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Prehistoric intercontinental dispersals are often used to explain the modern geographic distributions of various organisms, including birds. The extant Holarctic avifauna formed largely in the Neogene, and thus dispersals of various taxa during the Miocene likely have had a strong long-lasting effect upon the geographical pattern of the extant avian communities. However, the uneven fossil record of Neogene birds prevents accurate reconstruction of the biogeographic history of many bird clades, and the present evidence on dispersal of birds in the Neogene among continents is very limited. Past dispersals are most likely to be documented by taxa that are well represented in the fossil record, including diving ducks. Although these birds have a rather substantial fossil record in Europe and Asia, they remain very poorly known from the Neogene of North America. Here we document a new species of Miocene diving duck represented by a proximal humerus and a distal tibiotarsus from the Esmeralda Formation in Nevada (USA) and describe it as a new species of the primitive diving duck genus *Protomelanitta* Zelenkov (*Protomelanitta bakeri* sp. nov.), previously known only from the middle Miocene of Mongolia. Both species (from Mongolia and Nevada) are from the *ca* 11–12 Ma age range during the warm (though cooling) middle Miocene after the Middle Miocene Climatic Optimum and Middle Miocene Climate Transition. Given their proposed close relationship, it appears that *Protomelanitta* dispersed between Asia and North America, and this instance is the first clear indication of an aquatic bird dispersal between North America and Eurasia in the middle Miocene. This palaeobiogeographical event predates the famous immigration of *Hipparion* horses to the Old World and the late Miocene dispersals between continental Eurasian and North American faunas in general, but likely reflects one prolonged faunal interchange related to global climatic conditions and its effects.

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THE present geographic distribution of animals may be explained by various factors. Within one continent, ecological and climatic factors play a dominant role, whereas the distribution of taxa among continents may be at least partly influenced by historical factors. Although (volant) birds have great dispersal abilities, there are numerous examples that demonstrate that various taxa inhabited different territories in the deep past, as compared with their modern ranges. For example, bizarre South American hoatzin (Opisthocomiformes) likely immigrated to South America from Africa (Mayr *et al.* 2011, Mayr & De Pietri 2014), and the entire European Paleogene avifauna shows close affinities with the present-day South American avifauna (Mourer-Chauviré 1999, Mayr 2009).

The modern Holarctic avifauna largely formed in the Neogene (reviewed by Zelenkov 2014, 2016), thus dispersals of various taxa in the Miocene might have had a strong effect upon the geographical pattern of the extant avian communities. However, the palaeobiogeography of Neogene birds of the Northern Hemisphere remains poorly known, mostly because the vast majority of the Miocene and Pliocene birds described from disparate localities of remote regions of Eurasia and North America have not been compared reciprocally. Nevertheless, isolated finds indicate that episodes of avifaunal interchange did occur between Eurasia and North America during the Neogene. For example, Alvarez & Olson (1978) reported an unidentified shelduck (Tadorninae) from the earliest middle Miocene of North America, and Feduccia & Voorhies (1992) described an extinct species of the crowned crane (*Balearica*) from the late Miocene of Nebraska. Both shelducks and crowned cranes are now completely absent in North America. In addition, Zelenkov & Kurochkin (2012) reported the

presence of longspurs (*Calcarius*) in the late Pliocene of Mongolia, which are known from North America since the early Pliocene (Emslie 2007). These records are important but scarce, and data on other geographically widespread taxa are required to formulate a picture of the avifaunal interchanges between Eurasia and North America in the Miocene (paralleling that known for mammals). One of the best groups to study past dispersals is diving ducks, which have a reasonable fossil record, and usually broad geographic distributions.

Diving ducks are a non-monophyletic grouping that includes extant members of the clades Oxyurini (stiff-tailed ducks), Mergini (sea ducks and mergansers) and Aythyini (pochards), and they occur in aquatic environments around the globe. These groups have fossil records that extend into the Miocene and late Oligocene, indicating separate parallel radiations occurred among these different lineages through the Miocene. Each of these individual diving duck clades has undergone convergent evolution that is in large part related to foot propelled diving and the reduction in skeletal pneumaticity (e.g., O'Connor 2004). The exact timing of these individual evolutionary radiations among diving ducks is not known, but the oldest fossils are from the late Oligocene (basal Oxyurinae; Worthy 2009). However, the fossil record demonstrates that diving ducks dispersed around the world during the Miocene (e.g., Cheneval 1987, Livezey & Martin 1988, Worthy & Lee 2008, Worthy 2009, Zelenkov 2011, 2012a, 2012b, 2016, Stidham & Hilton 2016). This ecological evolution of a diving morphology was not restricted to the three extant clades, but also was present among unrelated extinct anatids, such as the Miocene *Cayaoa* from South America (Noriega *et al*. 2008). Overall, the fossil record demonstrates that the evolutionary road to diving specialization in waterfowl was filled with homoplasy, but that a diving lifestyle has been successful (in terms of biodiversity with many fossil and extant diving duck species) since the late Oligocene.

Despite the broader fossil record displaying such diversity, diving ducks are poorly known, both in terms of taxa and the amount of fossil material from the Miocene of North America, when compared with the fossil record of Asia, Australia/New Zealand and Europe, where several species have been described from several lineages (Kurochkin 1985, Cheneval 1987, Livezey & Martin 1988, Worthy & Lee 2008, Worthy 2009, Zelenkov 2011, 2012a, 2012b). At present, the North American record includes the early merganser *Mergus miscellus* (Alvarez & Olson 1978) from Virginia, the sea duck *Ocyplonessa shotwelli* (referred to *Histrionicus* by Olson & Rasmussen 2001) from Oregon (Brodkorb 1961; see Becker 1987a), material allocated to *Aythya* from North Carolina (Olson & Rasmussen 2001), the recently described stem stiff-tailed duck *Lavadytis* (Stidham & Hilton 2016), and *Oxyura* and *Aythya* specimens from the latest Miocene or Pliocene of Florida (Becker 1987b). *Dendrochen robusta* from the middle

Miocene of South Dakota (Miller 1944) has been hypothesized to be a relative of diving ducks (Livezey & Martin 1988), but that phylogenetic position has not been confirmed. Despite that sparse record, representatives of all three extant diving duck clades are known in the North American Miocene. Adding to that diversity, a previously unpublished proximal humerus collected over 100 years ago in Nevada represents a new species of diving duck that appears closely related to two taxa published from similar aged sediments in Mongolia (*Nogusunna* and *Protomelanitta*), and it is particularly similar to *Protomelanitta gracilis*, originally described as a probable primitive member of Mergini (Zelenkov 2011).

The presence of *Protomelanitta* in both Asia and North America suggests that at least some generic-level diving duck clades dispersed widely during the warm Miocene, and that the currently poor fossil record from North America might not be representative of the actual past diversity of waterfowl during that time. This same time period of the middle to late Miocene is well known for mammalian dispersal among the Northern Hemisphere continents (e.g., Kimura 2013, Flynn *et al*. 2014), and biogeographic linkages between North America and Asia among the avian fauna are, thus, not unexpected.

Institutional abbreviations. EK, personal collection of Evgeny Kurochkin stored at PIN; MNHN, Muséum national d'Histoire naturelle, Paris, France; NMNH, National Museum of Natural History, Washington, D.C., USA; PIN, Borissiak Paleontological Institute, Moscow, Russia; UCMP, University of California Museum of Paleontology, Berkeley, California, USA.

Osteological terminology follows Baumel & Witmer (1993) with English equivalents of many of the Latin terms used.

Systematic palaeontology

This published work and the nomenclatural act it contains have been registered in Zoobank: http://zoo bank.org/References/FC7C3A12-C3C9-43B6-AA4F-5B 082E7B5A72

Order ANSERIFORMES Wagler, 1831
Family ANATIDAE Leach, 1820

Protomelanitta Zelenkov, 2011

Protomelanitta bakeri sp. nov.
LSID. urn:lsid:zoobank.org:act: 663BB3AC-56D4-494C-BB07-00374B70BC5C

Holotype. UCMP 31460 is a proximal left humerus.

Etymology. Named in honor of Charles Lawrence Baker who was the lead on UCMP fossil collecting in Nevada (including this holotype and referred specimen) during 1911 and 1912.
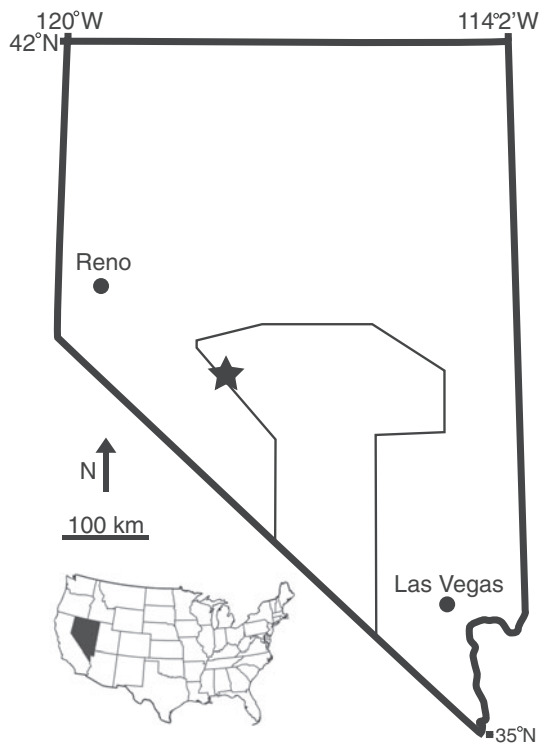
Fig. 1. Map of the United States with detail of the fossil locality within Nevada. Location of UCMP locality 2024 (Ione Valley 15) starred within Nevada (inside outline of Nye County).

Type locality and age. The holotype (and tentatively referred specimen) is from UCMP locality 2024 (Ione Valley 15) from the Esmeralda Formation in the Cedar Mountain area of Nye County, south-central Nevada (Fig. 1). It was collected in 1912 by a UCMP party (composed of Charles Lawrence Baker and John P. Buwalda). The mammals known from the locality include *Paracamelus* (UCMP 11627), *Merycodus furcatus* (UCMP 19807), *Pliauchenia* (UCMP 22294), *Procamelus* (UCMP 22295), *Aleurodon* (UCMP 61179), *Tomarctus* (UCMP 61186) and horses (Equidae). The last appearance of *Tomarctus* is in the late Clarendonian North American Land Mammal Age (NALMA), and the Clarendonian NALMA portion of the Esmeralda Formation is considered to be equivalent to Clarendonian 1 and 2 (Tedford *et al.* 2004). That biostratigraphic position would place the holotype fossil (at most) between *ca* 10 and 12.5 Ma in age (Hilgen *et al.* 2012), but likely closer to the middle portion of that age range.

Diagnosis. The new taxon differs from all Anatinae, except most representatives of the diving duck clades (Aythyini, Mergini and Oxyurinae) in the presence of a closed, non-pneumatic ventral pneumotricipital fossa, a notch in the proximal outline of the humerus between the humeral head and ventral tubercle, and a dorsally flattened deltopectoral crest. It differs from the genera of Mergini in having a short and moderate caudally protruding dorsal tubercle and the new taxon differs from crown-group Oxyurinae (*sensu* Worthy & Lee 2008) in

lacking a markedly reduced crus dorsale of the ventral pneumotricipital fossa. In addition, the distinctly non-concave dorsal surface of the deltopectoral crest distinguishes *Protomelanitta bakeri* from the primitive fossil members of Oxyurinae, and the extant *Thalassornis* and *Biziura*. *Protomelanitta bakeri* further differs from *Oxyura* and most specimens of species in *Aythya* by having a reduced, but present, capital shaft ridge. The presence of the non-pneumatic ('closed') ventral pneumotricipital fossa also distinguishes the new taxon from species of *Netta*, and the extinct *Aythya shihuibas* from the late Miocene of China (Stidham 2015). This new species is smaller than the older *Dendrochen robusta*, but similar in size to the coeval Mongolian taxa *Nogusunna conflictoides* and *Protomelanitta gracilis* (Tables 1, 2). It differs from *Nogusunna conflictoides* in that the capital shaft ridge in *Protomelanitta bakeri* ends adjacent to the dorsal tubercle, as in *P. gracilis*. Additionally, in *Protomelanitta bakeri*, the dorsal crus of the ventral pneumotricipital fossa is shorter (proximodistally) than in *Nogusunna conflictoides*, and the humeral head is proximodistally narrow and has a straight distal margin in caudal view. *Protomelanitta bakeri* differs from *P. gracilis* in its flatter fossa between the capital shaft ridge and the dorsal crus of the ventral pneumotricipital fossa, in addition to its smaller dorsal tubercle.

Tentatively referred material. UCMP 31461 is a distal left tibiotarsus from the same locality.

Description. The proximal humerus (holotype) is broken through the distal end of the bicipital crest and deltopectoral crest (Fig. 2). The dorsoventral depth of the specimen is 15.3 mm (Table 1). The ventral tubercle is partly damaged. The capital incisure can be seen in cranial view (Fig. 2B). The transverse ligamental groove is short and restricted to the area cranial to the ventral tubercle. The dorsal pneumotricipital fossa undercuts the head, and there is a dorsoventral line of foramina under the head. In the capital incisure, there is a small concave area on the ventral surface adjacent to the ventral tubercle. The deltopectoral crest is nearly flat dorsally (anconally). The proximal end of the dorsal tubercle makes a notch in the proximal humeral outline (as in *Protomelanitta gracilis* and *Nogusunna*). Its distal end is raised slightly, but is similar to the extent in specimens of *Aythya*. The dorsal tubercle is sub-triangular and is

Species/specimen	Proximal width
Protomelanitta bakeri UCMP 31460	15.3
Protomelanitta gracilis PIN 4869/151	14.8
Nogusunna conflictoides PIN 4869/197	14.9
Sharganetta mongolica PIN 4869/195	15.7
Dendrochen robusta UCMP 37364	20.6
'*Aythya*' *chauvirae* MNHN SA 10275	14.8

Table 1. Maximum dorsoventral width of the proximal end of the humerus in several Miocene diving ducks, in millimetres.

not considerably elongated proximodistally (Fig. 2A). Much of the surface of the bone is worn, not smooth. The proximal latissimus dorsi scar is preserved, and it is just proximal to the broken edge of the bone. There appears to be a weak capital shaft ridge, and it is directed towards the dorsal tubercle. The ventral pneumotricipital fossa has a bony wall inside, but several tiny foramina pierce it. It is not the open pneumatic fossa of the primitive state among diving ducks. The small fossa on the caudal ventral surface of the bicipital crest is dorsoventrally wider than some other taxa and bears a foramen. The area between the weak capital shaft ridge and the dorsal crus of the ventral pneumotricipital fossa is moderately concave.

The referred specimen (UCMP 31461) is broken distal to the fibular crest (Fig. 3A) and is 28.4 mm long. There is a deep concave fossa lateral to the supratendinal bridge (shared with the specimen referred to *P. gracilis*; Fig. 3B). The groove for the m. fibularis ('peroneus' groove) is on a lateral projection that abuts the proximal end of the lateral extensor retinaculum attachment with its distal end. The medial extensor retinaculum attachment does not overhang the extensor sulcus, but its distal end is medial to the proximal part of the supratendinal bridge (not entirely proximal to the bridge). The lateral condyle extends proximal to the medial condyle. The proximal end of the medial condyle has a lateral twist to it, and the medial condyle is less mediolaterally wide than the lateral condyle. There are two linear depressions in the intercondylar space. The medial epicondyle is quite large and visible cranially. There is a notch present in the distal end of the medial condylar rim. The lateral surface of the lateral condyle is relatively flat to slightly concave. The tibial cartilage articulation has a slightly convex area in the middle that is not a ridge, but the articular surface is not completely concave.

Comparisons. Among Miocene diving ducks, the new taxon is most similar to *Protomelanitta gracilis* and *Nogusunna conflictoides* from the late middle Miocene of Mongolia, and agrees with the former in the general outlines of the humeral head and ventral pneumotricipital fossa, and also in the fact that the capital shaft ridge is oriented towards the dorsal tubercle (Fig. 2). The position of the proximal latissimus dorsi scar in the new species is more distally positioned than the state among the extant species of *Aythya* and the extinct *Sharganetta*, and overall is more similar to that in *Nogunsunna conflictoides*. However, *Nogusunna* differs from *Protomelanitta* in that it has a well-pronounced capital shaft ridge that is oriented between the dorsal tubercle and humeral head, and a curved distal margin of the humeral head (Fig. 2E; Zelenkov 2011), similar to *Mionetta*. The most characteristic feature of both *Protomelanitta gracilis* and *P. bakeri* is the straight distal margin of the humeral head in caudal view, which has not been described for any other fossil duck (Fig. 2A, C), but

occurs in extant *Oxyura*. Our investigation of the osteology of modern ducks revealed no profound individual variation in this character. Additionally, *Protomelanitta bakeri* and *P. gracilis* share a dorsally widened transverse ligament groove (Fig. 2B, D). However, *Protomelanitta bakeri* can be distinguished easily from the Mongolian species by a smaller and more dorsally (anconally) oriented dorsal tubercle, which normally shows little individual variation in modern ducks. Additionally, the dorsal pneumotricipital fossa is more concave in *P. bakeri*, in contrast to the nearly flat state in *P. gracilis*. It should be noted, however, that the exact degree of concavity of the fossa in *P. gracilis* is not clear because the adjacent portion of the shaft is broken off in the holotype and only known proximal humerus of the Mongolian taxon.

Zelenkov (2011) described one distal tibiotarsus from the middle Miocene of Mongolia that was not assigned to a particular genus. This specimen (PIN 4869/222) agrees in size and morphology with the tibiotarsus from the Esmeralda Formation (Fig. 3; Table 2), so we hypothesize that it might belong to *Protomelanitta gracilis*. Both fossil tibiotarsi share the fossa on the lateral side of the supratendinal bridge, and similar overall proportions and morphologies (Fig. 3). Among the undescribed materials from the Sharga locality in Mongolia are two other morphologies of tibiotarsi that apparently can be allocated to *Nogusunna* and *Sharganetta* (NVZ, unpublished data), and those specimens differ from the Nevada tibiotarsus in their somewhat larger size (alleged *Sharganetta*) and narrower intercondylar incisure (alleged *Nogusunna*).

The new taxon differs from the coeval Mongolian *Sharganetta mongolica* by its more robust and somewhat ventrally displaced ventral tubercle (in *Sharganetta* and *Mionetta*, this tubercle is positioned roughly at the dorsoventral midpoint of the ventral pneumotricipital fossa), notably lowered and distally elongated dorsal tubercle, and a humeral head that does not overhang the dorsal pneumotricipital fossa in caudal view (see Zelenkov 2011).

Mionetta is known mostly from the latest Oligocene and early Miocene (see Mlíkovský 2002, Zelenkov 2012a), but has also been reported from the middle to late Miocene (Noriega 1995, Göhlich 2002), temporally overlapping with the new species described above. *Mionetta* has a notably elevated and very short dorsal tubercle, a more concave dorsal surface of the deltopectoral crest, a dorsally shifted ventral tubercle (that is positioned near the dorsoventral midpoint of the ventral pneumotricipital fossa, as in *Sharganetta*) and a strongly pronounced capital shaft ridge that all differ from the morphology in the new taxon.

'*Aythya*' *chauvirae* from the middle Miocene of Sansan (France) is similar to the new species in size (Table 1) and is known from several postcranial bones, including one proximal humerus (Cheneval 1987). '*Aythya*' *chauvirae* is interpreted to be a member of
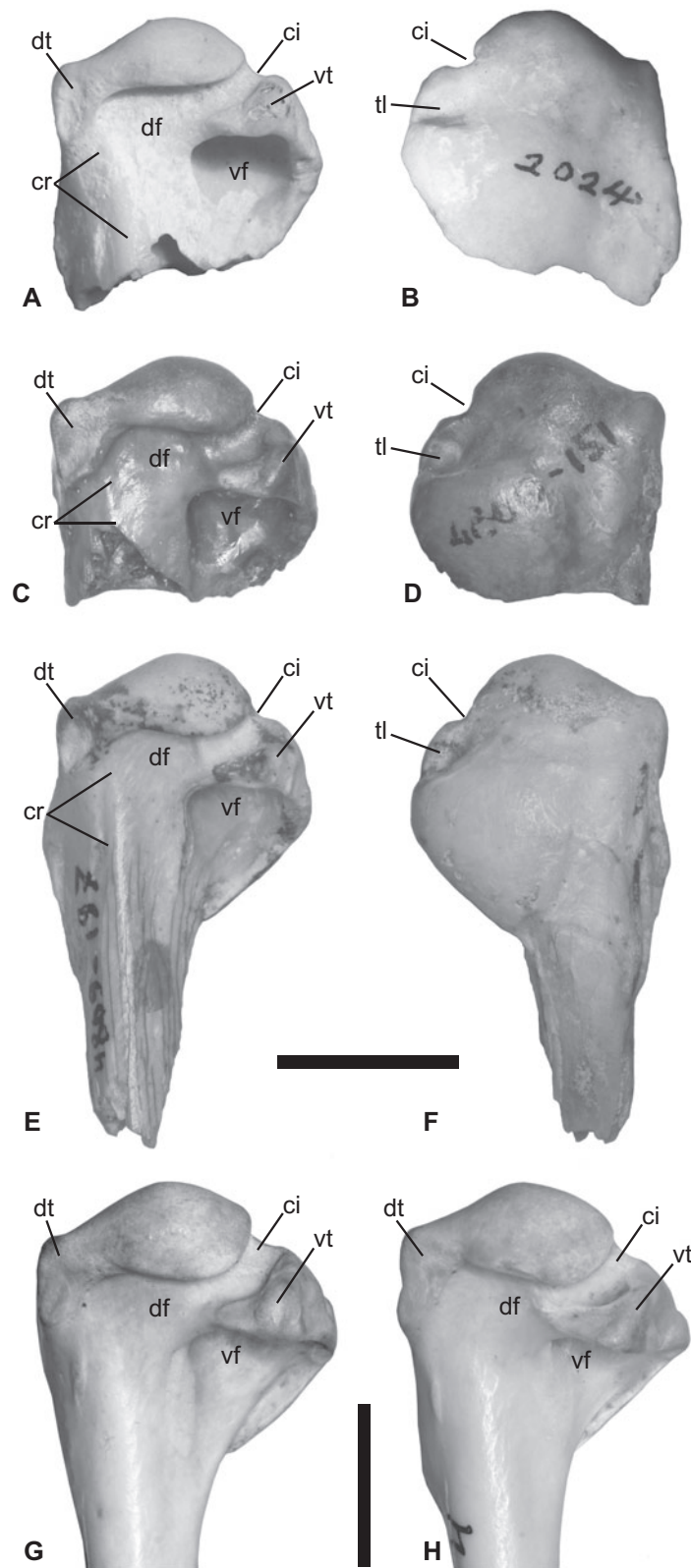
Fig. 2. Proximal left humeri of fossil and extant diving ducks. *Protomelanitta bakeri* holotype UCMP 31460 in **A**, caudal and **B**, cranial views. *Protomelanitta gracilis* PIN4869/151 in **C**, caudal and **D**, cranial views. *Nogusunna conflictoides* PIN 4869/197 in **E**, caudal and **F**, cranial views. *Aythya marila* EK 40–69-2 in **G**, caudal view. *Clangula hyemalis* EK 41–7-4 in **H**, caudal view. Scale bar = 10 mm. (Note panels **G** and **H** are at a slightly different scale.) Abbreviations: ci, capital incisure; cr, capital shaft ridge; df, dorsal pneumotricipital fossa; dt, dorsal tubercle; tl, transverse ligament furrow; vf, ventral pneumotricipital fossa; vt, ventral tubercle.
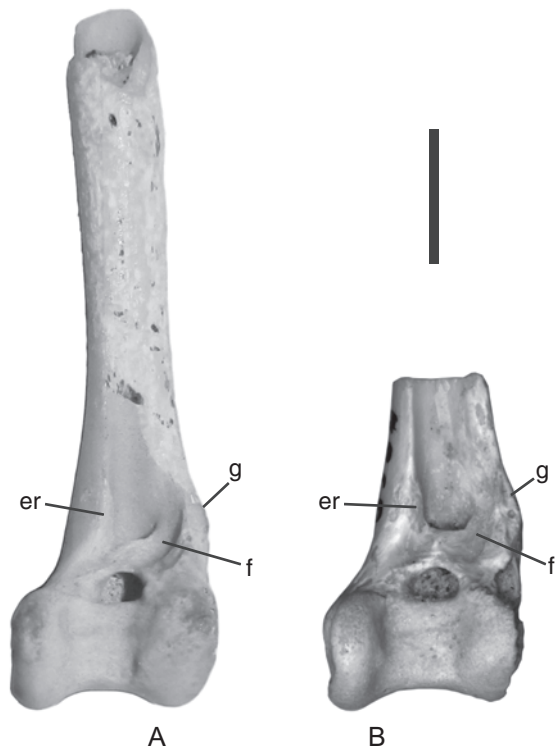
Fig. 3. Distal tibiotarsi referred to *Protomelanitta* in cranial view. **A**, UCMP 31461 referred to *Protomelanitta bakeri*. **B**, PIN 4869/222 referred to *Protomelanitta gracilis*. Scale bar = 5 mm. Abbreviations: er, extensor retinaculum; f, fossa (on the medial side of the supratendinal bridge); g, groove for m. tibialis.

Oxyurinae (Worthy *et al.* 2007, Worthy 2008). However, it should be compared with the diversity of Mongolian diving ducks (Zelenkov 2012a), given that some taxa of waterbirds (including ducks) had a wide distribution across Eurasia during the middle Miocene (Zelenkov 2013, 2015, 2016). The only known proximal humerus of 'Aythya' chauvirae has a markedly asymmetrical humeral head in caudal view (as in *Mionetta*) and, thus, clearly differs from *Protomelanitta*.

Two other diving ducks have been described from the middle Miocene of North America. *Ocyplonessa shotwelli* is known from remains of a tarsometatarsus and carpometacarpus from the Clarendonian NALMA of Oregon (Brodkorb 1961; see Becker 1987a). That species is morphologically similar to the extant *Histrionicus histrionicus*, and was even placed within this genus by Olson & Rasmussen (2001), who noted only minor differences from the extant Harlequin Duck. The

new species is unlikely to represent the same taxon because the Nevada humerus has a much more primitive morphology. In *Histrionicus*, the dorsal tubercle is very elongate, low, and distally directed, the humeral head has a distinctly different outline in distal view (with an angled dorsal half), and the dorsal pneumotricipital fossa is wider than in *Protomelanitta* and most other primitive ducks (e.g., *Mionetta*, *Nogusunna* and *Sharganetta*).

The other described middle Miocene North American diving duck is the merganser *Mergus miscellus* (Alvarez & Olson 1978), known from a series of hind limb bones and the pelvis from the older (Langhian; see Carnevale & Godfrey 2014) Calvert Formation of Virginia. This species was a fairly large bird (the size of the extant *Mergus serrator*), and is larger than the new taxon (Table 2). *Mergus miscellus* shares an apparently derived morphology of the tarsometatarsus with extant species in *Mergus*, but the fossil retains a presumably primitive structure of the pelvis, like that in extant *Mergellus* (Alvarez & Olson 1978). However, the new species of *Protomelanitta* differs markedly from both *Mergellus* and *Mergus*, which both have notably elongated dorsal tubercles (a characteristic of many modern lineages of ducks; see Zelenkov 2012a) and an asymmetrical (as in *Histrionicus*) humeral head. *Mergus* (along with the closely related *Lophodytes*) is unique among other diving ducks in that it possesses a pneumatized ventral pneumotricipital fossa, and *Mergellus* has deep dorsal pneumotricipital fossa.

Protomelanitta bakeri also differs from the recently described (Stidham & Hilton 2016) *Lavadytis pyrenae* from the middle Miocene of Nevada. That older species (allocated to Oxyurinae *sensu* Worthy & Lee 2008) has a closed ventral pneumotricipital fossa like that in *Protomelanitta*, but lacks a capital shaft ridge (as in extant *Oxyura*, but not *Protomelanitta* and *Nogusunna*).

Discussion

Extant diving ducks and their fossil relatives constitute a polyphyletic group of waterfowl whose apparent morphological similarities are most likely the result of convergent evolution of diving adaptations (Worthy & Lee 2008). Many of the adaptive changes in diving ducks are present in the hindlimb (as the propulsive mechanism), and thus accurate identification of lineages that diverged early in this group often is possible on the

Taxon/specimen	Distal width	Distal depth
Protomelanitta bakeri UCMP 31461	7.8	7.6
Protomelanitta gracilis PIN4869/222	7.7*	7.5*
Dendrochen robusta UCMP 37372	10.7	10.1
Dendrochen robusta UCMP 37373	10.3	9.7
Mergus miscellus NMNH 237150	8.8	–

Table 2. Measurements of the distal tibiotarsus in several Miocene diving ducks, in millimetres.
*Measurements in *Protomelanitta gracilis* are estimated.

basis of skeletal elements not strictly related to diving specialization, that were slower to evolve (e.g., the humerus). Given the morphology of the humerus in the new taxon, it can not be placed within Aythyini. The new taxon lacks the more proximal position of the latissimus dorsi scar found among Aythyini, in addition to other characters discussed above. *Protomelanitta bakeri* also has a capital shaft ridge unlike most species in *Oxyura*. Zelenkov (2011) originally proposed that *Protomelanitta* might be a member of Mergini, and he hypothesized that another coeval and morphologically similar taxon *Nogusunna* might be related to Oxyurinae (but not as a derived member of that group) or to 'Cairinini'. The similarities between the new taxon and *Protomelanitta gracilis* (and *Nogusunna conflictoides* to a lesser degree) strongly suggest that the new taxon and *Protomelanitta gracilis* are each other's closest relatives, hence their placement in the same genus. However, their placement within any specific diving duck clade is not clearly indicated, and they could be primitive members of Oxyurinae or another closely related group.

The evidence of mammalian interchange between North America and Asia during the middle and late Miocene is well known. For example, multiple dispersal events between North America and Asia have been hypothesized for one clade of sciurid rodents (Kimura 2013) in the late Clarendonian NALMA, and leporids are constrained to have dispersed from North America to Asia just after 8 Ma (Flynn *et al.* 2014). Another well-known and biochronologically very important dispersal event is the first occurrence of the *Hipparion* horses in the Old World which took place slightly before 11 Ma (Vangengeim *et al.* 2006, Wang *et al.* 2013). However, similar dispersal events have not been demonstrated to the same degree among birds, using the fossil record. Some faunal similarities between Asia and North America have been suggested, but mostly for the terminal Miocene. Crowned cranes (*Balearica*) are present in the late Miocene of North America (Feduccia & Voorhies 1992), and the genus is known from Europe since the early Miocene (Mourer-Chauviré 2001). Furthermore, Zelenkov (2012b) concluded that the late Miocene North American anseriform taxon *Branta woolfendeni* is a junior synonym of the coeval *Bonibernicla ponderosa* from Mongolia (Zelenkov 2012b). Zelenkov & Kurochkin (2015) further supposed that some of the bones from the latest Miocene of Mongolia, referred to *Anser liskunae*, might indeed belong to *A. arenosus*, a taxon initially described from the latest Miocene of North America (Bickart 1990).

The current age estimate for the Sharga locality (holotype locality of *Protomelanitta gracilis* and *Nogusunna conflictoides*) is around 11–13 Ma (Zazhigin & Lopatin 2000; see Wang *et al.* 2013 for the age of the MN7+8 biozone), which is close to the estimate (ca 10–12.5 Ma) for the age range of the type locality of *Protomelanitta bakeri* (see above). The presence of *Protomelanitta bakeri* and *P. gracilis* (as likely sister

species) in Mongolia and Nevada both between 10 and 12.5 Ma suggests that there was an intercontinental dispersal of this clade. That fairly wide age constraint (near two million years) leaves open the possibility that the specimens of *Protomelanitta* represent a chronospecies, reflecting anagenetic change within the clade, but this suggestion should be tested with more data and additional specimens. The inferred avian dispersal obviously predates the dispersal of *Hipparion* horses from North America to the Old World (notably, *Hipparion* is missing in the fauna of the Mongolian locality Sharga), and this may be explained by the ability of waterbirds to cross large forested regions of Beringia, which were unsuitable for horses.

Many modern diving ducks are marine, or at least spend winters in marine habitats with the breeding season occurring in freshwater or brackish habitats (see Livezey 1995), and that ecology could have facilitated large-scale dispersals of diving ducks in the deep past. However, it should be noted that current palaeontological data indicate that diving ducks might have been more continental in the middle Miocene, and that some extant diving ducks (e.g., some species of stiff-tailed ducks) are present in freshwater or nearshore habitats year round (Johnsgard & Carbonell 1996). With the limited known distribution data for *Protomelanitta*, it could have had either seasonal distribution pattern. Zelenkov (2012a) reviewed the fossil record of Holarctic diving ducks and noticed that these birds are abundant in continental deposits of middle Miocene age and absent from the coeval marine assemblages. For example, diving ducks are absent in the marine middle Miocene Pungo Formation in North Carolina (USA) that has produced various marine birds (Olson & Rasmussen 2001), but diving ducks are present in many continental faunas of the same age in both North America and Eurasia (see reviews by Zelenkov 2012a, 2016). Thus, the currently observed association of diving ducks with marine habitats may have been established in the late Miocene, and it might have been triggered by the increase in ocean productivity and decrease in continental lake productivity inferred for this time (see Zelenkov 2012a). Earlier, Olson (1984) noted a significant increase in the diversity of marine birds in the late Miocene, and related it to increased marine productivity. *Nogunsunna* and *Protomelanitta* also come from continental deposits, and thus the species of *Protomelanitta* were parts of the continental faunas (i.e., not exclusively marine), although they might have wintered in marine environments. Furthermore, the high productivity among continental lakes during the middle Miocene, inferred from the diversity of Mongolian freshwater fishes (Sytchevskaya 1989), in combination with warmer (overall) climates, might have facilitated or allowed diving ducks to spend their winters on land.

No matter what the precise ecology of *Protomelanitta* was, the dispersal event of these aquatic birds

and the latter Old World occurrence of *Hipparion* horses may reflect one prolonged faunal interchange related to (overall warm) global climatic conditions. That time period was much warmer than today, but less warm than the Middle Miocene Climatic Optimum that occurred a few million years earlier (Zachos *et al.* 2001, Hilgen *et al.* 2012). Furthermore, the 11–12 Ma period has been hypothesized to include climatic changes (warming and cooling) after the Miocene Climatic Transition (and after the Middle Miocene Climatic Optimum) and to encompass the oxygen isotope zone Mi5 (one of several cooling events correlated with sea level decrease and ice volume increase during the Miocene) and related lowered sea levels hypothesized to have facilitated Beringian dispersal (Miller *et al.* 1991, Garcés *et al.* 1997, Jiang *et al.* 2008). The overall warmer climate (including at higher latitudes where potential land bridges are among the Holarctic continents) and hypothesized lower sea levels could have facilitated avian dispersal, just as it is thought to have aided mammalian immigration. As the knowledge of the Miocene waterfowl in North America increases, it is likely that other biogeographic links to Asia (and Europe) will be found, reinforcing the pattern already known among the contemporaneous Miocene mammals.

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