A New Duck from the Middle Miocene of Mongolia, with Comments on Miocene Evolution of Ducks

N. V. Zelenkov

Borissiak Paleontological Institute, Russian Academy of Sciences, Profsoyuznaya ul. 123, Moscow, 117997 Russia
e-mail: nzelen@paleo.ru
Received May 18, 2011

Abstract—A new relatively large duck, *Chenoanas deserta* gen. et sp. nov. from the Middle Miocene of the Sharga locality, which is morphologically intermediate between the extant genera *Chenonetta* and *Tachyeres*, is described. The diversity of Early and Middle Miocene ducks is discussed. It is noted that some Middle Miocene duck remains are incorrectly referred to the genus *Mionetta*. The distribution of morphological characters of the humerus in Neogene and extant ducks shows that the present day diversity of ducks apparently results from extinction of some taxa which were formed in the Oligocene—Early Miocene. The distribution of morphological characters in the evolution of diving ducks is evidence that not only the formation of different morphotypes but also so-called "evolutionary maturation" of taxa also explains the modern diversity.

Keywords: Anatidae, parallel evolution, Miocene, Mongolia

DOI: 10.1134/S0031030112050139

INTRODUCTION

The Middle Miocene Sharga locality is the richest Neogene locality of Mongolian birds (Zelenkov and Kurochkin, 2010; Zelenkov, 2011a). The order Anseriformes is presented in Sharga by geese (Anserinae), shelducks (Tadorninae), and ducks (Anatinae); the last include several genera, some of which are extinct (Zelenkov, 2011a, 2011b; Zelenkov and Kurochkin, 2012). Sharga has yielded both diving ducks (genera *Sharganetta, Nogusunna*, and *Protomelanitta*) and nondiving anatids referred to the extinct genus *Mioquerquedula* and extant genera *Anas* and *Aix* (Zelenkov and Kurochkin, 2012).

In addition to previously described anatid taxa, the material from the Sharga locality contains remains of one more relatively large duck, which is described below. This form is larger than all other Anatinae from this locality; it is intermediate in morphology between the extant genera *Chenonetta* and *Tachyeres* and regarded here as a new genus.

The anatomical nomenclature (see also Zelenkov and Kurochkin, 2012) used in the present study follows *Nomina Anatomica Avium* (Baumel et al., 1993) and, in some cases, Ballmann (1969). The taxonomy of anseriforms follows Livezey (1986), with some modification; in particular, stiff-tailed ducks and relatives are ranked subfamily, Oxyurinae (Worthy and Lee, 2008; Worthy, 2009). In the case of primitive Anatinae (Anatinae tribus inc. sedis sensu Livezey, 1986), the name "Cairinini" is used for simplification. Recent phylogenetic studies have shown that this group is nonmonophyletic (Eo et al., 2009; Gonzalez et al., 2009; Worthy, 2009; Bulgarella et al., 2010); however, relationships of particular genera remain incompletely understood. The material is housed in the Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow (PIN).

SYSTEMATIC PALEONTOLOGY

Order Anseriformes

Family Anatidae Leach, 1820

Subfamily Anatinae Leach, 1820

Genus *Chenoanas* Zelenkov, gen. nov.

E t y m o l o g y. From the extant duck genera *Chenonetta* and *Anas*.

T y p e   s p e c i e s. *Chenoanas deserta* sp. nov.

D i a g n o s i s. In caudal view, caput humeri at least twice higher than wide; distal edge of caput humeri slightly concave in dorsal part and overhanging somewhat fossa pneumotricipitalis dorsalis; in cranial view, incisura capitis forming distinct relatively shallow incisure in proximal margin of bone; tuberculum dorsale subtriangular, its proximal part raised and positioned at level of caput humeri, and distal part almost fused with caudal bone surface or only slightly raising above it; impressio coracobrachialis distinct; fossa pneumotricipitalis ventralis deep and well pneumatized, its foramen facing distocaudally; dorsal surface of crista deltopectoralis slightly concave; at level of crista bicipitalis, bone shaft triangular in section.

S p e c i e s   c o m p o s i t i o n. Type species.

C o m p a r i s o n. *Chenoanas* differs from *Dendrocygna* and *Thalassornis* in the subtriangular tuberculum dorsale, with somewhat lowered distal margin and slightly concave dorsal surface of the crista deltopectoralis. It differs from *Stictonetta* in the concave distal margin of the caput humeri and the subtriangular tuberculum dorsale lowered to the level of the caudal bone surface. It differs from Anserinae, Tadorninae, and *Chenonetta* in the caput humeri dorsoventrally extended in caudal view. In the Anserinae and Tadorninae, the caput humeri is less than twice as high as wide. In addition, it differs from *Chenonetta* in the caput humeri overhanging the fossa pneumotricipitalis dorsalis. It differs from *Callonetta* in the presence of a concave distal margin of the caput humeri, the presence of well-pronounced impressio coracobrachialis and subtriangular tuberculum dorsale.

It differs from living *Oxyura* and the extinct Miocene genera *Manuherikia, Dunstanetta*, and *Mionetta* in the pneumatized fossa pneumotricipitalis ventralis. It additionally differs from *Mionetta* and *Manuherikia* in the slightly concave dorsal surface of the crista deltopectoralis; from *Mionetta* in the slightly extended subtriangular tuberculum dorsale with somewhat lowered distal edge; and from *Dunstanetta* in the fact that the caput humeri overhangs the fossa pneumotricipitalis dorsalis (Worthy and Lee, 2008).

It differs from *Matanas* from the Lower Miocene of New Zealand (Worthy et al., 2007) in the poorly projecting tuberculum dorsale and well-pronounced incisure in the dorsocaudal margin of the caput humeri.

It differs from *Tachyeres, Oxyura*, and all Anatinae in the tuberculum ventrale virtually not hanging over the fossa pneumotricipitalis ventralis, due to which the opening of this fossa looks widely open and distocaudally directed. In *Tachyeres* and Anatinae, the tuberculum ventrale is massive and overhangs the fossa pneumotricipitalis ventralis, considerably limiting the size of the opening of this fossa; as a result, the opening faces mostly distally.

It additionally differs from Anatinae in the subtriangular tuberculum dorsale raised above the caudal bone surface and in the well-pronounced impressio coracobrachialis. In addition, *Chenoanas* differs from the tribes Mergini and Aythyini in the pneumatized fossa pneumotricipitalis ventralis and from Anatini and "Cairinini" in the shaft triangular in cross section at the level of the crista bicipitalis.

R e m a r k s. In addition to the proximal humeral fragments, the type locality has yielded a coracoid fragment which (specimen PIN, no. 4869/57) is assigned here to *Chenoanas* based on similar size and general similarity to primitive Anatinae. This coracoid is characterized by a strongly concave sulcus m. supracoracoideus and the tuber brachialis overhanging it. In addition, the processus acrocoracoideus of the specimen from Sharga deviates only slightly medially,

which is also characteristic of primitive Anatinae. In this character, the coracoid of *Chenoanas* clearly differs from coracoids assigned to the Miocene genus *Matanas* (Worthy et al., 2007).

Distinctive features of the humerus of *Chenoanas* are the pneumatized fossa pneumotricipitalis ventralis, the shaft triangular in cross section, and somewhat raised subtriangular tuberculum dorsale. The pneumatized fossa pneumotricipitalis ventralis is a primitive condition for the crown group of Anatidae (nonpneumatized fossa is characteristic of Eocene–Oligocene Romainvillinae: Mayr, 2009), which is recorded in Dendrocygninae, Anserinae, Tadorninae, and some Anatinae, i.e., Anatini and "Cairinini." The triangular cross section of the shaft is characteristic of Dendrocygninae, Tadorninae, some Anatinae (Mergini, Aythyini), and some extinct Oxyurinae (Worthy and Lee, 2008). The tuberculum dorsale of primitive ducks is rounded and distinctly raises above the caudal surface (for example, in Dendrocygninae and Oligocene–Miocene *Mionetta*). In Anatinae, this tubercle is strongly extended and lowered to the level of the caudal bone surface, while in Tadorninae and *Chenonetta*, it is intermediate in morphology.

Although *Chenoanas* is similar to Tadorninae in the structure of the tuberculum dorsale, the Tadorninae are characterized by the caput humeri extended in caudal view, while in *Chenoanas*, the humeral head is dorsoventrally extended, as in Anatinae. In the extant genera *Chenonetta* and *Callonetta*, the head is intermediate in morphology. The two genera are traditionally referred to Anatinae, but molecular data suggest that both (Sraml et al., 1996) or only *Callonetta* (Bulgarella et al., 2010) are close to Tadorninae. Cladistic analysis of morphological characters places the genus *Chenonetta* between Tadorninae and Anatinae (Worthy, 2009). *Chenonetta* actually has an expanded caput humeri and shaft triangular in section, which is characteristic of Tadorninae. In contrast to *Chenonetta, Chenoanas* has a humeral head typical for Anatinae and probably represents an intermediate state between Tadorninae and Anatinae. The presence of intermediate forms, such as *Chenonetta* and *Callonetta*, in the modern fauna suggest that distinct boundaries between these subfamilies are absent.

Among Anatinae, *Chenoanas* is most similar to South American *Tachyeres*, which is united based on molecular data with other South American ducks, such as *Amazonetta, Speculanas*, and *Lophonetta*, as a sister group of *Anas* (Bulgarella et al., 2010). *Chenoanas* is similar to *Tachyeres* in the presence of a subtriangular tuberculum dorsale raised somewhat above the bone surface and in the processus acrocoracoideus of the coracoid not deviating medially. Nevertheless, the triangular cross section of the shaft and position of the tuberculum ventrale are evidence that *Chenoanas* is more primitive than *Tachyeres*. In addition, *Chenoanas* differs from all Anatinae in the widely open fossa tricipitalis ventralis.
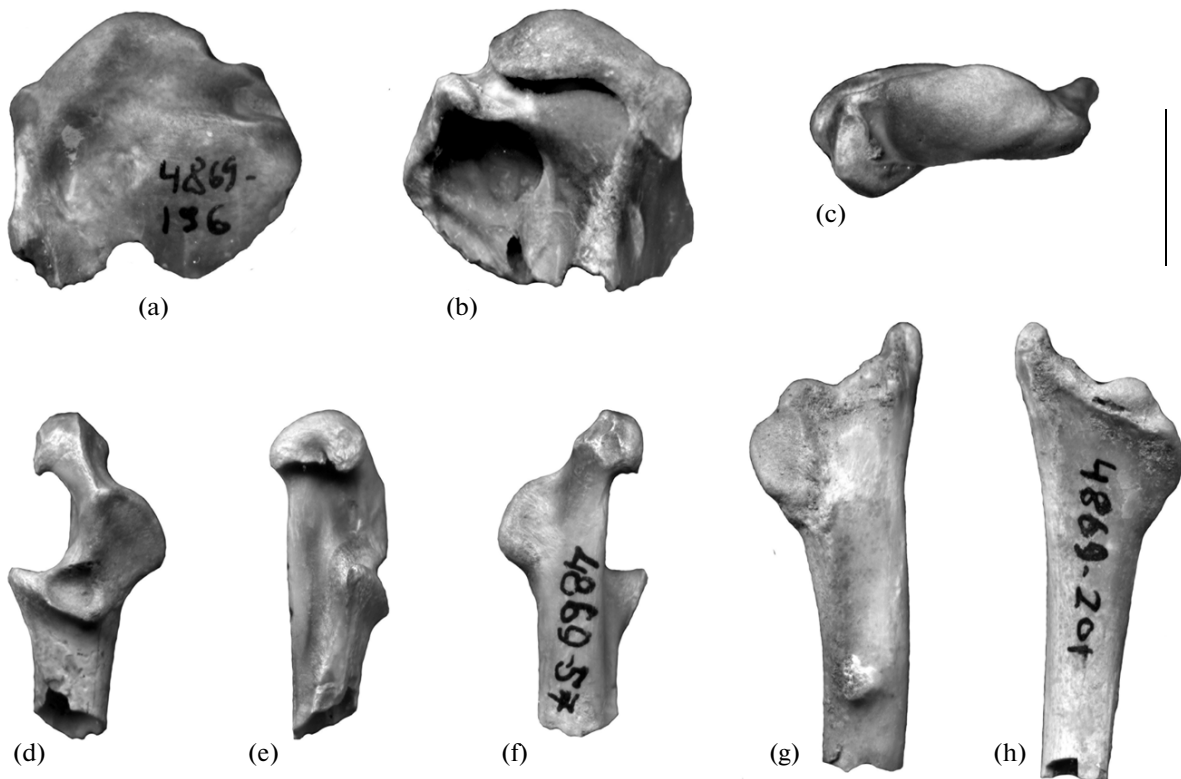
Fig. 1. *Chenoanas deserta* gen. et. sp. nov.: (a–c) holotype PIN, no. 4869/196, proximal fragment of the left humerus: (a) cranial, (b) caudal, and (c) proximal views; (d–f) specimen PIN, no. 4869/57, cranial fragment of the right coracoid: (d) dorsolateral, (e) medial, and (f) ventral Anatidae gen. indet.; (g, h) specimen PIN, no. 4869/201, cranial fragment of the left scapula: (g) lateral and (h) medial views. Scale bar, 1 cm.

Among extinct forms, *Chenoanas* is close to the Early Miocene genus *Matanas* from New Zealand and differs from it, along with the characters of the diagnosis, in the processus acrocoracoideus of the coracoid not deviating medially. *Matanas* is characterized by the projecting tuberculum dorsale (as in Tadorninae) and the caput humeri somewhat more widened in the caudal view, which is an undoubted primitive character. Among the nearest living relatives of *Matanas*, Worthy et al. (2007) indicated the genus *Chenonetta*, while *Chenoanas* is more advanced morphologically.

Anas sansaniensis Milne-Edwards, 1867 from the Middle Miocene of France and, presumably, the basal Upper Miocene of Austria (Cheneval, 1987; Göhlich, 2009) apparently belongs to *Chenoanas* or a closely related genus. The taxonomic position of this relatively large duck remains uncertain; Mlíkovský (2002) and Worthy (2008) proposed that it is hardly probable that this species belongs to the genus *Anas*. I agree with Worthy (2008) that the distal end of the tibiotarsus, which is designated as the lectotype of this species, does not provide characters distinguishing the genus *Anas* from a number of other duck genera. A new diagnosis of the species provided by Cheneval (1987, 2000) is based on a detailed comparison of *A. sansaniensis*

with species of the genus *Anas* and, hence, it is not informative if this species is placed beyond *Anas*. It seems plausible to regard *Anas sansaniensis* Milne-Edwards, 1868 as nomen dubium until this form is redescribed and its status is revised.

Chenoanas deserta Zelenkov, sp. nov.

E t y m o l o g y. From the Latin *desertus* (deserted).

H o l o t y p e. PIN, no. 4869/196, proximal fragment of right humerus; Mongolia, Gobi–Altai Aimag, Shargyn Govi, Sharga locality; terminal Middle Miocene, Oshin Formation.

D e s c r i p t i o n (Figs. 1, 2). A large duck, of the same size as living *Anas platyrhynchos*. The holotype is a well-preserved proximal end of the humerus, with the shaft base. The crista deltopectoralis is broken off in the middle and the crista bicipitalis is almost complete. See also the diagnosis of the genus.

M e a s u r e m e n t s in mm. Coracoid: length of cranial end from caudal edge of cotyla scapularis, 14.5; height of facies articularis humeralis, 5.9; width of shaft, 5.0. Humerus: width of proximal end, 19.4; height of caput humeri, 6.7.
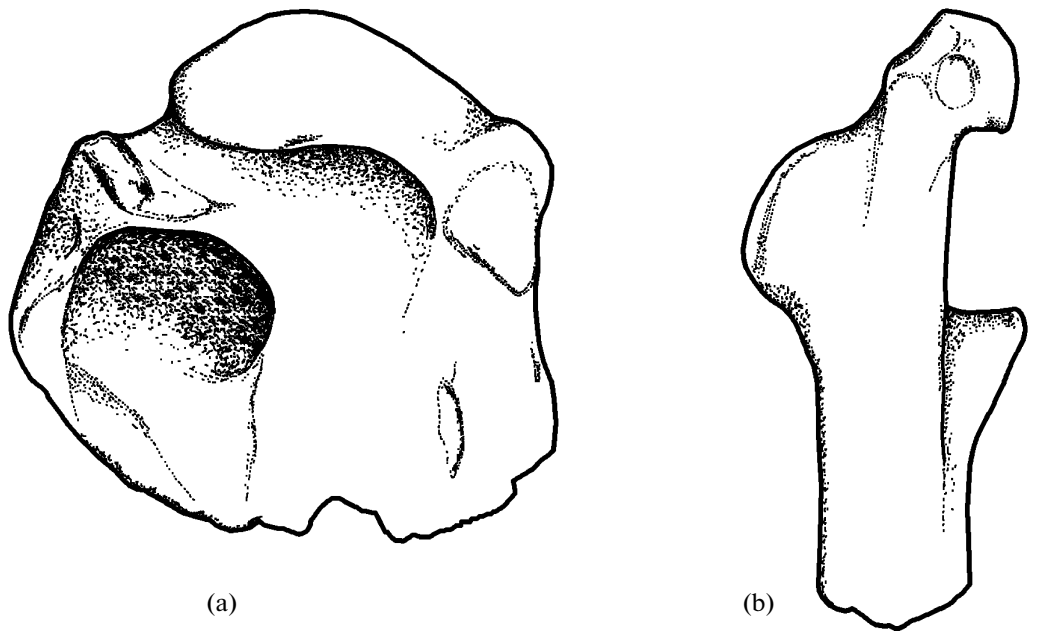
Fig. 2. *Chenoanas deserta* gen. et. sp. nov.: (a) holotype PIN, no. 4869/196, proximal fragment of the left humerus, caudal view; (b) specimen PIN, no. 4869/57, cranial fragment of the right coracoid, ventral view. Scale bar, 1 cm.

C o m p a r i s o n. The genus *Chenoanas* is monotypic.

M a t e r i a l. In addition to the holotype, specimen PIN, no. 4869/57, cranial fragment of the right coracoid from the type locality.

* * *

Anatidae gen. indet. The Sharga locality has also yielded two carpometacarpi (specimens PIN, nos. 4869/59, 205), which, judging from the relative size, could have belonged to *Chenoanas deserta* gen. et sp. nov. or *Aix praeclara* Zelenkov et Kurochkin, 2012; three coracoid fragments (specimens PIN, nos. 4869/18, 50, 51); a sternum fragment (specimen PIN, no. 4869/164); scapulae (specimens PIN, nos. 4869/9, 201); a radius fragment (specimen PIN, no. 4869/213); and a basal phalanx fragment of wing digit 1 (specimen PIN, no. 4869/98), which belonged to relatively large ducks. The two carpometacarpi differ morphologically: specimen PIN, no. 4869/59 has considerably deeper fossae on the ventral surface of the proximal end and a strongly developed fossa on the dorsal surface at the base of the os metacarpale alulare. The fossa on the dorsal surface of specimen PIN, no. 4869/205 is undeveloped, which occurs in *Anas*. It is impossible to assign with confidence these fragments to a certain taxon.

The coracoids (specimens PIN, nos. 4869/18, 50, 51) are similar in size to that of *Ch. deserta*, but differ from it in the elongated impressio lig. acrocoracohumeralis, the absence of a deep fossa in the cranial part of the sulcus supracoracoideus and, hence, the

tuber brachialis strongly overhanging it, and in the poorly pronounced caudal border of the cotyla scapularis and somewhat pointed facies articularis humeralis. This specimens apparently belong to a relatively large duck which is phylogenetically closer to extant *Anas* than to *Ch. deserta*. The presence in Sharga of one more large ducks, along with *Ch. deserta* and *Aix praeclara*, prevents reliable identification of fragments of the sternum, scapulae, radius, and phalanx, which are morphologically similar in various ducks. All of these fragments correspond in relative dimensions to the holotype of *Ch. deserta*.

Diversity of Early and Middle Miocene Ducks

To date, the Middle Miocene Sharga locality has yielded six duck genera and species (see also Zelenkov, 2011b; Zelenkov and Kurochkin, 2012): such a high generic diversity of ducks alone (not taking into account Anserinae and Tadorninae) is greater than in other Neogene localities with birds and expands considerably our knowledge of the evolution and diversity of ducks in the Early Neogene.

Undoubted anatids of the modern type (crown group of Anatidae) appeared in the fossil record in the Early Oligocene (Mayr and Smith, 2001). In the Late Oligocene, ducks are represented by the genera *Pinpanetta* Worthy, 2009 and *Australotadorna* Worthy, 2009 in Australia and the genus *Mionetta* Livezey et Martin, 1988 in France (Mourer-Chauviré et al., 2004; Worthy, 2009). The Anatidae of the modern type are also known in the Upper Oligocene of Kazakhstan and Argentina (Kurochkin, 1968; Agnolin, 2004); the

assignment of other Oligocene ducks (for example, Romainvillinae) to the crown group of Anatidae remains questionable (Mayr, 2009). Large Anatidae occurred in the Oligocene and Early Miocene; however, a review of geese (Anserinae) and other large anatids is beyond the scope of the present study.

The best known Early Miocene anatid genus *Mionetta* was established by Livezey and Martin (1988) for the duck *Anas blanchardi* Milne-Edwards, 1863, which is represented by abundant remains in the Saint-Gérand-le-Puy locality in France and a number of other Early Miocene localities of France, Germany, and Czechia. The species *A. consorbina* Milne-Edwards, 1867 from Saint-Gérand-le-Puy, which is distinguished from *A. blanchardi* by the somewhat larger size, and the small duck *A. natator* Milne-Edwards, 1867, which also comes from the Lower Miocene of France, Germany, and Czechia were referred to the genus *Mionetta*. It is sometimes proposed that *M. consorbina* is only represented by large individuals of *M. blanchardi* (Livezey and Martin, 1988; Mlíkovský, 2002); however, these species differ in morphology (Cheneval, 1983; Mourer-Chauviré, 2008). The taxonomic position of *M. natator* remains uncertain; a number of bones from Saint-Gérand-le-Puy assigned to this species may be incorrectly determined (Mlíkovský, 2002), while other specimens have not been revised. Outside Europe, the genus *Mionetta* has only been found in the Lower Miocene of Namibia (Mourer-Chauviré, 2008).

Although the genus *Mionetta* was repeatedly recorded in the Middle Miocene, some specimens are identified incorrectly; in particular, a humerus from the Credinta locality (Zone MN8) in Romania, which was assigned to *M. blanchardi*, demonstrates (judging from the figure) proportions that are not characteristic of *Mionetta* (thickened shaft and general shortening), much more massive caput humeri, and the epicondylus dorsalis projecting significantly dorsally (Kessler, 1992). A coracoid from the same locality differs from that of *Mionetta* from Saint-Gérand-le-Puy in the shape of the sulcus m. supracoracoideus and the inclined processus acrocoracoideus (in *Mionetta*, the processus acrocoracoideus extends parallel to the shaft). Heizmann and Hesse (1995) did not corroborate the presence of *Mionetta* in the Steinheim locality (Zone MN7) in Germany. The later Late Miocene and Pliocene European specimens (Mlíkovský, 2002) seem even more questionable. *Mionetta blanchardi* from the Sandelzhausen locality in southern Germany (Zone MN5) displays humeral morphology generally typical of this species, but differing in the unusual structure of the fossa pneumotricipitalis ventralis (Göhlich, 2002), which suggests that it could have belonged to a separate species. Judging from the structure of the humerus and coracoid, very small *M. natator* from the same locality should be referred to a separate genus, the relation of which to *Mionetta* is questionable (see below). *M. blanchardi* was also recorded in Zone MN5 of Czechia (Mlíkovský, 2003), although the paper did not contain figures of the bones. The find of *Mionetta* in Zone MN6 in Hungary (Gál et al., 2000) is very doubtful; the scapula from the Mátraszölös locality differs from that of *M. blanchardi* in the small tuber brachialis and the acromion projecting only slightly dorsally. It was proposed that "*Aythya*" *chauvirae* Cheneval, 1987 from the Middle Miocene (MN6) of France (Worthy et al., 2007; Worthy, 2008) should be referred to *Mionetta*, although it is likely related to one of primitive ducks from Sharga. Thus, to date, there is no reliable evidence of the presence of *Mionetta* in the deposits younger than Zone MN5. The disappearance of this genus from Europe at the Langhian−Serravalian boundary was possibly connected with a global fall in temperature at the end of the Langhian, 15−13.5 Ma (Flower and Kennett, 1994).

At present, it is generally accepted that *M. blanchardi* is phylogenetically close to the North American taxon *Dendrochen robusta* A. Miller, 1944, which was described based on a humerus from the Lower Miocene of South Dakota. Cheneval (1983) assigned *M. blanchardi* to the genus *Dendrochen* and attributed both species to the extant subfamily Dendrocygninae, one of the most primitive subfamilies of living anatids. Later, Livezey and Martin (1988) assigned the genera *Mionetta* and *Dendrochen* to a separate subfamily, Dendrocheninae, which they believed to be more advanced than Dendrocygninae, but more primitive than the extant Australian duck genus *Stictonetta*. Based on cladistic analysis of osteological characters, *Mionetta* was placed at the base of the oxyurine duck phylogenetic stem, which includes members of the extant subfamily Oxyurinae and *Stictonetta, Thalassornis, Malacorynchus*, and a number of extinct taxa (Worthy and Lee, 2008; Worthy, 2009). A presumable humerus of a member of Dendrocheninae (Oxyurinae sensu Worthy and Lee, 2008) was recorded in the Upper Miocene of Argentina (Noriega, 1995).

Cheneval (1987) proposed that a small duck, *Anas* ("*Querquedula*") *integra* A. Miller, 1944, from the Lower Miocene of South Dakota (United States) should be referred to the genus *Dendrochen*. Worthy and Lee (2008) also referred this taxon to the subfamily Oxyurinae sensu lato (see above). However, judging from the figure provided, the coracoid of "*Anas*" *integra* is closely similar to that of living *Anas*, while the coracoid of *M. blanchardi* strongly differs from that of dabbling ducks (see, e.g., Livezey and Martin, 1988). It is not improbable that North American *A. integra* and European *M. natator* belong to a different anatid genus (*?Mioquerquedula*), which is phylogenetically close to "Cairinini" or *Anas*; however, this conclusion requires an additional study.

A large duck, "*Anas*" *oligocaena* Tugarinov, 1940, from the Lower Miocene (originally Oligocene) of the Aral Region (for the age of this locality, see Lopatin, 2004) deserves particular attention. Mlíkovský and

Švec (1986) assigned this species to the genus *Dendrochen*. The holotype of *A. oligocaena* is a distal fragment of the humerus, the structure of which contradicts the assignment of this species to *Dendrochen* or affinity with *Mionetta*; at the same time, it suggests that this species is related to extant "Cairinini," in particular, the genus *Aix* (Zelenkov and Kurochkin, 2012). It is highly probable that *Matanas enrighti* Worthy et al., 2007 from the terminal Lower Miocene of New Zealand also belongs to this anatid lineage.

Early Miocene shelducks (Tadorninae) are represented by the genus *Miotadorna* Worthy et al., 2007 from New Zealand (Worthy et al., 2007). The taxonomic position of another duck species, *Anas luederitzensis* Lambrecht, 1929, which was described based on a proximal humeral fragment from the Lower Miocene of South Africa, remains uncertain (Worthy, 2008). The phylogenetic position of the Early Miocene duck *Cayaoa* Tonni et al., 1979 from Argentina (Noriega et al., 2008), which has lost ability to flight, is also uncertain; the humeral structure gives evidence that this taxon is rather primitive. One more primitive duck (genus *Ankonetta*) of uncertain phylogenetic position (combining characters of Dendrocygninae, Tadorninae, and Anserinae) has recently been described based on tarsometatarsal fragments from the Lower–Middle Miocene of Argentina (Cenizo and Agnolín, 2010).

Thus, at the Oligocene–Miocene boundary and in the Early Miocene, there were at least three anatid lineages: Oxyurinae, Tadorninae, and primitive Anatinae, the last are represented by *Matanas*, "*Anas*" *oligocaena*, and small ducks "*Mionetta*" *natator* and "*Anas*" *integra* (Table 1).

The existence in the Middle Miocene of Central Asia of Oxyurinae remains an open question. The extinct genera *Sharganetta* and *Nogusunna* from Sharga demonstrate certain similarity in humeral structure to primitive Oxyurinae, for example, *Manuherikia* (Zelenkov, 2011b). Although it is impossible to assign coracoids from Sharga to any genus known from this locality, all coracoids differ from that of *Oxyura* and *Manuherikia* and are more similar to coracoids of "Cairinini." On the other hand, members of Oxyurinae sensu Worthy and Lee, 2008 vary in coracoid structure (see, e.g., *Pinpanetta*). In my opinion, since *Sharganetta* and *Nogusunna* are more advanced than *Mionetta* in the majority of characters, they possibly represent a separate duck lineage, which, judging from the structure of coracoids from Sharga, are more closely related to Anatinae (Zelenkov, 2011b). The presence in Central Asia of ducks unrelated to Oxyurinae is also supported by the finding of "*Anas*" *oligocaena* in the Lower Miocene of Kazakhstan.

True Anatinae are represented in the Middle Miocene of Sharga by extinct members of the genera *Anas, Chenoanas* gen. nov., and *Mioquerquedula* Zelenkov et Kurochkin, 2012. *M. velox* and *A. sansaniensis* from Europe and, probably, a number of forms assigned to the genus *Anas* could have belonged to primitive Anatini. Precise phylogenetic position of *Chenoanas* remains uncertain; it is only possible to say that these ducks are more primitive in morphology than extant *Anas* and "Cairinini," to which they are similar in the pneumatized fossa pneumotricipitalis ventralis. *Chenoanas*, like the more ancient New Zealand genus *Matanas*, retains a number of features resembling primitive Tadorninae (Worthy et al., 2007; original data). More advanced "Cairinini" are known from the Middle Miocene of Sharga (*Aix praeclara*) and Upper Miocene of Czechia ("*Dendronessa*" sp.).

Remarks on the Evolution of Diving Ducks

The fossil record of diving ducks is remarkable. It is believed that, in the Early Miocene, the Oxyurinae were a dominant anatid group, the most primitive members of which (for example, the extinct genera *Mionetta* and *Pinpanetta* and extant genus *Stictonetta*) had not yet adapted for diving (Worthy and Lee, 2008; Worthy, 2009). The earliest diving duck belonging to this clade comes from the terminal Lower Miocene of New Zealand (genus *Manuherikia*). The phylogenetic position of one more diving duck which has lost ability to flight, *Cayaoa bruneti* Tonni, 1979 from the Lower Miocene of Argentina (Noriega et al., 2009), remains uncertain.

The earliest find of a diving duck of the modern type comes from the Oligocene of Kazakhstan and is represented by a distal ulnar fragment referred to the extant genus *Somateria* (Kurochkin, 1968). A reexamination of this specimen has shown that it is undoubtedly related to diving ducks of the tribe Mergini, in particular, the genus *Somateria*; however, it is impossible to assign it with certainty to the extant genus, because of fragmentariness (E.N. Kurochkin, personal communication). The extinct diving duck genus *Protomelanitta* is known from the continental Middle Miocene beds of Central Asia; it is closely related to extant Mergini; however, it had not yet not reached the evolutionary level of living members of this tribe. *Protomelanitta* is surprisingly similar in tarsometatarsal structure to extant Mergini; however, the humeral structure suggests that it occupies a basal position (Zelenkov, 2011b).

The diving duck *Aythya shihuibas* Hou, 1985 was described from the Upper Miocene of China based on a proximal humeral fragment; judging from a photograph (*Fossil Birds* ..., 2003), the holotype is characterized by a narrow caput humeri in caudal view, which is characteristic of the genus *Protomelanitta*, but has not been recorded in *Aythya* (Fig. 3). Thus, *A. shihuibas* should be transferred to the genus *Protomelanitta* and named *Protomelanitta shihuibas*. *P. shihuibas* differs from *P. gracilis* from the Middle Miocene of Mongolia in the dorsally displaced tuberculum ventrale (as in extant Mergini and Aythyini); the tuberculum dorsale of *P. shihuibas* is morphologically inter-

Table 1. Stratigraphic distribution of ducks in the Upper Oligocene–Miocene (Dendrocygninae, Anserinae, and others large Anatidae are excluded), based on the data of Miller (1944), Alvarez and Olson (1978), Yeh (1980), Cheneval (1983, 1987, 2000), Olson (1985), Becker (1987), Livezey and Martin (1988), Cheneval et al. (1991), Heizmann and Hesse (1995), Gál et al. (1998–1999, 2000), Olson and Rasmussen (2001), Göhlich (2002), Mlíkovský (2002, 2003), Mourer-Chauviré et al. (2004), Worthy et al. (2007, 2008), Mourer-Chauviré (2008), Noriega et al. (2008), Worthy (2008, 2009), Kessler (2009), Mayr (2009), Cenizo and Agnolin (2010), Zelenkov (2011a, 2011b), Zelenkov and Kurochkin (2012)

| | Oxyurinae | | Tadorninae | Anatinae | | Anatidae incertae sedis |
	traditional (diving)	sensu Worthy and Lee, 2008		Mergini, Aythyini, and basal members	Anatini	
Middle Miocene	"Oxyura" doksana (Czechia)	Mionetta blanchardi (Europe)	Tadorna sp. (Mongolia, Germany) Tadorninae gen. indet. (USA, Thailand)	Protomelanitta gracilis (Mongolia) Ocyplonessa shotwelli[1] (USA) "Mergus" miscellus (USA) "Mergus" minor (Hungary) "Mergus" sp. (Germany) "Clangula" matraensis (Hungary) "Bucephala" sp. (Hungary)	Anas soporata (Mongolia) ?Anas (USA) Aix praeclara (Mongolia) Mioquerquedula minutissima (Mongolia) Mioquerquedula velox (Europe) Chenoanas deserta (Mongolia) "Anas" sansaniensis (Europe)	Aythya chauvirae (France) Sinanas diatomas (China) Sharganetta mongolica (Mongolia) Nogusunna conflictoides (Mongolia)
Lower Miocene	Manuherikia lacustrina (New Zealand) Manuherikia minuta (New Zealand) Manuherikia douglasi (New Zealand)	Dendrochen robusta (USA) Mionetta blanchardi (Europe) Mionetta consorbina (Europe) Mionetta sp. (Namibia) Dunstanetta johnstoneorum (New Zealand)	Miotadorna sancti-bathansi (New Zealand)		"Aix" oligocaena (Kazakhstan) "Anas" integra (USA) Matanas enrighti (New Zealand)	"Mionetta" natator (Europe) "Anas" luederitzensis (Republic of South Africa) Cayaoa bruneti (Argentina) Ankonetta lariestrai (Argentina) Limicolavis pluvianellus (USA)
Upper Oligocene		Mionetta blanchardi (Europe) Pinpanetta tedfordi (Australia) Pinpanetta vickersrichae (Australia) Pinpanetta fromensis (Australia)	Australotadorna alecwilsoni (Australia)	"Somateria" sp. (Kazakhstan)		"Mionetta" natator (Europe) Teleornis impressus (Argentina)

[1] Ocyplonessa shotwelli described from the Middle–Upper Miocene.

mediate between that of *Protomelanitta*, on the one hand, and extant Mergini and Aythyini, on the other hand.

Presumable Mergini were also recorded in the Middle−Upper Miocene of North America ("*Mergus*" *miscellus*, *Ocyplonessa* ("*Histrionicus*") *shotwelli*: Brodkorb, 1961; Alvarez and Olson, 1978) and Eastern Europe ("*Clangula*", "*Mergus*": Gál et al., 1998–1999, 2000; Heizmann and Hesse, 1995). It is interesting that the Middle Miocene marine beds lack diving ducks of this morphological type; in particular, they have not been recorded in the Pungo Formation of the Lee Creek Mine locality (Olson and Rasmussen, 2001).

The fossil record of diving ducks essentially changes in the Upper Miocene−Lower Pliocene. In the Lower Pliocene of the Lee Creek Mine, diving ducks of the tribe Mergini compose a very rich fauna (Olson and Rasmussen, 2001). In the same period (Upper Miocene−Lower Pliocene), the true pochard *Aythya* (not known in the Upper Miocene) occurred in the continental beds of Mongolia and Mergini disappeared and, beginning from this level, were almost completely absent in the continental beds.

This distribution of diving ducks is possibly accounted for by the following: in the Middle Miocene, when the climate in Eurasia was rather humid, continental ponds of Eurasia and North America rich in animal food were occupied by diving ducks, such as *Protomelanitta* and *Ocyplonessa*. As aridity increased at the end of the Miocene, some of these ducks had to adapt to marine habitats richer in food. A presumable increase in productivity of the World Ocean, which was caused by the establishment of monsoon regime in Asia about 8 Ma and, hence, a global increase in transportation of some elements, primarily phosphorus, to the ocean, played an important role in this process (Filippelli, 1997). The formation of Mergini of the modern type could have been connected with this historical episode. Earlier, Olson (1984) noted probable connection of the increased diversity of marine birds with the growth of productivity of the ocean in the Late Miocene and proposed that, at that time, the range of a number of northern species could have moved southerly.

The similarity in morphology between Middle Miocene diving ducks and extant Mergini is evidence of direct affinity. Primitive diving ducks disappeared in the inland basins in the terminal Miocene simultaneously with the appearance of *Aythya*, which are probably descendants of primitive Mergini, strongly changed as a result of adaptation to changing conditions; however, it may well be that these two pochard groups are not connected as an ancestor and descendant. *Aythya spatiosa* Kurochkin, 1976 from the Lower Pliocene of Mongolia is intermediate between Aythyini and Mergini in the morphology of the femur (Zelenkov, 2011a) and tibiotarsus, supporting the affinity between the tribes Aythyini and Mergini. Late
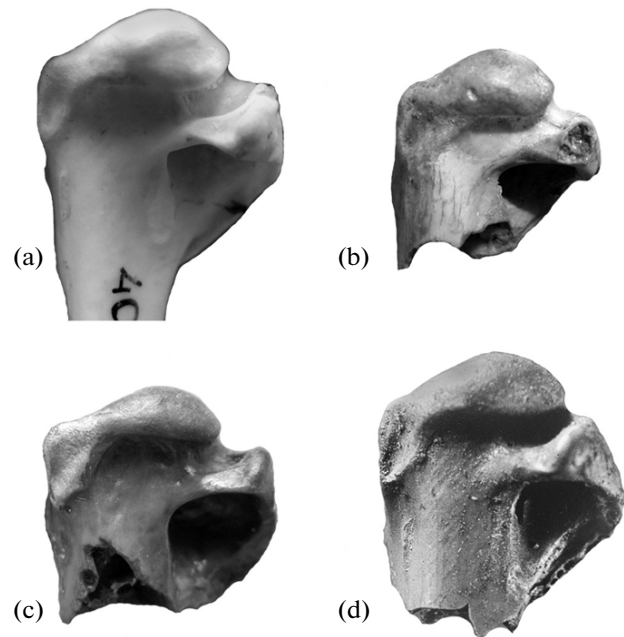

Fig. 3. Proximal parts of humeri in some Anatidae, caudal view: (a) *Aythya affinis* (Eyton, 1838), Recent; (b) *Anas* cf. *A. pullulans* Brodkorb, 1963, specimen PIN, no. 3222/50; Lower Pliocene, Khirgis-Nur 2 locality, Mongolia; (c) *Protomelanitta gracilis* Zelenkov, 2011, holotype PIN, no. 4869/151; Middle Miocene, Sharga locality, Mongolia; (d) *Protomelanitta shihuibas* (Hou, 1985), holotype; Upper Miocene, Shihuiba locality, China (after *Fossil Birds...*, 2003). Scale bar, 1 cm.

Miocene *P. shihuibas* is also intermediate in morphology (see above). Early Pliocene *Aythya* displays a high tuberculum dorsale (Zelenkov, 2011a), which is evidence that, even if ancestors of Aythyini did not belong to primitive Mergini, they had humeral features in common with some living primitive ducks (for example, *Stictonetta*) and Middle Miocene diving ducks, such as *Protomelanitta* (see below).

Parallel Evolution of Humeral Structures

The distribution of morphological characters in living and Early Neogene ducks shows that the presently observed distribution of advanced and primitive characters had not yet been achieved by the Early−Middle Miocene. A good example is provided by the humerus, the characters of which are given in Table 2. The humerus is a good marker of evolutionary advantage of anseriforms, which is considered to be one of the most suitable elements from the point of view of the phylogenetic signal (Woolfenden, 1961; Worthy, 2008). Table 2 shows that the subfamily Anatinae, which dominate the modern anatid fauna (including various ducks of several tribes), and phylogenetically remote *Oxyura* (Eo et al., 2009; Gonzalez et al., 2009) display the same set of advanced characters, distin-

Table 2. Distribution of proximal humeral characters in some Neogene and living ducks

	Dendrocygna and Thalassornis	Extant Oxyura	Extant Anatinae	Mionetta	Manuherikia (basal Oxyurinae)	Sharganetta	Stictonetta	Nogusunna	Protomelanitta
Tuberculum dorsale, lowered	−	+	+	−	−	−	−	+/−	+
Tuberculum dorsale, extended	−	+	+	−	−	−	−	+/−	+
Nonconcave dorsal surface of crista deltopectoralis	−	+	+	−	−	+	+/−	+	+
Well-pronounced capital shaft ridge absent	−	+	+	−	−	+/−	+/−	−	+/−
Tuberculum ventrale directed distocaudally, closing fossa pneumotricipitalis ventralis	−	+	+	−	+	−	−	−	−

guishing them from primitive *Dendrocygna* and *Thalassornis*. At the same time, Miocene genera display either a more or less complete set of primitive characters (*Mionetta, Manuherikia*) or a combination of primitive and advanced features (*Sharganetta, Nogusunna*). Among living ducks, this combination is only observed in some monotypic (and probably archaic) genera, such as *Stictonetta*.

Thus, the set of progressive humeral characters observed in the majority of living ducks was only one of morphological types of Early and Middle Neogene taxa. In this case, extant taxa, which are a certain horizontal section of phylogenetic tree of the group, differs strongly morphologically from the section of Early Neogene anatid diversity, in which the same groups (primitive Oxyurinae and Anatinae) were characterized by a different set of characters. Nevertheless, some Middle Miocene taxa (for example, *Protomelanitta*) already had a combination of characters close to that of anatids dominating the modern fauna. Thus, the Miocene duck diversity reflects early radiation of this group and the modern combinations of characters in ducks were probably formed as a result of extinction of the majority of intermediate aberrant taxa. In the modern diversity, these individual aberrant taxa (for example, *Stictonetta*) corresponding to Early and Middle Miocene anatids in the combination of characters are probably descendants of anatids that diverged at the Early Neogene evolutionary level. Apparently, primitive (such as *Dendrocygna*) and progressive forms (extant Anatinae and Oxyurinae) correspond to two opposite adaptive states, while intermediate Miocene forms reflect the states of adaptatiogenesis characterized by unstable morphology, which caused the appearance of a number of transitional morphotypes.

Remarkably, advanced morphology was independently acquired in at least two anatid lineages (Anatinae and Oxyurinae), suggesting a trend towards parallel evolution of at least humeral structures in this group. In particular, the raised tuberculum dorsale is characteristic of primitive ducks, such as Early Miocene *Mionetta* and Middle Miocene Mongolian *Sharganetta* and *Nogusunna* as well as extant Dendrocygninae. This structure of the tuberculum dorsale is characteristic of early members of Oxyurniae (genus *Manuherikia*) and Late Miocene (*Protomelanitta shihuibas*) and Early Pliocene pochards, but does not occur in living members of the genera *Oxyura* and *Aythya*. Middle Miocene members of *Protomelanitta* also demonstrate a rather primitive condition of this character compared with living members of the tribe Mergini.

Thus, the above consideration allows the conclusion that the humerus actually provides a criterion for judgment of the evolutionary level of anseriforms, although parallel evolution of particular characters complicate the use of this skeletal element for determination of the taxonomic position of primitive ducks.

ACKNOWLEDGMENTS

sidium of the Russian Academy of Sciences "Origin of Biosphere and Evolution of Geobiological Systems."

REFERENCES

Agnolín, F.L., Revisión systemática de algunas aves deseadenses (Oligoceno Medio) descriptas por Ameghino en 1899, *Rev. Mus. Argent. Cienc. Natur. N. Ser.*, 2004, vol. 6, pp. 239–244.

Alvarez, R. and Olson, S.L., A New Merganser from the Miocene of Virginia (Aves: Anatidae), *Proc. Biol. Soc. Wash.*, 1978, vol. 91, pp. 522–532.

Ballmann, P., Les oiseaux miocènes de La Grive-Saint-Alban (Isère), *Geobios*, 1969, vol. 2, pp. 157–204.

Baumel, J.J., King, A.S., Breazile, J.E., et al., *Handbook of Avian Anatomy: Nomina Anatomica Avium*, Publ. Nuttall Ornithol. Club, 1993, no. 23, pp. 1–779.

Becker, J.J., *Neogene Avian Localities of North America*, Washington, DC–London: Smithson. Inst. Press, 1987.

Brodkorb, P., Birds from the Pliocene of Juntura, Oregon, *Quart. J. Florida Acad. Sci.*, 1961, vol. 24, no. 3, pp. 169–184.

Bulgarella, M., Sorenson, M.D., Peters, J.L., et al., Phylogenetic Relationships of *Amazonetta, Speculanas, Lophonetta*, and *Tachyeres*: Four Morphologically Divergent Duck Genera Endemic to South America, *J. Avian Biol.*, 2010, vol. 41, no. 2, pp. 186–199.

Cenizo, M.M. and Agnolín, F.L., The Southernmost Records of Anhingidae and a New Basal Species of Anatidae (Aves) from the Lower–Middle Miocene of Patagonia, Argentina, *Alcheringa*, 2010, vol. 34, no. 4, pp. 493–514.

Cheneval, J., Les Anatidae (Aves, Anseriformes) du gisement aquitanien de Saint-Gérand-le-Puy (Allier, France), in *Act. Sympos. Paléontol. G. Cuvier*, Buffeteaut, E., Mazin, J.M., and Salmon, E., Eds., Montbéliard: Ville de Montbéliard, 1983, pp. 85–98.

Cheneval, J., Les Anatidae (Aves, Anseriformes) du Miocène de France: Révision systématique et évolution, *Doc. Lab. Géol. Lyon*, 1987, vol. 99, pp. 137–156.

Cheneval, J., The Avifauna of Sansan, *Mém. Mus. Nat. Hist. Natur.*, 2000, vol. 183, pp. 321–388.

Cheneval, J., Ginsburg, L., Mourer-Chauviré, C., and Ratanasthien, B., The Miocene Avifauna of the Li Mae Long Locality, Thailand: Systematics and Paleoecology, *J. South. Asian Earth Sci.*, 1991, vol. 6, no. 2, pp. 117–126.

Eo, S.H., Bininda-Emonds, O.R.P., and Carroll, J.P., A Phylogenetic Supertree of the Fowls (Galloanserae, Aves), *Zool. Scr.,* 2009, vol. 38, no. 5, pp. 465–481.

Filippelli, G.M., Intensification of the Asian Monsoon and a Chemical Weathering Event in the Late Miocene–Early Pliocene: Implications for Late Neogene Climate Change, *Geology*, 1997, vol. 25, no. 1, pp. 27–30.

Flower, B.P. and Kennett, J.P., The Middle Miocene Climatic Transition: East Antarctic Ice Sheet Development, Deep Ocean Circulation and Global Carbon Cycling, *Palaeogeogr. Palaeoclimatol. Palaeoecol.*, 1994, vol. 108, nos. 3–4, pp. 537–555.

Fossil Birds of China, Hou, L.H., Chuong, Ch.-M., Yang, A., et al., Eds., Yunan: Sci. Technol. Press, 2003.

Gál, E., Hár, J., Kessler, E., et al., Middle Miocene Fossils from the Sections at the Rákóczi Chapell at Mátraszölös, *Fol. Hist. Natur. Mus. Matraensis,* 1998–1999, vol. 23, pp. 33–78.

Gál, E., Hár, J., Kessler, E., et al., Middle Miocene Fossils from the Section of the Road at the Rákóczi Chapell, Mátraszölös: 2. Locality Mátraszölös 2, *Fol. Hist. Natur. Mus. Matraensis*, 2000, vol. 24, pp. 39–75.

Göhlich, U.B., The Avifauna of the Miocene Fossil–Lagerstatte Sandelzhausen (Bavaria, Southern Germania), *Zitteliana*, 2002, vol. 22, pp. 169–190.

Göhlich, U.B., The Early Vallesian Vertebrates of Atzelsdorf (Late Miocene, Austria): 5. Aves, *Ann. Naturhist. Mus. Wien*, 2009, vol. 111A, pp. 509–514.

Gonzalez, J., Düttman, H., and Wink, M., Phylogenetic Relationships Based on Two Mitochondrial Genes and Hybridization Patterns in Anatidae, *J. Zool.*, 2009, vol. 279, no. 3, pp. 310–318.

Heizmann, E.P.J. and Hesse, A., Die mittelmiozänen Vogel- und Säugetierfaunen des Nördlinger Ries (MN 6) und des Steinheimer Beckens (MN 7)—ein Vergleich, *Cour. Forsch. Senckenb.*, 1995, vol. 181, pp. 171–186.

Kessler, E., Review of the Neogene Waterfowl (Aves: Anatidae) of Eastern Paratethys, *Stud. Univ. Babes-Bolyai. Biol.*, 1992, vol. 37, no. 2, pp. 47–54.

Kessler, E., New Results with Regard to the Neogene and Quaternary Avifauna of the Carpathian Basin: Part I, *Földt. Közl*, 2009, vol. 139, pp. 67–81.

Kurochkin, E.N., New Oligocene Birds of Kazakhstan, *Paleontol. Zh.*, 1968, no. 1, pp. 92–101.

Livezey, B.C., A Phylogenetic Analysis of Recent Anseriform Genera Using Morphological Characters, *Auk*, 1986, vol. 103, no. 4, pp. 737–754.

Livezey, B.C. and Martin, L.D., The Systematic Position of the Miocene Anatid *Anas* [?] *blanchardi* Milne-Edwards, *J. Vertebr. Paleontol.*, 1988, vol. 8, no. 2, pp. 196–211.

Lopatin, A.V., Early Miocene Small Mammals from the North Aral Region (Kazakhstan) with Special Reference to Their Stratigraphic Significance, *Paleontol. J.*, 2004, vol. 38, suppl. 3, pp. 217–223.

Mayr, G., *Palaeogene Fossil Birds*, Berlin–Heidelberg: Springer Verlag, 2009.

Mayr, G. and Smith, R., Ducks, Rails, and Limicoline Waders (Aves: Anseriformes, Gruiformes, Charadriiformes) from the Lowermost Oligocene of Belgium, *Geobios*, 2001, vol. 34, no. 5, pp. 547–561.

Miller, A.H., An Avifauna from the Lower Miocene of South Dakota, *Univ. Calif. Publ. Bull. Depart. Geol. Sci.*, 1944, vol. 27, no. 4, pp. 85–100.

Mlíkovský, J., *Cenozoic Birds of the World: Part 1. Europe*, Praha: Ninox Press, 2002.

Mlíkovský, J., Middle Miocene Birds of Františkovy Lázně, Bohemia, *J. Nat. Mus. Natur. Hist. Ser.*, 2003, vol. 172, pp. 109–113.

Mlíkovský, J. and Švec, P., Review of the Tertiary Waterfowl (Aves: Anseridae) of Asia, *Věst. čs. Společ. Zool.*, 1986, vol. 50, pp. 249–272.

Mourer-Chauviré, C., Birds (Aves) from the Early Miocene of the Northern Sperrgebiet, Namibia, *Mem. Geol. Surv. Namibia*, 2008, vol. 20, pp. 147–167.

Mourer-Chauviré, C., Berthet, D., and Hugueney, M., The Late Oligocene Birds from the Créchy Quarry (Allier, France) with a Description of Two New Genera (Aves: Pelecaniformes: Phalacrocoracidae, and Anseriformes: Anseranatidae), *Senckenb. Lethaea*, 2004, vol. 84, pp. 303–315.

Noriega, J.I., The Avifauna from the "Mesopotamian" (Ituzaing Formation: Upper Miocene) of Entre Ríos Provincem Argentina, *Cour. Forsch. Senckenb.*, 1995, vol. 181, pp. 141–148.

Noriega, J.I., Tambussi, C.P., and Cozzuol, M.A., New Material of *Cayaoa bruneti* Tonni, an Early Miocene Anseriform (Aves) from Patagonia, Argentina, *Neues Jahrb. Geol. Paläontol. Abh.*, 2008, vol. 249, no. 3, pp. 271–280.

Olson, S.L., A Brief Synopsis of the Fossil Birds from the Pamunkey River and Other Tertiary Marine Deposits in Virginia, in *Stratigraphy and Paleontology of the Outcropping Tertiary Beds in the Pamunkey River Region, Central Virginia Coastal Plain*, Lauck, W.W. and Krafft, K., Eds., Atlantic Coast. Plain Geol. Ass., 1984, pp. 217–223.

Olson, S.L., The Fossil Record of Birds, in *Avian Biology*, Farner, D.S., King, J.R., and Parkes, K.C., Eds., New York: Acad. Press, 1985, vol. 8, pp. 79–252.

Olson, S.L. and Rasmussen, P.C., Miocene and Pliocene Birds from the Lee Creek Mine, North Carolina, *Smithson. Contrib. Paleobiol.*, 2001, vol. 90, pp. 233–365.

Sraml, M., Christidis, L., Easteal, S., et al., Molecular Relationships within Australasian Waterfowl (Anseriformes), *Aust. J. Zool.*, 1996, vol. 44, no. 1, pp. 47–58.

Woolfenden, G.E., Postcranial Osteology of the Waterfowl, *Bull. Florida St. Mus. Biol. Sci.*, 1961, vol. 6, pp. 1–129.

Worthy, T.H., Tertiary Fossil Waterfowl (Aves: Anseriformes) of Australia and New Zealand, *Unpublished PhD*, Adelaide: Univ. Adelaide, 2008, pp. 1–415.

Worthy, T.H., Descriptions and Phylogenetic Relationships of Two New Genera and Four New Species of Oligo–Miocene Waterfowl (Aves: Anatidae) from Australia, *Zool. J. Linnean Soc.*, 2009, vol. 156, no. 2, pp. 411–454.

Worthy, T.H. and Lee, M.S.Y., Affinities of Miocene Waterfowl (Anatidae: *Manuherikia, Dunstanetta* and *Miotadorna*) from the St Bathans Fauna, New Zealand, *Palaeontology*, 2008, vol. 51, no. 3, pp. 677–708.

Worthy, T.H., Tennyson, A.JD., Jones, C., et al., Miocene Waterfowl and Other Birds from Central Otago, New Zealand, *J. Syst. Palaeontol.*, 2007, vol. 5, no. 1, pp. 1–39.

Worthy, T.H., Tennyson, A.J.D., Hand, S.J., and Scofield, R.P., A New Species of the Diving Duck *Manuherikia* and Evidence for Geese (Aves: Anatidae: Anserinae) in the St Bathans Fauna (Early Miocene), New Zealand, *J. Roy. Soc. N. Zeal.*, 2008, vol. 38, no. 2, pp. 97–114.

Yeh, H.K., Fossil Birds from Linqu, Shandong, *Vertebr. PalAsiat.*, 1980, vol. 18, no. 2, pp. 116–125.

Zelenkov, N.V., Birds of the Neogene of Central Asia, *Candidate's Dissertation in Biology*, Moscow: Paleontol. Inst. Russ. Acad. Sci., 2011a, pp. 1–304.

Zelenkov, N.V., Diving Ducks from the Middle Miocene of Western Mongolia, *Paleontol. Zh.*, 2011b, no. 2, pp. 70–77.

Zelenkov, N.V. and Kurochkin, E.N., Birds of Central Asia in the Neogene, in *Materialy XIII Mezhdunarodnoi Ornitologicheskoi Konferentsii Severnoi Evrazii: Ornitologiya V Tsentral'Noi Evrazii* (XIII International Ornithological Conference of Northern Eurasia on Ornithology in Central Eurasia), Orenburg: Orenb. Gos. Ped. Univ., 2010, pp. 133–134.

Zelenkov, N.V. and Kurochkin, E.N., Dabbling Ducks (Aves: Anatidae) from the Middle Miocene of Mongolia, *Paleontol. Zh.*, 2012, no. 4, pp. 88–95.