoi*（新種）について報告する．*U. onoi*はほぼ完全な上腕骨を含む複数の単離した骨化石によりその存在が認められる大型種で，その大きさは現生のウミガラス類を大きく上回る．飛翔性のウミスズメ科鳥類における体重と上腕骨長のスケーリング式より推定される*U. onoi*の体重は約1.5キログラムで，先行研究による化石オオハシウミガラス類*Alca*の推定体重と同様，一般に知られる飛翔性の翼推進性潜水鳥類の体重の「上限」約1キログラムを上回っている．これらの例はウミスズメ科の2つの系統で独立に大型種の進化と絶滅が起こったことを示している．

キーワード：更新世，ウミスズメ科，ウミガラス属，生物地理，体重推定