

Dabbling Ducks (Aves: Anatidae) from the Middle Miocene of Mongolia

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Abstract—A new genus and two new species of ducks (Aves: Anatidae) from the Middle Miocene Sharga locality are described. *Mioquerquedula minutissima* gen. et sp. nov. is a very small duck. *Anas velox* Milne-Edwards, 1868 from the Middle Miocene of France is transferred to the genus *Mioquerquedula*. *Aix praeclara* sp. nov. described here is the oldest record of the modern genus *Aix*. A revision of the previously described small duck *Anas saporata* Kurochkin, 1976 shows that only the specimens from the Sharga locality should be referred to this species. The status of other small ducks from the Neogene of Europe and North America is discussed. The diversity of herbivorous and diving ducks in the Sharga locality indicates that Miocene Shargyn Govi Lake was rich in food resources.

Keywords: Anatidae, *Anas*, *Aix*, Miocene, Asia, Mongolia.

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INTRODUCTION

Remains of anatids (family Anatidae) are relatively frequent in the fossil record; however, rather uniform osteology of these birds essentially complicates identification of their bones and, hence, reconstruction of the evolution and phylogeny of the group. In particular, within the extensive extant genus of dabbling ducks (*Anas* L., 1758) from Oligocene and Neogene deposits, a great number of extinct species was described; at the same time, according to the modern concept, many forms possibly occupy an isolated taxonomic position (Mlíkovský, 2002; Worthy, 2008). A prominent example is provided by the Oligocene–Early Miocene ducks *Anas blanchardi* Milne-Edwards, 1863 and *A. natator* Milne-Edwards, 1867, which are represented by abundant remains from several localities of Europe (Mlíkovský, 2002). These species, originally described within the genus *Anas* (and the species *A. consorbina* Milne-Edwards, 1867, the validity of which is frequently put in doubt), were transferred to the extinct genus *Dendrochen* of the extant subfamily of whistling ducks, Dendrocygninae (Cheneval, 1983). Later, *A. blanchardi* and *A. natator* were referred to a separate genus, *Mionetta* Livezey et Martin, 1988, and their close affinity to Dendrocygninae was rejected (Livezey and Martin, 1988; Worthy and Lee, 2008; Worthy, 2009). Since the Dendrocygninae are the most primitive subfamily of extant Anatidae, it was attempted to assign to this subfamily some other species of extinct anatids that display certain primitive

characters. In particular, Mlíkovský and Švec (1986) referred a small duck from the Neogene of Mongolia, *Anas saporata* Kurochkin, 1976, to the extant genus *Dendrocygna* Swainson, 1837.

The holotype of *A. saporata* comes from the Middle Miocene of the Sharga locality (which was originally dated Middle Pliocene) and is represented by an incomplete coracoid (Kurochkin, 1976). A number of other bones from the Upper Miocene and Lower Pliocene (originally Lower and Middle Pliocene) Yavor 1, Hyargas Nuur 2, and Chono Harayh localities in western Mongolia, which were then considered to be of the same age as Sharga, were also assigned to *A. saporata* (Devyatkin, 1981; Kurochkin, 1985).

A reinvestigation of the previously described material of *A. saporata* has shown that this species should not be assigned to the genus *Dendrocygna*; it is retained in *Anas*, probably representing an early stage of the evolution of this genus. At the same time, specimens from the Yavor 1, Hyargas Nuur-2, and Chono Harayh localities do not belong to *A. saporata*. They are more similar in morphology to living species of the genus *Anas* and, hence, they will be described in a future publication. At the same time, new material from Sharga contains two coracoid fragments, which we assign to *A. saporata*.

In Sharga, fossils of another very small duck (somewhat smaller than *A. saporata*) are rather common; we describe it within a separate genus, *Mioquerquedula* gen. nov. In addition, based on a coracoid, we recognized the presence in Sharga of one more (larger) duck, which we assign to a new species of the extant

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genus *Aix*. From the Sharga locality (see the data on the locality and references in Zelenkov and Kurochkin, 2009), diving ducks have previously been described (Zelenkov, 2011a). Like members of the genera *Anas* and *Aix*, ducks of the genus *Mioquerquedula* were not specialized divers, because they had a pneumatized fossa tricripitalis ventralis.

The anatomical nomenclature in the present study follows *Nomina Anatomica Avium* (Baumel et al., 1993) and, in some cases, Ballmann (1969). To designate the medially oriented surface of the processus acrocoracoideus (which is connected through a ligament with the furcula), we use the term tuber brachialis, because, in the Anatidae, the facies articularis clavicularis is not developed (in contrast to, for example, Accipitridae, which is taken for example of the facies articularis clavicularis in a figure in *Nomina Anatomica Avium*).

The taxonomy of Anseriformes follows Livezey (1986), with slight modification; in particular, the stiff-tailed ducks and their relatives was ranked subfamily Oxyurinae (Worthy and Lee, 2008; Worthy, 2009). In the case of primitive members of Anatinae (Anatinae tribus inc. sedis sensu Livezey, 1986), the taxon “Cairinini” is used for simplicity, with putting this name in inverted commas. Phylogenetic studies confirmed that this tribe is paraphyletic (Woolfenden, 1961; Livezey, 1986; Eo et al., 2009; Gonzalez et al., 2009; Worthy, 2009; Bulgarella et al., 2010); however, relationships of particular genera remain uncertain.

The fossil specimens described here were collected from time to time in the Sharga locality by parties of the Joint Russian–Mongolian Paleontological Expedition and are housed in the Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow (PIN).

We use the following abbreviations: (PIN) Borissiak Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia; (MNHN) Paris Natural History Museum, France; and (MTC) Muzeul Ţării Crişurilor, Oradea, Romania.

SYSTEMATIC PALEONTOLOGY

Order Anseriformes

Family Anatidae Vigors, 1825

Genus *Aix* Boie, 1828

Aix praeclara Zelenkov et Kurochkin, sp. nov.

Plate 17, fig. 1

Etymology. From the Latin *praeclara* (excellent).

Holotype. PIN, no. 4869/92, cranial end of right coracoid; Mongolia, Gobi–Altai Aimag, Shargyn Govi, Sharga locality; terminal Middle Miocene, Oshin Formation.

Description (Figs. 1f, 1g). The processus acrocoracoideus is elongated, impressio lig. acrocora-

cohumeralis is only slightly widened at the apex; the medial surface of the tuber brachialis is slightly convex, with a slightly concave caudal margin; the sulcus m. supracoracoidei is not pneumatized; the shaft and processus acrocoracoideus are narrow in ventral view.

Measurements in mm: total length of the fragment, 23.1 (holotype) and 20.5 (specimen PIN, no. 4869/67); length from cranial bone edge to caudal edge of cotyla scapularis, 14.2 (holotype); minimum width of diaphysis, 4.4 (holotype); dorsoventral height of facies articularis humeralis, 5.4 (holotype) and 5.2 (specimen PIN, no. 4869/67); greatest diameter of cotyla scapularis, 3.8 (holotype and specimen PIN, no. 4869/67).

Comparison. The genus *Aix* includes two extant species. *A. praeclara* differs from *A. galericulata* (L., 1758) in the significantly thinner shaft and processus acrocoracoideus, nonconcave medial surface of the tuber brachialis (Figs. 1g, 1h), and in the slightly cut caudal edge of the tuber brachialis. It differs from *A. sponsa* (L., 1758) in the slightly widened impressio lig. acrocoracoideus and somewhat more elongated processus acrocoracoideus. Extinct species of the genus *Aix* have not been described.

Remarks. The coracoid is rather unusual in “Cairinini” and, in particular, in *Aix*; this allows the determination of the form from Sharga to genus. *A. praeclara* differs from *Dendrocygninae* and *Mergini* in the plane of the acrocoracoid positioned in parallel to the plane of sternal expansion; it differs from *Anas* in the narrow diaphysis at the level of facies articularis humeralis and the narrow processus acrocoracoideus, and from *Aythya* in the processus acrocoracoideus projecting medially relative to the shaft. It differs from *Chenonetta* in the gracile shaft and processus acrocoracoideus, from *Callonetta* in the elongated processus acrocoracoideus, from *Nettapus* in the slightly medially displaced processus acrocoracoideus. Of living species of the genus *Aix*, the extinct species is most similar to *A. galericulata*. The coracoids from the Sharga locality, which presumably belong to *Sharganetta* or *Nogusunna* (Zelenkov, 2011a) differ from the coracoid of *A. praeclara* in the smaller size.

From the Lower Miocene of the Aral Region (Kazakhstan), a duck similar in size, *Anas oligocaena* Tugarinov, 1940, which is represented by several skeletal elements, was described. Mlíkovský and Švec (1986) transferred this species to the genus *Dendrocygna*. Reinvestigation of the material shows affinity of *A. oligocaena* to ducks of the tribe “Cairinini” and to the genus *Aix* (original data). The coracoid fragment housed in PIN (specimen PIN, no. 217/758) probably belongs to *A. oligocaena* and differs from that of *A. praeclara* in the craniocaudally extended and low facies articularis humeralis, large cotyla scapularis, the weak depression in the dorsal part of the sulcus m.

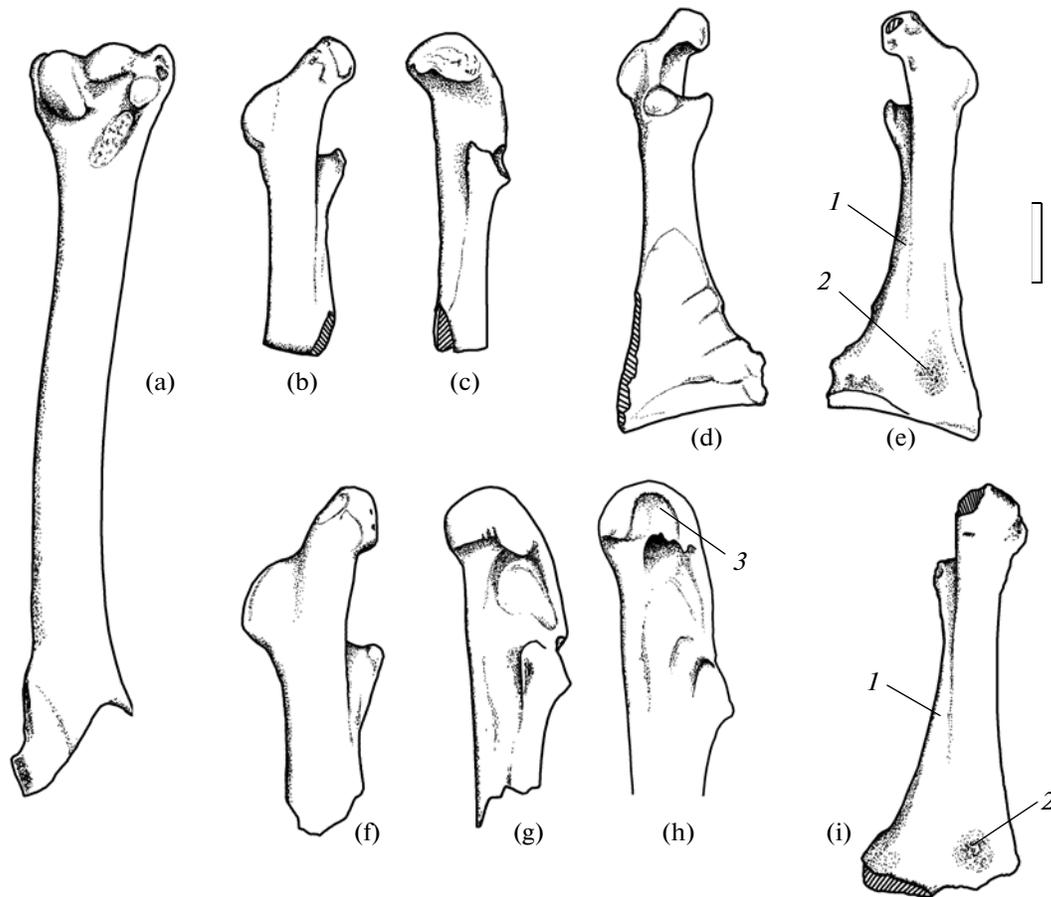


Fig. 1. Anatids from the Middle Miocene of the Sharga locality in comparison with extant members of the family: (a) Anatinae gen. indet. (*Anas* aut *Mioquerquedula*), specimen PIN, no. 4859/54, left humerus fragment, cranial view; (b, c) *Anas soporata* Kurochkin, 1976, holotype PIN no. 2614/95, cranial part of right coracoid: (b) ventral and (c) medial views; (d, e) *Mioquerquedula minutissima* gen. et sp. nov., holotype PIN, no. 4869/193, left coracoid: (d) dorsal and (e) ventral views; (f, g) *Aix praeclara* sp. nov., holotype PIN no. 4869/92, cranial fragment of right coracoid: (f) ventral and (g) medial views; (h) *Aix galericulata* L., Recent, specimen PIN, no. 40-11, right coracoid, medial view; and (i) *Mioquerquedula* sp., specimen PIN, no. 4869/143, left coracoid, ventral view. Designations: (1) groove extending onto the ventral surface of the coracoid; (2) well-developed impressio m. supracoracoidei; and (3) concave tuber brachialis with a concave caudal margin. Scale bar, 0.5 cm.

supracoracoidei, and in the shorter and narrower processus acrocoracoideus.

Fossil remains of *Aix* have been recorded in the Upper Miocene of Austria: a coracoid from the Götzendorf locality is referred to this genus based on the absence of a pneumatized sulcus m. supracoracoideus (Mlíkovský, 1991). In the coracoid from Sharga (holotype), this sulcus is also nonpneumatized; however, we have revealed pneumatization of this region at least in one specimen of the extant species *A. galericulata*.

An almost complete carpometacarpus, which is referred to as Anatinae gen. indet. and closest to *Aix* and *Cairina*, was recorded in the Middle Sarmatian of Moldova (Kurochkin and Ganya, 1972).

Material. Holotype; specimen PIN, no. 4869/67, fragment of the cranial end of a left coracoid from the type locality.

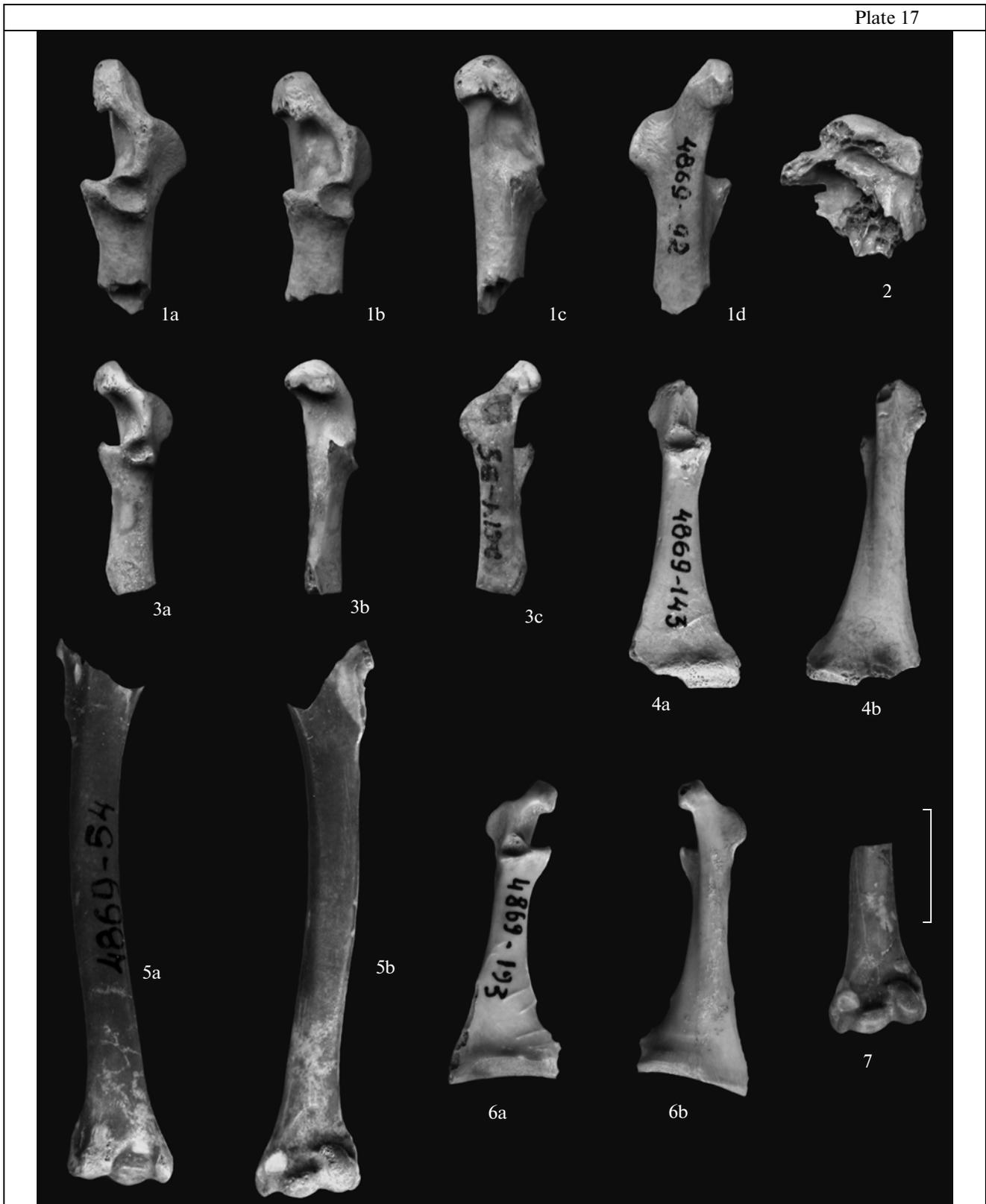
Genus *Mioquerquedula* Zelenkov et Kurochkin, gen. nov.

Etymology. From the Miocene and *Querquedula*, a presently unused generic name of small living dabbling ducks of the genus *Anas*.

Type species. *Mioquerquedula minutissima* sp. nov.

Diagnosis. In coracoid, plane of ventral surface of processus acrocoracoideus subparallel to plane of sternal expansion; tuber brachialis nonconcave, overhanging sulcus m. supracoracoidei; groove between processus procoracoideus and shaft of coracoid extending distally and passing onto ventral surface of bone; ventral surface of extremitas sternalis having relatively shallow, but distinct depression (impressio m. supracoracoidei).

Species composition. *M. velox* (Milne-Edwards, 1868) and *M. minutissima* sp. nov. from the Middle Miocene of France and Mongolia.



C o m p a r i s o n. *Mioquerquedula* is distinguished from all other Anatidae, except for Anatini and some “Cairinini,” in the processus acrocoracoideus of the coracoid the plane of which is positioned subparallel to the sternal expansion of this bone. In Dendrocygninae, Anserinae, Tadorninae, Mergini, and partly Aythyini, the plane of the acrocoracoid is subperpendicular to the plane of the sternal expansion or positioned at 45° to it. Among “Cairinini,” *Mioquerquedula* reliably differs in this character from *Cairina* and *Pteronetta* and, to some extent, from *Chenonetta*, which shows an intermediate condition. It additionally differs from *Chenonetta* in the notched cranial part of the sulcus m. supracoracoidei and the tuber brachialis not overhanging this notch. *Aix sponsa* and *A. galericulata* differ from each other in the pneumatization of the sulcus m. supracoracoidei, which is pneumatized in *A. sponsa* and variably pneumatized in *A. galericulata*. Nevertheless, in both members of *Aix*, the pneumatic fossa in the cranial part of the sulcus m. supracoracoidei is always formed beginning from its dorsal part (sometimes it also expands onto the ventral part); in *Mioquerquedula*, the deepest and nonpneumatized fossa is positioned in the ventral part of the sulcus m. supracoracoidei. In addition, the medial surface of the tuber brachialis of *Aix* in concave (an incisure is occasionally formed in place of this concavity), while in *Mioquerquedula*, this concavity is indiscernible and the incisure is very weak. *Mioquerquedula* differs from *Callonetta* in the nonpneumatized sulcus m. supracoracoidei; in addition, it lacks a rib extending from the dorsal edge of the tuber brachialis and separating the sulcus m. supracoracoidei from the pneumatic fossa located more cranially, which is characteristic of *Callonetta* (in other anatids with pneumatized cranial end of the coracoid, the pneumatic fossa is inseparable from the sulcus m. supracoracoidei). The new genus differs from *Nettapus* in the relatively slender processus acrocoracoideus, the absence of an incisure in the medial margin of the bone caudal to the processus procoracoideus, and in the facies articularis humeralis projecting weakly ventrally relative to the shaft.

In addition, *Mioquerquedula* differs from Anatinae (including *Anas* and the majority of “Cairinini”) in the groove (which begins between the processus procora-

coideus and the shaft of the coracoid) extending distally and passing onto the ventral surface of the coracoid shaft and in the presence of a distinct impressio m. supracoracoidei on the sternal expansion of the bone. A similar groove is present in *Nettapus* and, to a lesser extent, in *Chenonetta*. In *Anas*, this groove is almost always absent: of 38 skeletons investigated, it is recognized in two, *A. sibilatrix* and *A. penelope* (although it is much more poorly developed). It is noteworthy that the same specimens additionally have a deep fossa in the cranial part of the sulcus m. supracoracoidei and a hardly discernible impressio m. supracoracoidei: both characters are characteristic of *Mioquerquedula* and usually absent in *Anas*.

Mioquerquedula is smaller in size than all Anseriformes, except for *Nettapus*.

R e m a r k s. The diagnosis and comparison of the genus *Mioquerquedula* are based on the characters observed in the Mongolian species *M. minutissima*.

The coracoid structure (in particular, the parallel orientation of the processus acrocoracoideus and plane of the extremitas sternalis) indicates that *Mioquerquedula* belongs to the clade including *Anas* and advanced “Cairinini.” The concave cranial part of the sulcus m. supracoracoidei, which is characteristic of *Mioquerquedula*, is observed in many “Cairinini” and, as rare exception, in *Anas*. *Mioquerquedula* is similar in some characters to different members of “Cairinini” (in particular, to *Nettapus*); however, cannot be positioned close to any. It is noteworthy that the main characters distinguishing *Mioquerquedula* from *Anas* are observed in some specimens of *Anas* simultaneously (see above); this suggests affinity between these two genera. If this is the case, the similarity with “Cairinini” seems plesiomorphic.

The coracoid of *Mioquerquedula* is most reliably distinguished by the combination two characters. The first is the presence of a distinct groove beginning between the processus procoracoideus and the shaft (and actually continuing the sulcus m. supracoracoidei) and passing onto the ventral surface of the bone. The presence of such a groove is a progressive character of Anatidae, which only occurs in some “Cairinini” and, as rare exception, in *Anas*. The second distinctive character of *Mioquerquedula* is the well-developed impressio m. supracoracoidei. The presence of

Explanation of Plate 17

All specimens come from the Oshin Formation (terminal Middle Miocene) of the Sharga locality, Mongolia.

Fig. 1. *Aix praeclara* sp. nov., holotype PIN, no. 4869/92, cranial fragment of right coracoid: (1a) dorsolateral, (1b) dorsal, (1c) medial, and (1d) ventral views.

Figs. 2 and 4. *Mioquerquedula* sp.: (2) specimen PIN, no. 4869/107, proximal fragment of right humerus, caudal view; (4) specimen PIN, no. 4869/143, left coracoid: (4a) dorsal and (4b) ventral views.

Fig. 3. *Anas sporata* Kurochkin, 1976, holotype PIN, no. 2614/95, cranial part of right coracoid: (3a) dorsal, (3b) medial, and (3c) ventral views.

Figs. 5 and 7. Anatidae gen. indet. (*Anas* aut *Mioquerquedula*): (5) specimen PIN, no. 4869/54, fragment of left humerus: (5a) caudal and (5b) cranial views; (7) specimen PIN, no. 4869/56, distal fragment of left humerus, cranial view.

Fig. 6. *Mioquerquedula minutissima* gen. et sp. nov., holotype PIN, no. 4869/193, left coracoid: (6a) dorsal and (6b) ventral views. Scale bar, 1 cm.

this imprint is a primitive character of Anatidae, which is characteristic of Dendrocygninae and the Miocene genera *Mionetta* and *Manuherikia* (Livezey and Martin, 1988; Worthy and Lee, 2008), but does not occur in “Cairinini” and *Anas*. In *Mioquerquedula*, this impressio is small, in contrast to *Dendrocygna*, but distinct, while in *Anas*, it is almost always indiscernible.

From the Miocene beds of Europe and North America, several small anatids, probably related to *Mioquerquedula* have been described. A very small duck, *Anas velox* Milne-Edwards, 1868, similar in size to *M. minutissima*, comes from the Middle Miocene (MN6) of the Sansan locality (France). This species is also recorded in the Middle Miocene of Germany, Romania, and, presumably, in the Upper Miocene of Hungary (Mlíkovský, 2002). The coracoid of *Anas velox* (specimen MNHN SA 1232), which is figured in the studies of Milne-Edwards (1869–1871) and Cheneval (1987), has a groove passing onto the ventral surface of the bone, resembling that of *M. minutissima*, and, hence, the species *Anas velox* possibly belongs to the genus *Mioquerquedula*. The fragmentariness of this specimen (MNHN SA 1232) prevents the recognition of the second distinctive feature of this genus, i.e., a well-pronounced impressio m. supracoracoidei. Three coracoids of *Anas velox* (Cheneval, 2000) are known; the largest (paralectotype MNHN SA 1232) is larger than the holotype of *M. minutissima*; the specimens from Sharga referred to as *Mioquerquedula* sp. are also somewhat larger (see below).

Several coracoid fragments and some other bones from the Lower Miocene of the Dolnice locality (Czechia) were referred to *Anas velox* (Švec, 1981); Mlíkovský (2002) transferred them to *Mionetta natator* (Milne-Edwards, 1867). In our opinion, the generic assignment of *M. natator* requires revision. In particular, judging from the figures provided by Švec, presumable coracoids of *M. natator* differ from coracoids of *Mionetta blanchardi* from the same locality. It is possible that *M. natator* is related to Middle Miocene *Mioquerquedula*. The specimens of *M. natator* from Dolnice differ from *M. minutissima* and *M. velox* in the distinctly larger size; if they belong to *Mioquerquedula*, that, they undoubtedly represent separate species.

From the Upper Miocene of Hungary, a small duck, *A. albae* Jánossy, 1979, was described based on a carpometacarpus fragment. Mlíkovský (2002) proposed that the generic status of this specimen is uncertain; perhaps, *A. albae* also belongs to the genus *Mioquerquedula*. Recently, fragments of a scapula and tibiotarsus from the Upper Pliocene and Pleistocene (MN15–MN16 and MN17) of Hungary (Kessler, 2009) were referred to *A. albae*. Since it is impossible to compare these specimens with the holotype of *A. albae* and they differ in age, the scapula and tibiotarsus should only be determined as *Anas* sp. The distal fragment of a tibiotarsus from the Middle Miocene of Romania (Subpiatră locality, MN 6) has recently been referred to *A. albae* (Kessler and Venczel, 2009). How-

ever, this specimen (MTC, no. 24452), judging from the photograph provided, should not be referred to Anatidae, since it is characterized by a strongly developed epicondylus medialis (which is distinct in both cranial and distal views of the specimen, whereas it is absent in ducks), a deep incisure between the condyles in cranial view (poorly developed in ducks), and a short and relatively wide condylus medialis (in ducks, this condyle is narrow and more extended).

The small duck *Anas integra* Miller, 1944 from the Lower Miocene of South Dakota (United States) possibly also belongs to *Mioquerquedula*. Although it is not known whether or not this form had a groove passing onto the ventral side of the bone, the coracoid of *A. integra* is in general similar to that of *M. minutissima*. It was previously proposed that this species is probably close to *Dendrochen* (Cheneval, 1987); however, the coracoid of *A. integra* has much in common with that of extant *Anas*, while the coracoid of *Mionetta* differs essentially (see, for example, Livezey and Martin, 1988).

One more small duck, *Anas pullulans* Brodkorb, 1961, was described from the basal Upper Miocene of Oregon based on the proximal fragment of a carpometacarpus (Brodkorb, 1961). This species differ from *M. velox* (judging from the figures provided by Milne-Edwards and Brodkorb) in the wider os metacarpale minus (as in *Anas*), the lower os metacarpale alulare, and the proximally compressed trochlea carpalis. Thus, the taxonomic position of *A. pullulans* remains uncertain, although the shape of the trochlea carpalis suggests that it is close to living *Anas* rather than *M. velox*. The carpometacarpus of *M. minutissima* is not known.

Mioquerquedula minutissima Zelenkov et Kurochkin sp. nov.

Plate 17, fig. 6.

E t y m o l o g y. From the Latin *minutissima* (tiny).

H o l o t y p e. PIN, no. 4869/193, almost complete left coracoid; 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. 1d, 1e). A very small duck, as large as living *Nettapus auritus*. The sulcus m. supracoracoidei is concave in the caudal part; the impressio lig. acrocoracohumeralis is approximately constant in width throughout its extent; the processus acrocoracoideus projects slightly medially relative to the shaft.

M e a s u r e m e n t s in mm. Coracoid: greatest length, 28.6; length from the most cranial edge to caudal edge of the cotyla scapularis, 8.5; minimum width of the end, 3.2; dorsoventral height of the facies articularis humeralis, 3.2; greatest diameter of the cotyla scapularis, 2.3.

C o m p a r i s o n. The new species differs from the *M. velox* in the distinctly medially displaced processus acrocoracoideus.

M a t e r i a l. Holotype.

Genus *Anas* L., 1758***Anas soporata* Kurochkin, 1976**

Plate 17, fig. 3

Anas soporata: Kurochkin, 1976, p. 61, text-fig. 8; 1985, p. 43, text-fig. 18, pl. V. figs. 1–6.*Dendrocygna soporata*: Mlíkovský and Švec, 1986, p. 262

H o l o t y p e. PIN, no. 2614/95, cranial part of right coracoid; 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. 1b, 1c). Small-sized ducks. The processus acrocoracoideus of the coracoid is displaced distinctly medially relative to the shaft; the impressio lig. acrocoracohumeralis is extended, its dorsal margin is arched; the tuber brachialis is nonconcave and undivided into two parts, it is dorsoventrally extended and overhangs the cranial part of the sulcus m. supracoracoidei, which contains a pneumatic foramen; at the level of the facies articularis humeralis, the ventral surface of the shaft is flattened, and the margo medialis is pointed; the sulcus m. supracoracoidei is deep in dorsolateral view.

M e a s u r e m e n t s in mm: greatest length of the fragment, 21 (holotype) and 17.0 (specimen PIN, no. 4869/144); length from the cranial edge of the bone to the caudal edge of the cotyla scapularis, 10.7 (holotype); dorsoventral height of the facies articularis humeralis, 3.4 (holotype) and 3.7 (specimens PIN, nos. 4869/102, 144); minimum width of the diaphysis, 3.4 (holotype, specimen PIN, no. 4869/102) and 3.2 (specimen PIN, no. 4869/144).

C o m p a r i s o n. *A. soporata* is a small duck, somewhat smaller than living *Anas crecca*. It differs from extant members of the genus in the presence of a pneumatic foramen in the cranial part of the sulcus m. supracoracoidei, the flattened ventral surface of the bone at the level of the facies articularis humeralis, the wide and arched dorsal margin of the impressio lig. acrocoracohumeralis, and the deep sulcus m. supracoracoidei in dorsolateral view. In addition, *A. soporata* is characterized by the nonconcave tuber brachialis undivided into two parts (in *Anas*, this tubercle is usually concave and frequently divided by an incisure into two parts), and the distinctly medially displaced processus acrocoracoideus. In *A. soporata*, the processus acrocoracoideus projects medially relative to the shaft for a distance approximately equal to the diameter of the cotyla scapularis; among small ducks, a distinctly projecting processus acrocoracoideus is only characteristic of *A. crecca*, although it projects to a lesser extent.

A. soporata is most similar to *A. crecca* and differs from it in addition to the above-listed characters in the pointed margo medialis at the level of the facies articularis humeralis (in *A. crecca*, the condition of this character is close to that of *A. soporata*) and in the tuber brachialis overhanging the sulcus m. supracoracoidei. An overhanging tuber brachialis is observed in

some species of *Anas*, in particular, in some specimens of *A. penelope* and *A. sibilatrix* (original data); the two species have a deep fossa under the tuber brachialis, which does not contain a pneumatic foramen characteristic of *A. soporata*. In addition to the above-mentioned characters, *A. soporata* differs from other small ducks, *A. querquedula* and *A. discors*, in the absence of an incisure in the sulcus m. supracoracoidei at the level of the base of the processus acrocoracoideus and the convex medial edge of the processus acrocoracoideus (in *A. querquedula* and *A. discors*, this edge is subparallel to the bone medial edge).

R e m a r k s. Morphological differences of the coracoid of *A. soporata* from that of living ducks, which are manifested among other things in the presence of a pneumatic foramen, the narrow sulcus m. supracoracoidei, and the flattened ventral surface of the bone at the level of the facies articularis humeralis, are undoubted evidence of species independence of *A. soporata* and probably characterize an early stage in the evolution of dabbling ducks. *A. soporata* is somewhat more similar to extant *A. crecca* in the extended tuber brachialis and medially displaced processus acrocoracoideus.

A. soporata shows certain similarity to extant *Nettapus*. This is observed in the presence of a medially displaced processus acrocoracoideus, the development of a pneumatic foramen (observed in one specimen of *N. auritus*), pointed margo medialis, deep sulcus m. supracoracoideus, and flattened ventral surface of the shaft at the level of the facies articularis humeralis. At the same time, *A. soporata* differs from *Nettapus* in the structure of the processus procoracoideus (in *Nettapus*, it has an incisure homologous to the foramen n. supracoracoidei), the curved impressio lig. acrocoracohumeralis, ovate facies articularis humeralis, and in the dorsoventrally extended tuber brachialis (which is short and high in *Nettapus*). These differences provide reliable differentiation between *A. soporata* and *Nettapus* and, hence, similarity in the above-listed characters is probably primitive. A much more important point is general similarity of *A. soporata* to living members of *Anas* in the general outline of the bone and the structure of the facies articularis humeralis and similarity to *A. crecca* in the structure of the processus acrocoracoideus.

Mlíkovský and Švec (1986) assigned *A. soporata* to the genus *Dendrocygna*, indicating four characters distinguishing it from *Anas*. Although two of these four characters actually distinguish *A. soporata* from extant *Anas* (medially displaced processus acrocoracoideus and deep sulcus m. supracoracoidei), it is impossible to assign this species to *Dendrocygna*, because, among other things, the plane of the ventral surface of the processus acrocoracoideus of *Dendrocygna* is subperpendicular to the plane of the sternal expansion of the bone. This coracoid structure is primitive for the order Anseriformes (also observed in Anhim-

idae and Anseranatidae). In *A. saporata*, the plane of the processus acrocoracoideus subparallel to the plane of the sternal expansion of the bone, as in extant Anatini and "Cairinini."

A. saporata differs from the other small duck from the Sharga locality, *Mioquerquedula minutissima*, in the dorsoventrally extended tuber brachialis with a pneumatic foramen under it, the processus acrocoracoideus projecting strongly medially relative to the shaft, and in the absence of a distinct groove passing onto the ventral surface of the bone. It differs from *M. velox* from the Middle Miocene of France in the somewhat smaller size (in comparison with the paralectotype, see above) and the distinctly medially displaced processus acrocoracoideus.

An ulna fragment (specimen PIN, no. 2614/119) from the Sharga locality and a number of other bones from localities of the Great Lakes Depression were previously referred to this species (Kurochkin, 1985). The material from the Yavor 1, Hyargas Nuur 2, and Chono Harayh localities belong to dabbling ducks closer in general pattern to living forms and, hence, should be excluded from *A. saporata*. The taxonomic position of the ulna fragment (specimen PIN, no. 2614/119) is impossible to determine to genus (see below). At the same time, the Sharga locality has yielded two more coracoid fragments (specimens PIN, nos. 4869/102, 144) similar to the holotype of *A. saporata* and assigned to this species. These specimens differ from *Mioquerquedula* in the absence of a distinct groove passing onto the ventral surface of the bone.

Material. Holotype and specimens PIN, nos. 4869/102, 144, cranial fragments of right coracoids from the type locality.

We assign to *Mioquerquedula* sp. a proximal fragment of a right humerus (specimen PIN, no. 4869/107) and fragmentary coracoids (specimens PIN, nos. 4869/71, 143, 189, 192) from the Sharga locality (Pl. 17, figs. 2, 4; Fig. 1i). The humerus, although poorly preserved, is reliably distinguished from that of *Anas* in the subtriangular tuberculum dorsale, as in primitive anatids (in *Anas*, this tubercle is always elongated). The coracoids display a groove passing onto the ventral side, which is characteristic of this genus (see above). In addition, specimens PIN, nos. 4869/143 and 189 have an impressio m. supracoracoideus, as the holotype *M. minutissima*, and specimen PIN, no. 4869/143 is similar to the holotype of *M. minutissima* in the structure of the sulcus m. supracoracoideus (the cranial part of the sulcus contains a fossa, but a pneumatic foramen characteristic of *A. saporata* is absent). At the same time, the specimens in question differ from the holotype of *M. minutissima* in the somewhat larger size and, hence, could have belonged to a separate species. Because of incomplete preservation, it is impossible to determine more precisely the taxonomic status of these specimens.

Remains of small dabbling ducks are rather common in Sharga. The collection of PIN from this locality contains (Pl. 17, figs. 5, 7; Fig. 1a) fragments of a coracoid (specimen PIN, no. 4869/223), scapula (specimen PIN, no. 4869/80), humerus (specimens PIN, nos. 4869/25, 54, 56, 115), ulna (specimens PIN, nos. 2614/19, 119, 4869/215), and femur (PIN, nos. 4869/5, 99) identified as Anatinae gen. indet.; it is impossible to assign them with certainty to *Mioquerquedula* or *Anas*.

CONCLUSIONS

Thus, remains of herbivorous dabbling ducks from the Middle Miocene of the Sharga locality provide evidence of significant diversity of anatids inhabiting at that time the area of modern Mongolia. On the other hand, diving ducks, living members of which feed mostly on benthos, were also diverse in Sharga (Zelenkov, 2011a); the same is true of herons (Zelenkov, 2011b), which inhabit shores of water bodies rich in animal food. This is evidence of the presence of a lake rich in various food resources, which was located at the end of the Middle Miocene in the area of the modern Shargyn Govi Desert. This situation contrasts with the impoverishment of the aquatic fauna in the Early (and particularly Late) Pliocene (Sytchevskaya, 1983), which was accompanied by an increase in salinity in water bodies and, in particular, a decrease in taxonomic diversity of diving ducks.

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