A shelduck coracoid (Aves: Anseriformes: *Tadorna*) from the arid early Pleistocene of the Qinghai-Tibetan Plateau, China

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ABSTRACT

An avian coracoid from the early Pleistocene Qigequan Formation in the Qaidam Basin, Qinghai Province, China, in the northern part of the Qinghai-Tibetan Plateau represents one of the few avian fossils from the region. The specimen is from an individual of a shelduck (*Tadorna* sp.), and its phylogenetic position is supported by the presence of a procoracoid notch (where the procoracoid foramen is greatly reduced) and other osteological characters. The previous hypothesis of extreme aridity in the Qaidam Basin during the early Pleistocene is lessened by the presence of a shelduck (along with the fossil record of proboscideans) that is part of a clade that occurs and breeds on the arid Qinghai-Tibetan Plateau today. In addition, the occurrence of Chinese shelducks in arid environments today likely evolved in combination with the increase in elevation and intensifying aridity in the plateau region since the early Pleistocene.

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INTRODUCTION

The Tibetan region has long been an area of study because of its high elevation and related cold climate. The uplift of the Qinghai-Tibetan Plateau, in combination with the glacial-interglacial climatic shifts of the Pleistocene, is thought to have driven speciation and the origin of many Tibetan endemic species (e.g., Lei et al., 2014). The biota on the Qinghai-Tibetan Plateau today includes endemic birds and artiodactyls, and has been hypothesized as the center of origin for some cold climate adapted mammals (e.g., Deng et al., 2011) and some avian taxa (Lei et al., 2014) that have spread
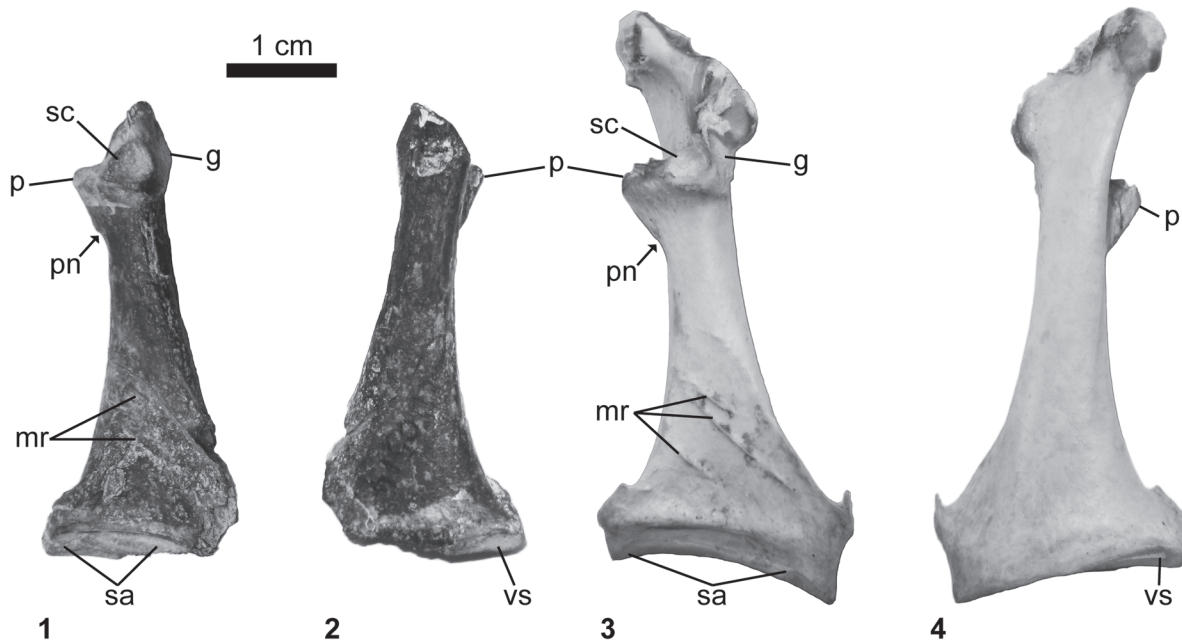
FIGURE 1. Comparison of the fossil *Tadorna* sp. (IVPP V20114) in **1** and **2**, and the coracoid of *Tadorna ferruginea* (IVPP OV1745) in **3** and **4**. **1** and **3** are in dorsal view, and **2** and **4** are in ventral view. Abbreviations: g-glenoid; mr-muscular ridges; p-procoracoid process; pn-procoracoid notch; sa-sternal articulation; sc-scapular cotyle; and vs-ventral sternal articulation.

to lower elevation environments during past periods of climate change. However, hypotheses of the timing of clade divergences, as well as any taxon's past presence in those montane regions (i.e., Pleistocene refugia), largely are not derived from the sparse fossil (avian and mammalian) record in the region. Occupation of such high elevations and arid environments has led to the evolution of morphological and molecular adaptations among the organisms there. For example, late Cenozoic aridification on the Qinghai-Tibetan Plateau has been hypothesized to have led to the evolution of thick-boned cyprinid fish (Chang et al., 2008). Within birds, several species of waterfowl, including the South American tadornine *Chloephaga melanoptera*, that live at such high elevations are known to have evolved convergent modifications to their hemoglobin as an adaptation to the lowered oxygen levels present at those altitudes (e.g., McCracken et al., 2009, 2010). Furthermore, the Ground Tit (*Pseudopodoces humilis*) that lives across the Tibetan Plateau exhibits evolutionary changes to its cardiac function that are thought to be modifications for high altitude life (Cai et al., 2013). Documentation of fossil vertebrates at high elevation is relatively rare, limiting the detailed

study of vertebrate evolution (including tempo) and adaptations to those environments.

In general, the fossil record of vertebrates is poorly known from the Qinghai-Tibetan Plateau (Wang et al., 2013, 2014), and the known avian fossils from the region are restricted to a lost trackway from the Oligocene or early Miocene (Xing et al., 2013), late Miocene eggshell fragments initially referred to as *Struthio*, and a coracoid initially identified as *Anas* sp. (misspelled as "*Ana* sp." in Wang et al., 2007, p. 374; Figure 1). The eggshell fragments previously published as *Struthio* are not from *Struthio camelus*, but possibly are referrable to the paleognath ootaxon *Struthiolithus*. That eggshell is currently under study along with other Neogene eggshell from across China. A re-examination of the waterfowl specimen (see below) demonstrates that while it is an anatid, it is not a member of *Anas*. Instead, it appears to belong to another anatid clade; allied to the species in *Tadorna*. That specimen comes from the Qaidam Basin in the northern Qinghai-Tibetan Plateau, China (Figures 2, 3), and it was deposited during a period of increasing aridity and is among the few fossil bird specimens known from the Tibetan Plateau.
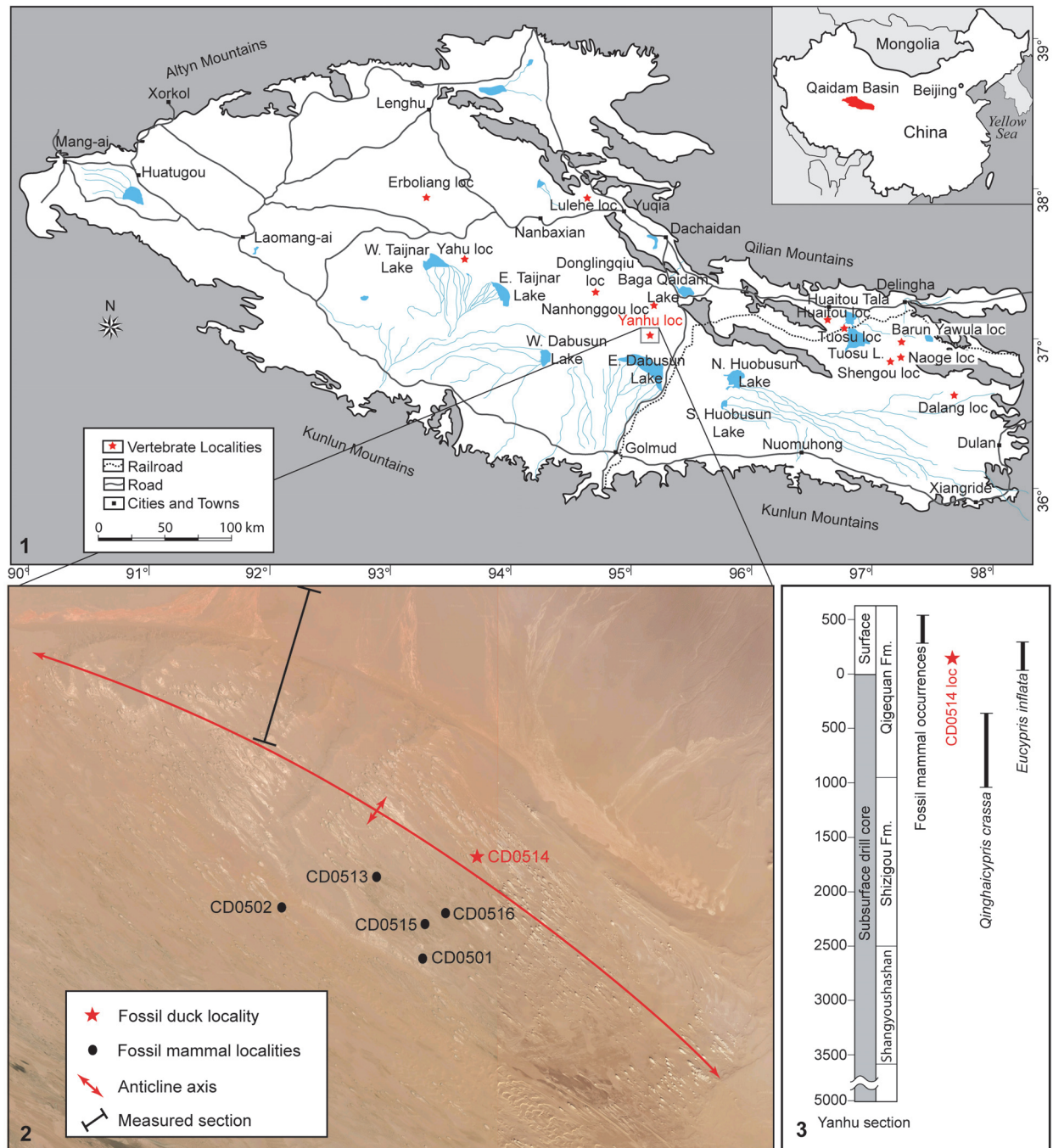
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FIGURE 2. 1 map of Qaidam Basin showing major areas of vertebrate fossil-producing localities (modified from Wang et al., 2007, figure 1). **2** satellite image of the Yanhu Anticline showing the location of the fossil bird locality (CD0514) and other fossil mammal localities. **3** stratigraphic occurrences of vertebrate and ostracod fossils. Yanhu surface and drill sections, as well as ostracod occurrences, are based on unpublished data of Sun Zhencheng, archived in the China University of Petroleum.

Members of the Tadornini include extant and extinct species on all continents except Antarctica and are known as fossils back into the late Oligocene and early and middle Miocene (e.g., Olson, 1985; Alvarez and Olson, 1978; Worthy and Pledge, 2007; Worthy et al., 2007; Worthy, 2009; Zelenkov, 2013). The extant genera of Tadornini include *Tadorna*, *Cyanochen*, *Alopochen*, *Chloephaga*, and *Neochen* (e.g., Livezey, 1997). Worthy and Lee (2007) discuss the oldest potential

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FIGURE 3. Photograph of the Yanhu Anticline exposures. The wind-eroded exposures are mostly oriented along the prevailing winter northwesterly winds, roughly coinciding with the axis of the anticline. Person in foreground for scale (photo by Xiaoming Wang).

records of the Tadornini, including *Miotadorna* in the early-middle Miocene of New Zealand (Worthy et al., 2007), and Worthy (2009) described *Australotadorna* from the late Oligocene of Australia. The shelducks (species in the genus *Tadorna*) are composed of seven species of extant birds that occur across the Old World (including the possibly extinct Crested Shelduck, *Tadorna cristata*, from eastern Asia) (Livezey, 1997). The phylogenetic relationships among the members of Tadornini vary depending on the taxonomic composition of the species sampled and the data used (osteological vs. molecular), but they indicate that the species of *Tadorna* are closely related to *Alopochen* and *Chloephaga* within Tadornini (Donne-Goussé et al., 2002; Worthy and Lee, 2008; Worthy, 2009; Fulton et al., 2012). The placement of *Miotadorna* within the crown clade of Tadornini constrains the origin of that clade to at least the early or middle Miocene (Worthy and Lee, 2008; Worthy, 2009), and that result is consistent with molecular clock estimates for the timing of Tadornini diversification (Fulton et al., 2012).

There are several Neogene records of specimens of *Tadorna* and other potential Tadornini/*Tadorna* fossils in the Miocene and Pliocene of Asia. Kurochkin (1985) described tadornine bones from the late Pliocene of the Transbaikal area of Russia (Asia), Zelenkov and Martynovich (2013) reported tadornine bones from the early-middle Miocene of Baikal, and Zelenkov and Kurochkin (2011) mention middle Miocene *Tadorna* specimens from Mongolia. In addition, there is a scapula that may belong to Tadornini from the middle Miocene of Thailand (Cheneval et al., 1991). Furthermore, Zelenkov (2013) discussed the evolution of the tadornine birds in Asia and potential role of aridification in their geographic and temporal distribution during the Neogene. He suggests that aridification might be the cause of the absence of Tadornini in the latest Miocene deposits in Eurasia (Zelenkov, 2013). With the known fossil record, it appears that the shelduck group was present across large parts of Asia in the Miocene and Pliocene. Thus, their past presence in Qinghai-Tibetan Plateau is not unexpected given Tadornini fossil records in adjacent areas and the occurrence of species of *Tadorna* on the plateau today (MacKinnon and Phillipps, 2000; Lang et al., 2007; Yang et al., 2009; Li et al., 2010). The age of this Qaidam fossil falls within the early Pleistocene, a time that overlaps with the hypothesized temporal origin of some of the Tibetan endemic mammalian and avian lineages (Lei et al., 2014), in addition to one hypothesized speciation event within the crown group of *Tadorna* (e.g., *Tadorna tadornoides* vs. *T. ferruginea* + *T. cana*; Fulton et al., 2012). The description below uses the osteological terminology of Baumel and Witmer (1993) with English equivalents of the Latin terms.

SYSTEMATIC PALEONTOLOGY

AVES Linnaeus, 1758
ANSERIFORMES Wagler, 1831
ANATIDAE Leach, 1820
TADORNINI Reichenbach, 1849-1850
TADORNA sp. Boie, 1822

Material. IVPP V20114 (Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, China) is a partial right coracoid collected by Xiaoming Wang on August 5, 2005 (Figure 1).

Locality and Horizon. The specimen is from IVPP locality CD0514 (N37°13'32.8" E95°11'08.3" elevation 2,791 ± 5.1 m), near the axis of the Yanhu Anticline, central Qaidam Basin, Qinghai Province, China (Figures 2, 3). It is from the Qigequan Formation and is early Pleistocene in age based on biochronology of ostracods and subsurface records in petroleum geologic explorations (Figure 2.3). Specifically, occurrences of the ostracod species *Qinghaicypris crassa* and *Eucypris inflata* below and above CD0514, respectively, are characteristic of basal Quaternary strata in central and eastern Qaidam Basin and have been calibrated to span the Matuyama magnetochron (C2r.1r-C2r.2r), that ranges between 1.945 and 2.581 Ma (Sun et al., 1995; Yang et al., 1997; Hilgen et al., 2012). Wang and coauthors (2007) state that only astragali of an "antelope-sized" artiodactyl were found nearby (at localities CD0501 and CD0502), but enamel fragments of a gomphothere proboscidean also were found in the Yanhu anticline region (CD0515 locality; see Figure 2). Those Pleistocene proboscidean fossils have not been mentioned previously in the literature. Unfortunately, mammalian records are too fragmentary to be of help in age determination.

Specimen Description. The preserved bone is dark brown to black in color, and much of the bone surface is worn with many small bone flakes missing. The coracoid is broken just cranial to the scapular cotyle on the dorsal surface, and the area ventral to the scapular cotyle is missing. The lateral sternal corner is broken, and much of the sternal articulation surface is missing. The craniocaudal length of the specimen is 41.5 mm. The bone surface is not 'spongy', and therefore the morphology and the specimen's size likely represent that of an adult individual (e.g., Watanabe and Matsuoka, 2013).

The scapular cotyle is a deep cup located near the lateral edge of the bone (Figure 1). The tip of the procoracoid is broken away leaving a blunt triangular process. There is no procoracoid foramen. However, there is a slight notch at the caudal base of the procoracoid and no evidence of an ossified ligament in the area (Worthy and Lee, 2008, character 42; Figure 1). Only the caudal end of the glenoid is preserved and is localized to the lateral surface of the bone. Caudal to the scapular cotyle, there are several subparallel muscular ridges on the dorsal surface that are oriented roughly at 45 degrees to the long axis of the bone. The dorsal area just cranial to the sternal articulation is slightly concave and does not have any pneumatic foramina (Worthy and Lee, 2008, character 47). The ventral surface of the caudal end of the coracoid is relatively flat (Worthy and Lee, 2008, character 48). The medial sternal articulation on the ventral surface does not extend above the adjacent areas of bone (Worthy and Lee, 2008, character 49). The dorsal surface of the preserved portion of the sternal articulation extends to the broken caudolateral edge. The medial edge of the coracoid shaft exhibits a low ridge extending from caudal to the base of the procoracoid to the level of the muscular ridges. The cranial tip of the preserved bone in the supracoracoideus fossa is slightly concave suggesting that the area below the glenoid was excavated (Worthy and Lee, 2008, character 46).

Taxonomic Comparisons. The presence of the procoracoid foramen is a crown group bird plesiomorphy, and its absence is a derived state found among some crown anatids (and convergently in other avian crown clades) (e.g., Mayr and Clarke, 2003). The reduction/absence of the procoracoid foramen (to a notch) in this Qinghai specimen supports its position within Anatidae since that foramen is present in the outgroups to Anatidae (within Anseriformes), but some anatids including some individuals and species from *Anser*, *Branta*, and *Cygnus* have a procoracoid foramen or notch formed by ossified ligaments (appendix 1 of Worthy and Lee, 2008, character 42). The absence of a pneumatic foramen on the dorsal sternal end of the coracoid is a derived character among *Presbyornis* + Anatidae (Worthy and Lee, 2008, character 47) and reinforces the identification of the fossil as an anatoid anseriform. Worthy and Lee (2008) mention that species of *Tadorna* exhibit at least a slight notch at the base of the procoracoid (not associated with ossified ligaments), as in this fossil (Figure 1). That particular morphology (character state) appears to be present only among species and individuals of *Tadorna* (a putative synapomorphy of the group), and it is reportedly absent in their close relatives *Alopochen* and *Chloephaga* (appendix 1 and data matrix from Worthy and Lee, 2008). While

the depth, and even presence, of that notch may vary across individuals of *Tadorna*, the clear presence of the character state in this Qinghai fossil and among specimens of *Tadorna* supports their taxonomic placement together to the exclusion of other taxa that never exhibit the trait. The absence of a concave area on the ventral surface cranial to the sternal articulation (appendix 1 and data matrix from Worthy and Lee, 2008, character 48) eliminates *Dendrocygna, Stictonetta, Thalassornis,* most species of *Oxyura, Malacorhnychus, Plectropterus, Mionetta, Manuherikia,* and *Nettapus* (Worthy and Lee, 2008) as potential taxonomic affiliations for this fossil given its flat ventral surface. The ventral articular facet with the sternum is not a distinct raised facet elevated above the adjacent coracoid (Worthy and Lee, 2008, character 49), but exhibits an articulation nearly identical to that in *Tadorna ferruginea* (IVPP OV1745). That absence means that the Qaidam fossil is inconsistent with the character states in *Dendrocygna, Thalassornis, Biziura, Nettapus, Cereopsis, Branta, Anser, Cygnus, Alopochen, Chloephaga,* and *Miotadorna* (appendix 1 and data matrix from Worthy and Lee, 2008). The concavity below the glenoid in the supracoracoideus fossa (Worthy and Lee, 2008, character 46) is a homoplastic character among anatids and varies even within some genera (e.g., *Miotadorna* and *Tadorna*; appendix 1 and data matrix from Worthy and Lee, 2008). Thus, its utility for aiding in identification of this fossil specimen is limited. However, its presence in this fossil specimen eliminates *Tadorna radjah* (appendix 1 and data matrix from Worthy and Lee, 2008) as a possible identification. The fossil also shares size and subtle morphological features that are difficult to define with *Tadorna*. Among those features, the morphology, position, and size of the ridge on the medial side of the coracoid shaft, the relative position and size of the muscular ridge area, the morphology and size of the dorsal surface of the sternal articulation, and the position of the scapular cotyle are all extremely similar to those present in *Tadorna ferriginea* (IVPP OV1745).

Given those combinations of traits and their phylogenetic distribution, many anatid genera, can be excluded from consideration. The presence of the procoracoid notch (not associated with ossified ligaments) in this Qaidam specimen, however, points to allocation of this fossil among the species of *Tadorna*. Worthy and Lee (2008, appendix 1) mention a potentially homologous procoracoid notch (formed by ossified ligaments) also being present sometimes in specimens of *Cygnus*

(swans) and some geese. However, those taxa are larger bodied as adults than the individual who produced IVPP V20114, and those larger birds also have a different state for Worthy and Lee's (2008) character 49 (above) than what is present in this fossil. Additionally, the absence of the notched procoracoid character in most anatid taxa and the close outgroups to *Tadorna* (e.g., *Alopochen*) would seem to indicate that the notches are instead analogous, and that the notch in *Tadorna* (not formed by a ligament) could be a distinct synapomorphy (appendix 1 and data matrix from Worthy and Lee, 2008). That notch character has not been reported from species allocated to *Anas*, even though species in that grouping share many of the above phylogenetic character states with this fossil (appendix 1 and data matrix from Worthy and Lee, 2008); thus, the prior assignment to *Anas* is rejected.

Livezey (1997) did not include any coracoid characters in his analysis of shelduck phylogeny, and the more recent work by Worthy (e.g., Worthy, 2009) has not focused on interspecific relationships within genera. Analyses of Tadornini phylogeny have given different results depending on the data analysed and the taxonomic composition of the analyses (e.g., Worthy, 2009; Fulton et al., 2012). In some studies, the species of *Tadorna* form a clade, and in other studies *Alopochen* is placed within the *Tadorna* group (Worthy, 2009). Thus, the combination of the fragmentary nature of the Qaidam specimen and the current knowledge of the phylogenetic distribution of coracoid characters limits the resolution of this specimen's taxonomic allocation. The Qaidam fossil appears to be from a non-*Alopochen*, non-*Chloephaga* tadornine based on the data available (i.e., *Tadorna*), and IVPP V20114 is nearly identical to extant species of *Tadorna* (Figure 1). In particular, the specimen is nearly equal in size to that of *Tadorna ferruginea* (IVPP OV1745), a species present on the Qinghai-Tibet Plateau today with a body mass averaging ~1.1 to 1.3 kg (larger than most species of *Anas;* Dunning, 2008). While this coracoid may belong to an extant species, it also is possible that it derives from a currently unknown extinct species. The data present in the specimen do not support a species level identification, and we refrain from attempting to over-identify the specimen.

DISCUSSION

There are several lakes in the Qaidam Basin today (Figure 2), and the paleontological and geological record demonstrates that lakes (freshwater,

brackish, and saline) were present in the basin extending back into the Miocene (Wang et al., 2007; Chang et al., 2008; Yang et al., 2013; Mischke et al., 2010; Madsen et al., 2014). Despite the presence of Neogene and Quaternary lacustrine deposits in the Qaidam Basin, its geological and paleontological record indicates a long-term trend towards aridification that may correlate with the uplift of the Qinghai-Tibetan Plateau (e.g., Chang et al., 2008), and the basin is currently quite arid (see Figures 2.2 and 3 for images of the Yanhu Anticline). That aridification is seen in pollen records (Wu et al., 2011), in the increase in gypsum deposits, and the absence of fish faunas in the Pleistocene Qigequan Formation (Chang et al., 2008), but fish fossils have been reported in younger sediments elsewhere in the Qaidam Basin (Mischke et al., 2010). Other changes are present in lacustrine and paleontological records in the basin (e.g., Yang et al., 2013, Wu et al., 2011, Cai et al., 2012), and overall they indicate a significant shift to drier climates near 2.5 or 2.6 Ma, with additional (stepwise) aridity through the Pleistocene. Cai and others (2012) state that the vegetation in the western part of the basin during the same time interval when the shelduck fossil was deposited was a period with decreasing tree diversity, increasing shrubs and herbs, was cooler than the time before ~2.6 Ma, and is considered by them to be classified as steppe desert. The age of this shelduck fossil is within Stage 2 of the core studied by Yang and others (2013) that appears to be climatically arid, but wetter than during the younger Pleistocene time intervals. The basin also has been argued to have been drier than present before 1.8 Ma, but climatic changes after ~1.8 Ma appear to have been increasingly arid (Zhuang et al., 2014; Li et al., 2014).

Palynological data from the Yanhu (Yahu in their usage) Anticline suggest a shift to drier climates near ~2.6 Ma that is nearly coincident with a change in ostracod faunas to a slightly brackish species (i.e., *Qinghaicypris crassa*) (Wu et al., 2011). That shift detected near 2.6 Ma is consistent across the basin with other records supporting an increase in regional aridity (e.g., Cai et al., 2012). However, the Yanhu Anticline data (Wu et al., 2011) show botanical variability through the time interval when the shelduck fossil was deposited (their Stage III) with increases and decreases in various plant taxa, and a short lived burst of coniferous trees near 2.0 Ma that likely indicates past climatic variability through that time interval.

Two species of *Tadorna* (i.e., *T. ferruginea* and *T. tadorna*) occur in the Qinghai-Tibet Plateau region today (and other parts of China and the world), and the Ruddy Shelduck (*T. ferruginea*) also can be locally common there (Cheng, 1987; MacKinnon and Phillips, 2000; Lang et al., 2007; Brazil, 2009; Li et al., 2010). Species of *Tadorna* occur in a wide variety of habitats across the Old World (MacKinnon and Phillips, 2000), but their occupation of high elevation arid habitats is restricted to Asia. Therefore, the past occurrence of shelducks during the early Pleistocene in the Qaidam Basin likely would indicate (and is consistent with) the past presence of aquatic habitats (open water or marsh/reedy habitat), although Chinese Ruddy Shelduck populations inhabit more terrestrial habitats during the winter outside of the plateau (Luo et al., 2013). The Common Shelduck (*T. tadorna*) also is known to occupy brackish and saline bodies of water (e.g., MacKinnon and Phillips, 2000), and both Chinese shelduck species will associate with water bodies in arid areas, but they are not restricted to that habitat (Cheng, 1987; Brazil, 2009). However, that habitat inference is consistent with the occurrence of ostracods in the Qigequan Formation.

Furthermore, brackish or saline water conditions in arid landscapes are within the realized niches of the two extant Chinese species of shelduck and likely those tolerances were present in individuals of those species in the deep past, although those (arid) habitats have not been posited previously for the Miocene and Pliocene fossils of this clade. The age range of the Qinghai *Tadorna* fossil (1.945 – 2.581 Ma: the magnetochron's length) includes many glacial and interglacial cycles (Pillans and Gilbert, 2012) across a background of increasing regional aridity, and we cannot constrain during which particular climate regime this individual was present in the Qaidam Basin. Additionally, we cannot assume that the current occupation of the Qinghai-Tibetan Plateau by shelducks in the spring and summer seasons (with their migration to lower elevations in winter; Luo et al., 2013) occurred during the early Pleistocene. This individual may have been a resident (i.e., nonmigratory) or perhaps even only spent the winter in the basin. However, the presence of this adult shelduck individual at a minimum indicates the very likely past presence of both dietary items (such as invertebrates and plants) and aquatic habitats used by shelducks in the Qaidam Basin at one point in the early Pleistocene. Furthermore, it is possible that shelducks have inhabited this

region continuously from the early Pleistocene to the present, but they also might have been absent during the hypothesized hyper arid intervals after 1.8 Ma, only returning later when large, possibly freshwater lakes were present in the basin (e.g., Mischke et al., 2010, Madsen et al., 2014). While Li and others (2014) state that large mammals (such as elephants, rhinoceroses, and giraffes) are absent from Quaternary deposits in the basin (as an indicator of faunal change in response to the climatic/vegetational shifts), the presence of gomphothere tooth fragments in the Yanhu Anticline (see above and Figure 2), demonstrates that proboscideans actually occurred in the basin during those early Pleistocene arid climates (contra Li et al., 2014). In combination with this *Tadorna* specimen, it would appear that the (vertebrate) faunal response to increasing aridity may have been more gradual than currently appreciated or that the interpreted level of aridity may not have been as extreme at that time.

Obviously, the late Cenozoic diversity of birds in Qinghai-Tibetan Plateau must have been higher than the current fossil record suggests (i.e., a turkey-sized bird, a large paleognath, and an anatid), but the Qaidam vertebrate fossil record dominated by mammals and fish (e.g., Wang et al., 2007) will require more research effort in order to expose more avian fossils and to derive the evolutionary and biogeographic data only hinted at by published molecular analyses. However, this anatid fossil from the northern Qinghai-Tibetan Plateau suggests that some birds, along with many mammal groups, that currently inhabit the high elevations of the Qinghai-Tibet Plateau may have a long history in the region extending at least into the early part of the glacial-interglacial cycles and increasing aridity of the Pleistocene. Their dispersal, speciation, and local adaptation at those high altitudes may have proceeded on pace with the changes in climate and elevation that occurred across the plateau, and over a long period of geologic time rather than the result of more recent post-glacial dispersals. The occurrence (and perhaps even preference) of some shelduck species for arid habitats also may have evolved during the climatic change associated with the uplift of the Qinghai-Tibetan Plateau.

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