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RESEARCH PAPER

Three bird taxa (Aves: Anatidae, Phasianidae, Scolopacidae) from the Late Miocene of the Sea of Azov (Southwestern Russia)

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Abstract European Late Miocene avian faunas are very insufficiently known. Until now, no Mio-Pliocene birds have been described from the eastern part of the Eastern Paratethys, and the entire record of birds from the Eastern Paratethys is restricted to several poorly described taxa from Ukraine and Moldova. Here we describe the remains of three bird species from the recently discovered Late Miocene vertebrate locality Morskaya-2, which has yielded the first known avian fauna of this age in the European part of Russia and also the easternmost Neogene avian fauna in Europe. The three taxa represent the families Phasianidae, Anatidae and Scolopacidae, which have not been documented from the Miocene of the Eastern Paratethys before. A small quail from Morskaya is assigned to *Plioperdix hungarica* comb. nov., which was previously known from the Late Miocene of Hungary. We show that the morphology of the acrocoracoid process of the coracoid is very diagnostic in phasianids and fits the molecular phylogeny of the family relatively well. Apomorphic characters indicate that *Plioperdix* is a sister taxon of the extant genus *Coturnix*. A medium-sized duck is assigned to the genus *Anas* s.s. and described as a new species, *A. kurochkini* sp. nov. Although metrically close to *S. clypeata*, this duck is morphologically distinct from all extant dabbling ducks. The presence of the quail and the duck indicates a certain degree of similarity between the avian faunas across the northern borders of the Central and Eastern Paratethys in the latest Miocene. The third reported taxon is a large snipe, which is described here as *Gallinago azovica* sp. nov.

Keywords Miocene · Avian faunas · Paratethys · Anatidae · Phasianidae · Scolopacidae

Kurzfassung Europäische Avifaunen des späten Miozäns sind nur sehr ungenügend bekannt. Es sind bisher keine Nachweise von mio-pliozänen Vogelresten aus dem östlichen Teil der Ost-Paratethys beschrieben worden. Die komplette Überlieferung fossiler Vögel aus der östlichen Paratethys beschränkt sich auf einige, sehr dürftig beschriebene Taxa aus der Ukraine und aus Moldavien. Es werden Reste von drei Vogelarten aus der kürzlich entdeckten, obermiozänen Vertebratenfundstelle Morskaya-2 beschreiben. Diese Lokalität lieferte den Erstnachweis einer Avifauna aus dieser Zeit des Europäischen Teils von Russland und zugleich die östlichste in Europa gefundene Avifauna aus dem Neogen. Die drei beschriebenen Taxa repräsentieren die Familien Phasianidae, Anatidae und Scolopacidae, welche bisher aus dem Neogen der östlichen Paratethys unbekannt waren. Eine kleine Wachtel von Morskaya wird als *Plioperdix hungaricus* comb. nov. bestimmt, welche bereits aus dem späten Miozän von Ungarn bekannt ist. Wir zeigen, dass die Morphologie des Processus acrocoracoides des Coracoids ein gutes diagnostisches Merkmal der Phasanidae darstellt und relativ gut mit der molekularen Phylogenie dieser Familie korreliert. Die apomorphen Merkmale weisen darauf hin, das *Plioperdix* ein Schwester-Taxon der noch vorhandenen Gattung *Coturnix* darstellt. Ein mittelgroßer Vertreter der Entenvögel wird der Gattung *Anas* s.s. zugeordnet und als neue Art *A. kurochkini* nov. sp. beschrieben. Obwohl die

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metrischen Daten diese Art auch annähernd zu *S. clypeata* passen, unterscheidet sich dieser Entenvogel jedoch morphologisch von allen vorhandenen Vertretern dieser Gattung. Das Auftreten von Wachtel- und Entenvögeln deutet zuverlässig auf eine Ähnlichkeit der spätmiozänen Avifaunen über die nördlichen Grenzen der Zentral und Östlichen Paratethys hin. Das dritte überlieferte Taxon, eine große Schnepfe, wird als *Gallinago azovica* nov. sp. beschrieben.

Schlüsselwörter Miozän · Avifaunen · Paratethys · Anatidae · Phasianidae · Scolopacidae

Abbreviations

IPEE	Laboratory of biocenology and historical ecology of the A.N. Severtsov Institute of Ecology and Evolution of the Russian Academy of Sciences, Moscow
MNHN	Muséum national d'histoire naturelle Paris
NMNH	National Museum of Natural History Kiev
PIN	Borissiak Paleontological Institute of the Russian Academy of Sciences Moscow
SMNS	Staatliches Museum für Naturkunde Stuttgart
ZIN	Zoological Institute of the Russian Academy of Sciences, Saint Petersburg

Introduction

It has long been understood that the origin of modern bird faunas began in the Neogene, a period when the vast majority of modern bird genera appeared in the fossil record for the first time. However, the details of the formation of modern avian faunas remain poorly known. In Europe, environmental conditions varied significantly through time and space during the Miocene, which itself seriously influenced the taxonomical and ecological structures of the communities of terrestrial animals (Fortelius et al. 1996). As a result, different groups of mammals, now inhabiting the Western Palearctic, have drastically different evolutionary histories (Bernor et al. 1996).

The fossil record of birds is still too incomplete to draw evolutionary conclusions for particular avian taxa. We know a lot about the Early and Middle Miocene terrestrial bird faunas of Western and Central Europe (see Mlíkovský 2002), but growing independent evidence from various groups of birds (Manegold et al. 2004; Manegold 2008; De Pietri et al. 2011; De Pietri and Mayr 2012) indicates that the avian communities of this time were comprised mostly of extinct lineages, and recent genera were rare (see, for example, the list of bird taxa from the famous Early Miocene Saint-Gérand-le-Puy locality in Mourer-Chauviré et al. 2013). A turnover that led to the origin of the modern taxonomic diversity of birds in Europe probably occurred during the Late Miocene, but avian remains of this age are extremely rare in Western and Central Europe. Late Miocene birds are much better known from Eastern Europe, with the most important bird localities occurring in Hungary, Moldova and Ukraine (e.g., Kurochkin and Ganea 1972; Jánossy 1991; Kessler 2009a, b). Unfortunately, data from Eastern territories are still of very limited use for reconstruction of the evolution of avian communities because bird taxa were often very superficially described and extensive comparisons were limited (Jánossy 1979, 1991, 1993; Sobolev and Marisova 2011).

Here we describe remains of a quail, a duck and a large snipe from the recently discovered (Titov et al. 2006) locality Morskaya-2 in Southern Russia (Sea of Azov region; Fig. 1). This is the first Neogene locality with avian remains from the territory of European Russia and is the eastern-most Neogene avian locality in Europe. The closest localities that have yielded Late Miocene birds are those in the eastern Ukraine and Moldova, which are some 600 km away from Morskaya. Details of the locality and associated Turolian (late MN 12-early MN 13) fauna are provided elsewhere (Titov et al. 2006; Titov and Tesakov 2013). The three bird taxa described here represent families that are very common in the fossil record; thus, they can be used to compare different avian faunas. A small quail from Morskaya-2 is referred to a species previously described from Hungary, which is here transferred to the genus *Plioperdix*. A medium-sized duck is described as a new species, probably close to Mallards (*A. platyrhynchos*; *A. poecilorhyncha,* and others) but much smaller. The third reported taxon is a large extinct snipe, which is also described here as a new species.

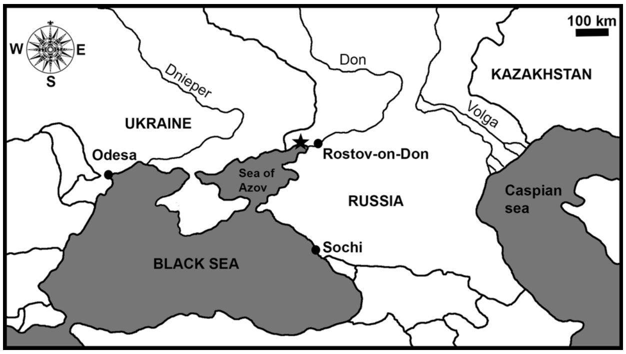

Fig. 1 Map of the Black Sea region showing the location (*star*) of the Morskaya-2 locality near Taganrog (Rostov Oblast; Russia)

Materials and methods

For comparative purposes, Miocene birds were examined in the collections of the PIN (see list of abbreviations below), MNHN, NMNH and SMNS as well as the natural history museums in Vienna, Berlin and Stuttgart and the Paläontologisches Museum München. Comparative osteological collections of the PIN, IPEE, MNHM, NMNH and ZIN were used (see Appendix). Osteological nomenclature follows Nomina Anatomica Avium (NAA; Baumel and Witmer 1993). For the medial surface of the acrocoracoid process of the coracoid, which serves as an attachment site for the ligg. acrocoracoclavicularii, we use the term "tuberculum brachiale" (Ballmann 1969; Baumel and Witmer 1993) rather than "facies articularis clavicularis," because the articulation between the coracoid and furcula is not developed in the studied groups of birds (it is present, for example, in accipitriforms and some "pelecaniforms" where the ventrally oriented articular facet is distinct from the medially oriented surface of the acrocoracoid process). The ventral surface of the acrocoracoid process bears impressions or tubercles for the origin of m. coracobrachialis cranialis and the coracoid head of m. biceps brachii. Elzanowski and colleagues (Elzanowski et al. 2012) name these structures "impressio coracobrachialis" and "impressio bicipitalis", respectively. In Galliformes, there is only one well-developed impression here, which was called "impressio bicipitalis" by Butendieck (1980). Indeed, m. coracobrachialis cranialis is inconspicuous in Phasianidae and may even have its origin on the proximal tendon of m. biceps brachii (Sych 1985). Thus, we use "impressio bicipitalis" for the attachment site situated on the ventral surface of the acrocoracoid. The taxonomy of the extant birds follows Dickinson and Remsen (2013).

Systematic paleontology

Order GALLIFORMES Temminck, 1820
Family PHASIANIDAE Vigors, 1825
Genus ***Plioperdix*** Kretzoi, 1955
Plioperdix hungarica (Jánossy 1991), comb. nov.

Referred specimens Partial notarium (ZIN PO 7344); sympheseal portion of furcula (ZIN PO 7348); incomplete right (ZIN PO 7337, 7338, 7335, 7350, 7353, 7359, 7513) and left (ZIN PO 7333, 7334, 7336, 7351, 7352, 7354, 7356, 7358, 7512) coracoids; cranial fragments of right (ZIN PO 7345) and left (ZIN PO 7346) scapulae; distal fragment of right tarsometatarsus (ZIN PO 7343)-see Fig. 2a, b, j, l, m.

Occurrence Late Miocene (MN 12-13) of Hungary and Southeast Russia.

Measurements (mm) Coracoid: dorsoventral depth of tuberculum brachiale 3.6 (ZIN PO 7335, 7353, 7512), length of facies articularis humeralis + facies articularis scapularis 6.5 (ZIN PO 7335, 7350, 7353), 6.6 (ZIN PO 7512), dorsoventral depth at the level of processus procoracoideus 2.9 (ZIN PO 7335), 2.8 (ZIN PO 7335), 2.7 (ZIN PO 7350, 7512), minimal mediolateral shaft width 2.2 (ZIN PO 7350). Scapula: maximal height (dorsoventral) of the caput scapulae 5.3 (ZIN PO 7345), minimal shaft height (just caudal to the facies articularis humeralis) 2.2 (ZIN PO 7345).

Differential diagnosis The coracoid of *P. hungarica* differs from that of *P. pontica* in the considerably mediolaterally narrower but dorsoventrally thicker shaft and better developed incisure in the caudal margin of the acrocoracoid process (Fig. 2, Character 1) as well as in the presence of a longitudinal depression on the medial surface of the tuberculum brachiale. From *P. africana* Mourer-Chauviré et Geraads, 2010, it differs by the considerably smaller size. *P. hungarica* differs from *Palaeocryptonyx* in the straight caudal margin of the tuberculum brachiale (concave in *Palaeocryptonyx*), non-prominent impressio bicipitalis (sensu Elzanowski et al. 2012) and thinner shaft at the level of the facies articularis humeralis. *P.hungarica* differs from *Palaeortyx* in the short facies articularis humeralis with a bulbous ventral labrum, the strongly cranially protruding and caudally unhooked processus acrocoracoideus and the distinct (although flat) medially shifted impressio bicipitalis. From *Bantamyx* it differs in the medially shifted process acrocoracoideus. From extant *Coturnix* (including early Pleistocene *Chauvireria* Boev 1997) it differs in the less pronounced incisure in the caudal margin of the processus acrocoracoideus. From all other extant genera it differs in the medially offset acrocoracoid and narrow shaft at the level of the facies articularis humeralis.

Description and comparisons The small phasianid bird from Morskaya agrees in size with *Palaeocryptonyx hungaricus* Jánossy 1991 from the Late Miocene (MN 13) of Hungary (Jánossy 1991; Kessler 2009b). Both the Morskaya and Hungarian fossils show features characteristic of the genus *Plioperdix* (see below); hence, *Palaeocryptonyx hungaricus* is moved here to *Plioperdix*.

Palaeocryptonyx hungaricus, illustrated by Jánossy (Jánossy 1991; Fig. 2), has the typical morphology of the genus *Plioperdix*. In the coracoid, the extremitas omalis is not inclined medially, and a notch in the caudal margin of the acrocoracoid process is present. Thus, the medial margin of the shaft at the level of the facies articularis humeralis runs roughly parallel to the lateral margin and is not inclined medially (Jánossy 1991). This condition is

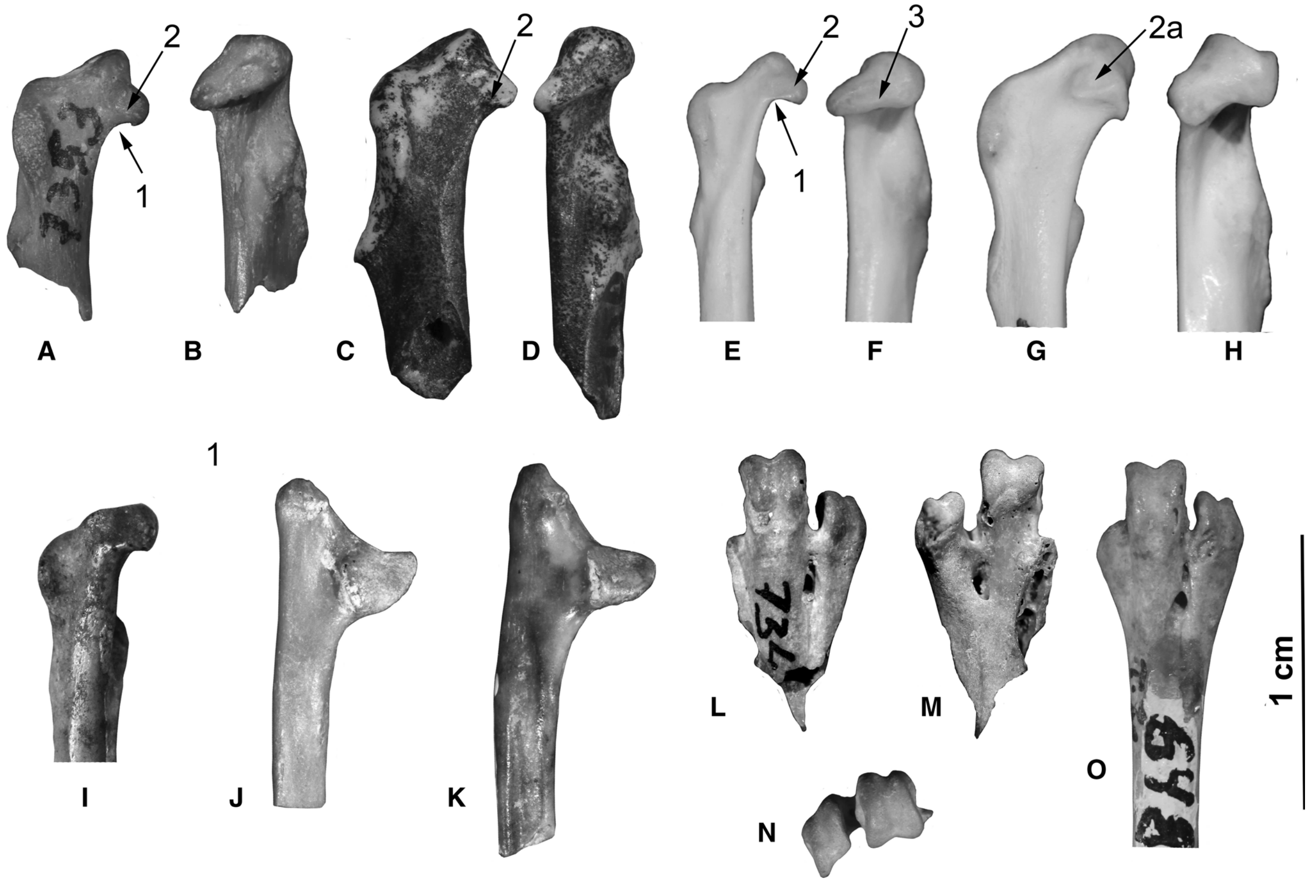

Fig. 2 *Plioperdix hungarica* from the Late Miocene of Morskaya-2 (Southern Russia) compared with other small Phasianidae. **a**, **b**, **j**, **l**, **m**, **n** *Plioperdix hungarica*: **a**, **b** right coracoid ZIN PO 7353, ventral (**a**) and medial (**b**) views; **j** right scapula ZIN PO 7345, lateral view; **l**–**n** distal fragment of right tarsometatarsus ZIN PO 7343, dorsal (**l**), ventral (**m**) and distal (**n**) views. **c**, **d**, **k**, **o** *Plioperdix pontica*. **c**, **d** left coracoid (reversed) PIN 2975-120, Late Pliocene of Beregovaya (Transbaikalia), ventral (**c**) and medial (**d**) views. **k** Right scapula PIN 2614-139, Early Pliocene of Kotlovina (Ukraine), lateral view; **o** right tarsometatarsus ZIN 6489, lectotype, Early Pliocene of Odessa catacombs (Ukraine), dorsal view. **e**, **f** *Coturnix japonica*, extant, right coracoid PIN 49-67-1, ventral (**e**) and medial (**f**) views. **g**, **h** *Ammoperdix griseogularis*, extant, right coracoid PIN 49-2-2, ventral (**g**) and medial (**h**) views. **i** *Palaeortyx brevipes*, Early Miocene of Saint-Gérand-le-Puy (France), left coracoid (reversed) MNHN Av 2897, ventral view. Designations: *1* well-developed notch in the caudal margin of the acrocoracoid process; *2* medially shifted and ventrally not-protruding impressio bicipitalis; *2*a strongly ventrally protruding impressio bicipitalis; *3* straight (non-concave) caudal margin of tuberculum brachiale

clearly advanced since it is not present in most Phasianidae. In the figured specimens of *Palaeocryptonyx* from different localities and age, the medial margin of the shaft is considerably inclined medially (Sánchez Marco 2009; Pavia et al. 2012; Bedetti and Pavia 2013; own observations by NVZ). The humerus of *Plioperdix* is very characteristic in that its pectoral crest is offset from the shaft distally (Fig. 3; see also Kurochkin 1985); this is also present (although to a lesser degree) in the holotype humerus illustrated by Jánossy (Jánossy 1991; Figs. 2, 6). This feature is visible in both cranial and caudal views. *Coturnix* has a somewhat similar (although less offset) pectoral crest, and other Phasianidae completely lack such morphology (Fig. 3). This unambiguous synapomorphy of the humerus further supports the clade *Plioperdix* + *Coturnix,* and also the inclusion of *Chauvireria balcanica* into *Coturnix* (see below). In the tarsometatarsus, the trochlea metatarsi IV is pressed to the trochlea metatarsi III in *P. hungaricus* and *P. ponticus* (see below). The above features demonstrate that *Palaeocryptonyx hungaricus* is indeed a member of the genus *Plioperdix*.

The type species of the genus *Plioperdix* is *P. pontica,* which is known from the late Early Pliocene of Ukraine and Moldova and the Late Pliocene of Mongolia and Transbaikalia (see Zelenkov and Kurochkin 2009). Although complete coracoids of the small phasianid bird from Morskaya are not known, several partial fragments allow reconstruction of most of the details. Importantly, the preserved cranial fragments of the coracoid show almost no variation in morphology.

The coracoid of *P. hungarica* from Morskaya looks smaller than the corresponding bone of *P.pontica* (Fig. 2),

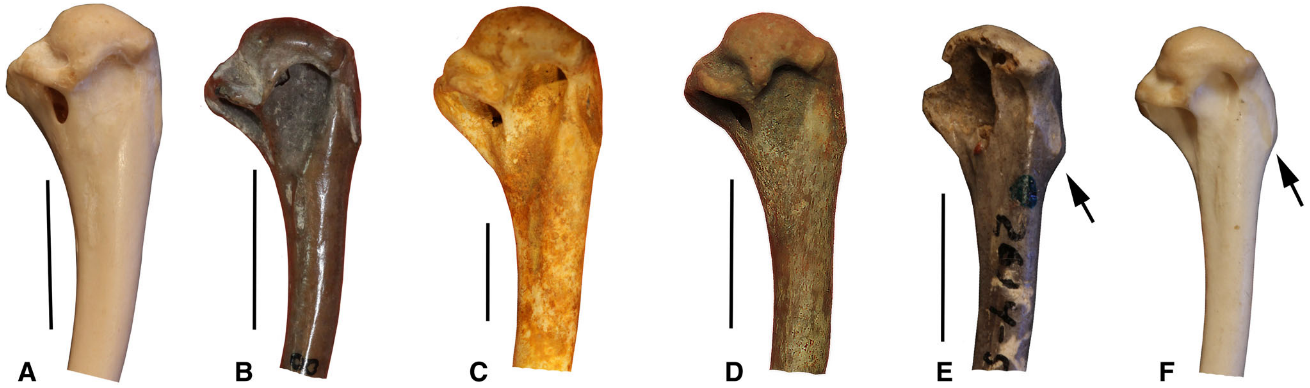

Fig. 3 Proximal humeri of small phasianids in caudal views. **a** *Bambusicola thoracica*, extant, PIN 49-102-1; **b** *Palaeortyx brevipes*, MNHN Av 2898; Early Miocene of Saint-Gérand-le-Puy (France); **c** *Palaeortyx intermedia*, Paläontologisches Museum München 18001 (reversed), Early Miocene of Wintershof-West (Germany); **d** *Palaeocryptonyx depereti*, MNHN uncatalogued, Middle Miocene of la Grive-Saint-Alban (France); **e** *Plioperdix pontica*, PIN 2614-59, Early Pliocene of Etulia (Moldova); **f** *Coturnix japonica*, extant, PIN 49-67-1. Arrows indicate the apomorphically offset distal end of the pectoral crest in *Coturnix* and especially *Plioperdix*

but this effect may result from the reduced shaft width in the former species because the length of the facies articularis humeralis + cotyla scapularis is roughly similar in both species. The extremitas omalis is not well preserved in the only known coracoid of *P. africana*, but the African species is on average 30 % larger than *P. pontica* (Mourer-Chauviré and Geraads 2010). In *P.hungarica,* the impressio bicipitalis on the ventral surface of the acrocoracoid is non-prominent (like in *P. pontica, Coturnix* and *Synoicus*; Fig. 2). This condition is here considered a synapomorphy of the clade *Plioperdix* + *Coturnix* and distinguishes both genera from other phasianids where this facies is prominent (projecting ventrally), including *Palaeocryptonyx* (see discussion below). Another characteristic feature of the acrocoracoid in *P. hungarica* is that the whole impressio bicipitalis (together with the ventral part of the tuberculum brachiale) is shifted medially (Fig. 2). This character is found in several evolutionarily advanced genera of phasianids (*Alectoris, Francolinus, Coturnix, Synoicus*), but is not characteristic of the primitive Rollulinae and the extinct genus *Palaeortyx*, where the impressio is more laterally situated (Figs. 2i, 4). The primitive (perhaps secondary) condition is illustrated in *Ammoperdix* (Fig. 2g). The acrocoracoid process of *P. hungarica* from Morskaya is protruding cranially to a larger extent than in *Palaeocryptonyx* and especially *Palaeortyx*, and it is similar to the condition in *P. pontica* and extant *Ammoperdix* and *Coturnix*. This is evidently an advanced evolutionary character because primitive forms have an acrocoracoid that is less protruding cranially (a discussion of the evolutionary transformation of the coracoid in Phasianidae is given below).

The impressio lig. acrocoracohumeralis is rather short and oval in shape (as in *Palaeocryptonyx*), while it is more elongate in *P. pontica*. The ventral margin of this impressio is slightly convex—an advanced character (based on the phylogeny of Wang et al. 2013; see below) found only in *Ammoperdix* + *Coturnix* clade and in *P. pontica.* The tuberculum brachiale is craniocaudally low and dorsoventrally oblong in medial view, as in *Palaeocryptonyx* and *P. pontica,* and slightly overhanging the sulcus m. supracoracoideus; the caudal margin of the tuberculum brachiale is straight (another probable synapomorphy of the *Coturnix* + *Plioperdix* clade) and marked by a distinct ridge that is also present in *P. pontica* but is not evident in *Palaeocryptonyx*. On the medial surface of the tuberculum brachiale there is a shallow but well visible longitudinal excavation. A similar excavation is present in extant *Coturnix* and all specimens of *P. hungarica* from Morskaya, but not in *P. pontica* and *Palaeocryptonyx*. At the level of the facies articularis humeralis, the shaft is considerably narrower mediolaterally than in *P. pontica*, *Palaeocryptonyx* and *Palaeortyx*. The shaft is also thinner (dorsoventrally narrower) in *P. hungarica* than in *Palaeocryptonyx* and *Palaeortyx,* but is still thicker than in *P. pontica* (the latter species has an autapomorphically thin shaft).

The angulus medialis of the extremitas sternalis protrudes medially to a considerably smaller degree than in *Palaeocryptonyx* and *P. africana*. The facies articularis sternalis is less curved than in *P. africana*. In these two features, the sternal fragments of the coracoid from Morskaya are similar to Hungarian specimens. The extremitas sternalis of *P. pontica* is not known. The specimen PIN 3381/452, illustrated by Zelenkov and Kurochkin (2009), indeed belongs to a Scolopacid wader (new identification by NVZ).

The scapula (ZIN PO 7345) is also slightly smaller than the corresponding element of *P. pontica* (Fig. 2j, k). The

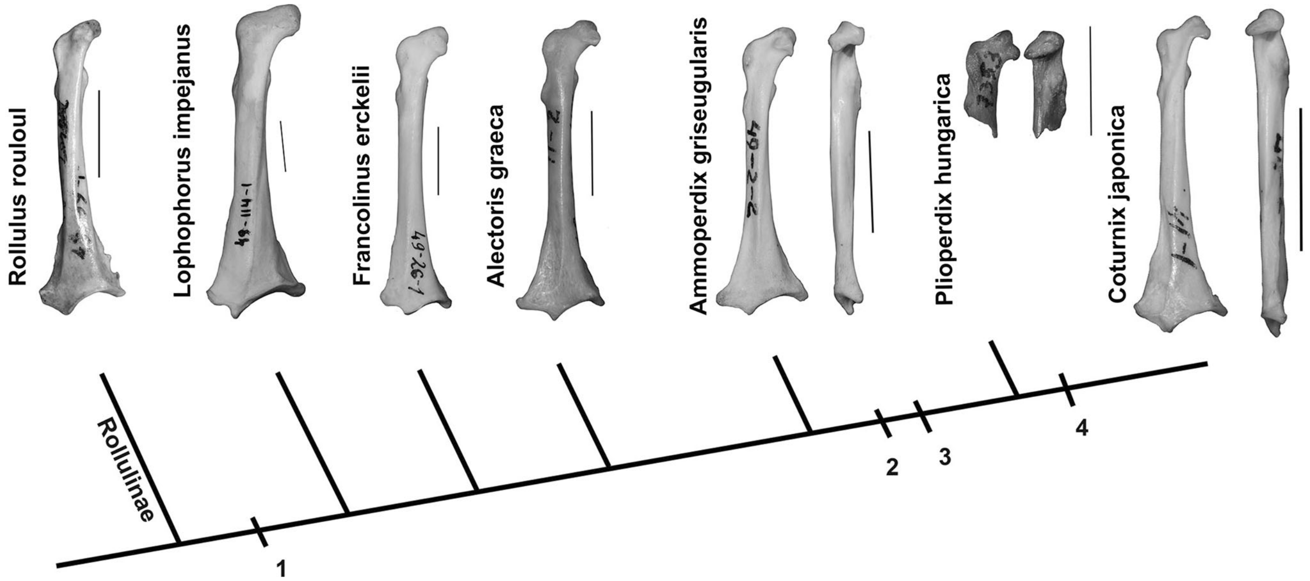

Fig. 4 Simplified phylogeny of Phasianidae (after Wang et al. 2013) showing the evolution of the coracoid morphology on the way to extant *Coturnix* quails. Apomorphies: *1* medially shifted acrocoracoid; *2* tuberculum brachiale with straight caudal margin; *3* flat (not protruding) impressio bicipitalis; *4* well-developed incisure in the caudal margin of the acrocoracoid process. *Scale bar* 1 cm

acromion is shorter than in *P. pontica, Palaeortyx* and extant *Ammoperdix*. The facies articularis humeralis is craniocaudally longer and dorsoventrally lower than in *P. pontica* (the craniocaudal length of the facies is sub-equal to its dorsoventral length in *P. hungarica*). The scapular blade is thin, its lateral surface is flat, and a groove characteristic of *P. pontica* is missing. Like in *P. pontica,* but in contrast to *Palaeortyx*, the tip of the acromion is not laterally widened, and thus the acromion is almost twice as narrow as the facies articularis humeralis in cranial view (in *Palaeortyx*, the acromion is wider than the facies articularis humeralis in cranial view). The scapula of *Palaeocryptonyx* spp. has not been described.

The tarsometatarsus (ZIN PO 7343) generally resembles that of the extant genus *Coturnix*. The shaft appears to be wide at the level of the fossa metatarsi I, wider than in *P. pontica,* but the trochleae are the same size as in *P. pontica* (Fig. 2l–o). The whole bone thus was probably more robust than in *P. pontica,* but this feature is subject to individual variation at least in *Ammoperdix* (our data). The trochlea metatarsi IV is only slightly narrower than the trochlea metatarsi III in distal view and less offset from the trochlea metatarsi III than in *Ammoperdix*. The same morphology is visible in the specimen of *P. hungarica* illustrated by Jánossy (Jánossy 1991; Fig. 2), in which the trochlea metatarsi II seems to be less pressed to the trochlea metatarsi III than in *P. pontica*. In this clearly primitive feature, *P. hungarica* is more similar to *Ammoperdix*. The trochlea metatarsi III is thin in *P. hungarica,* as in *P. pontica* (wide in *P. africana*). The articular surface of the trochlea metatarsi III on the ventral side is strongly asymmetrical, with a short medial semi-condyle—a somewhat similar condition is also found in *Coturnix coturnix*. In *P. pontica*, the articular surface of the third trochlea is longer in ventral view and only slightly asymmetrical. *Palaeortyx* and *Palaeocryptonyx* appear to be undistinguishable from each other on the basis of the distal tarsometatarsus alone (see Göhlich and Mourer-Chauviré 2005). The degree of asymmetry of the trochlea metatarsi III varies among different *Palaeortyx* species (our data).

Other skeletal elements are either poorly preserved or non-diagnostic. They are referred to this species based on the relative size and resemblance with the corresponding bones of *Coturnix coturnix*.

Remarks In order to evaluate the systematic significance of the characters of the coracoid, we have mapped them onto the most comprehensive recent phylogeny of Phasianidae (Wang et al. 2013) and found that this bone has a high phylogenetic signal, especially compared to other postcranial elements, which are very uniform in phasianids. A series of examined skeletons of wild birds shows that the acrocoracoid region has a very stable morphology and shows very limited intraspecific variation. Representatives of the subfamily Rollulinae (Dickinson and Remsen 2013), which were recovered as the sister clade of the other Phasianidae, have a rather uniform morphology of the coracoid, with the whole cranial one-third of the bone (shaft + acrocoracoid) essentially shifted medially (Fig. 4). The acrocoracoid, in turn, is not protruding medially relative to the shaft (Fig. 4). This morphology, which allows distinguishing Rollulinae from other Phasianidae, was found in *Arborophila* and *Rollulus*. Also in Rollulinae, the impressio bicipitalis is positioned laterally, i.e., close to the long axis of the bone. A similar structure of the coracoid is retained in *Pavo*, which evidently represents a primitive condition, because peacocks were resolved as a sister group of the remaining Phasianidae in one analysis (Wang et al. 2013). In the remaining lineages, it is not the cranial-one third of the bone but the acrocoracoid process that is inclined medially. Primitive taxa within different phylogenetic lineages (*Argusianus, Ithaginus, Tragopan, Lophophorus*) are hardly distinguishable from one another, and they all have strongly medially shifted acrocoracoids and usually a labrum of the facies articularis humeralis that is not protruding below the ventral margin of the bone (exemplified by *Lophophorus*, Fig. 4). Importantly, the ventral plane of the acrocoracoid is continuous with the ventral plane of the bone in these taxa. In the *Perdix-Phasianus* lineage (*Perdix, Phasianus, Crossoptilon, Lophura, Syrmaticus, Chrysolophus, Cathreus* were examined; see Wang et al. 2013), the acrocoracoid approaches the shaft and its ventral plane rotates ventrally; thus, the whole cranial end becomes narrower. In this lineage, the acrocoracoid process is more ventrally protruding than the rest of the bone, which is obviously a synapomorphy of this clade. In the *Francolinus-Coturnix* lineage (see Wang et al. 2013), to which we assign *Plioperdix*, the acrocoracoid remains shifted medially, but the impressio bicipitalis protrudes further medially (*Coturnix, Plioperdix, Alectoris*) than the medial margin of the process. Importantly, the ventral rotation of the coracoid is not present in this lineage. In *Coturnix* the whole extremitas omalis is considerably modified in comparison with its close relatives (*Alectoris, Ammoperdix, Francolinus*). In *Coturnix* there is a notch in the caudal margin of the acrocoracoid process just caudal to the impressio bicipitalis (Fig. 2), the impressio itself is not protruding ventrally (which is obviously a secondary condition), and the caudal margin of the tuberculum brachiale is straight (Figs. 2, 4). Closely related taxa (*Alectoris, Ammoperdix, Francolinus*) differ in these morphologies. *Plioperdix* has a similarly advanced (as in *Coturnix*) morphology except for the notch, which is less developed in this fossil genus. However, in *Plioperdix* this notch is larger than in any other phasianids, approaching the condition of *Coturnix*. Thus, *Plioperdix* is probably a sister genus or even an ancestor of the extant *Coturnix*. However, *Plioperdix* has a more specialized morphology of the pectoral crest (see above); thus, a sister group relationships with *Coturnix* seems more likely. Judging from the published photographs, the early Pleistocene (MN 17) European small phasianid genus *Chauvireria* (Boev 1997) is identical to *Coturnix* in coracoid morphology (and apparently other elements) and thus can be treated as a junior synonym of this extant genus. Notably, the *Francolinus-Coturnix* lineage has a clear evolutionary tendency of size decrease (Fig. 4); in accordance with this tendency, the Mio-Pliocene *Plioperdix* is bigger than all extant quails of the genus *Coturnix*.

It is noteworthy that in *Alectoris, Plioperdix* and *Coturnix*, the impressio bicipitalis is shifted medially in such a manner that it protrudes further medially than the cranial end of the acrocoracoid process. In Rollulinae, in contrast, the facies is positioned at the level of the shaft (Fig. 4). The extinct Oligocene-Miocene genus *Palaeortyx* (Mourer-Chauviré 1992; Göhlich and Mourer-Chauviré 2005) is intermediate between Rollulinae and basal Phasianinae (like *Lophophorus*) in the structure of the acrocoracoid. This observation is in agreement with conclusions by other authors: Ballmann (1969) considers *Palaeortyx* to be close to *Arborophila* (Rollulinae), and Mayr and colleagues (Mayr et al. 2006) noticed that the hind limb proportions of *Palaeortyx* were different from those of the crown Phasianidae.

The genus *Plioperdix* has been reported from the late Early Pliocene (MN 15) of the Black Sea region in Eastern Europe (Kurochkin 1985; Bocheński and Kurochkin 1987) and from the Late Pliocene (MN 16) of Mongolia and Russian Transbaikalia in Asia (Kurochkin 1985; Zelenkov and Kurochkin 2009). The recently described African representative of the genus, *Plioperdix africana* from the Late Pliocene of Morocco (Mourer-Chauviré and Geraads 2010), apparently lacks an apomorphically offset pectoral crest of the proximal humerus, but has a narrow distal tarsometatarsus (particularly a trochlea metatarsi II that is pressed to the trochlea metatarsi III), as in *Coturnix* and *Plioperdix*.

Order ANSERIFORMES Wagler, 1831
Family ANATIDAE Vigors, 1825
Genus ***Anas*** Linnaeus, 1758
Anas kurochkini sp. nov.

Etymology In honor of paleornithologist Evgeny Kurochkin

Holotype ZIN PO 7281, complete right coracoid (Fig. 5a, d, f).
Referred material ZIN PO 7282, 7287, partial left coracoids.

Type locality and horizon Locality Morskaya-2 near Morskaya railroad station, Rostov Oblast, northeastern Sea of Azov region, Russia. Greenish clay member, Middle Turolian (late MN 12–early MN 13).

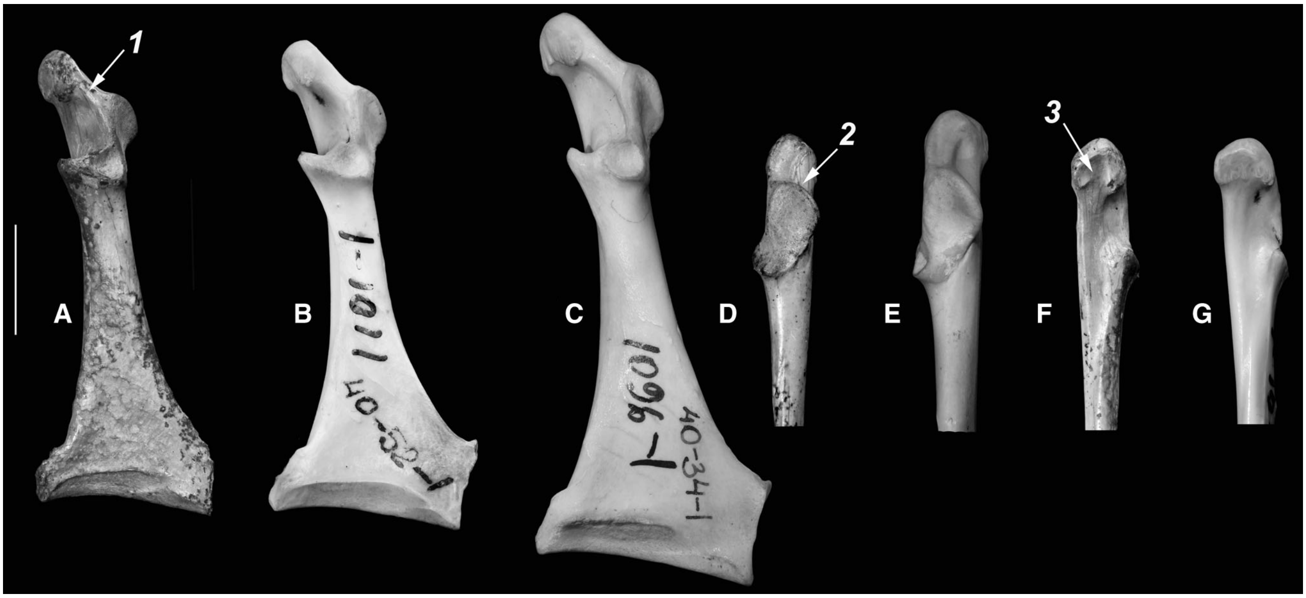

Fig. 5 *Anas kurochkini* sp. nov. from the Late Miocene of Morskaya-2 (Southern Russia) compared with extant dabbling ducks. **a**, **d**, **f** *Anas kurochkini* sp. nov., holotype right coracoid ZIN PO 7281, dorsal (**a**), lateral (**d**) and medial (**f**) views. **b**, **g** *Spatula clypeata*, extant, right coracoid PIN 40-52-1, dorsal (**b**) and medial (**g**) views. **c**, **e** *Anas poecilorhyncha*, extant, right coracoid PIN 40-34-1, dorsal (**c**) and lateral (**e**) views. Designations: *1* unusually thin ridge connecting cranial angle of facies articularis humeralis with tuberculum brachiale; 2 wide cranial angle of facies articularis humeralis; *3* dorsoventrally thin tuberculum brachiale. *Scale bar* 1 cm

Table 1 Measurements of the coracoid in the fossil species *Anas kurochkini* and several extant species of ducks. Cranial end is measured from the cranial end to the caudal margin of cotyla scapularis

Taxon	*N*	Total medial length (cm); *M* ± σ (min–max)	Minimal shaft width (cm); *M* ± σ (min–max)	Length of cranial end (cm); *M* ± σ (min–max)
Anas kurochkini sp. nov.	1	40.3	4.9	14.1
Spatula clypeata	14	41.2 ± 1.3 (39.3–43.1)	4.6 ± 0.2 (4.2–5.0)	14.2 ± 0.5 (13–14.9)
Spatula querquedula	12	35.9 ± 1 (34.5–37.7)	3.8 ± 0.2 (3.4–4.1)	12.1 ± 0.4 (11.4–12.9)
Sibirionetta formosa	2	37.4, 38.9	3.9, 4.2	12.5, 12.6
Mareca penelope	20	43.0 ± 2.2 (38.1–45.4)	5.1 ± 0.3 (4.2–5.6)	15.4 ± 0.9 (14.3–16.3)
Mareca strepera	12	44.7 ± 1.4 (42.3–48.2)	5.3 ± 0.3 (4.8–5.8)	16.4 ± 0.4 (15.7–16.9)
Anas acuta	13	44.6 ± 2 (40.5–47.4)	5.1 ± 0.5 (4.4–5.6)	15.9 ± 0.9 (14–17.5)

Occurrence Type locality and probably other Late Miocene (Turolian) localities in Ukraine and Hungary (see "Remarks").

Measurements See Table 1.

Differential diagnosis Dabbling duck intermediate in size between extant *Spatula clypeata* and *Sibirionetta formosa*, being metrically closer to the former species. Differs from all extant species of dabbling ducks (*Anas* s. l.) in the combination of the following three characters: (1) facies articularis humeralis craniocaudally short, with obtuse cranial angle; (2) crista acrocoracoidea thin and very short; (3) tuberculum brachiale dorsoventrally narrow. Differs from Aythyini and Mergini in that the ventral plane of the processus acrocoracoideus lies sub parallel to the ventral plane of the extremitas sternalis. From primitive members of Anatinae (the paraphyletic tribe "Cairinini") it differs in the medially inclined extremitas omalis.

Description and comparisons The new species can be referred to the dabbling ducks (genus *Anas* s. l.) and differs from Aythyini and Mergini in that the ventral plane of the processus acrocoracoideus lies subparallel to the ventral plane of the extremitas sternalis. In the mentioned tribes, the ventral plane of the processus acrocoracoideus is inclined with respect to the plane of the extremitas sternalis. The tribe Aythyini is likely a sister group of Anatini (Gonzalez et al. 2009); thus, the characters that are present in Aythyini are considered primitive in the following comparisons and discussion.

The tuberculum brachiale is craniocaudally high and dorsoventrally narrow (Fig. 5), which is clearly a primitive condition typical of diving ducks (*Aythya*) and retained in *Sibirionetta*. In *Anas* and *Mareca*, this tuberculum is usually much wider dorsoventrally and narrower craniocaudally. However, a similar condition was found in one examined specimen of *A. platyrhynchos,* suggesting affinities of *A. kurochkini* to recent Mallards (see below).

In the holotype of the new species, the sulcus m. supracoracoidei is excavated in its lateral part, just next to the facies articularis humeralis. Such a well-defined excavation is characteristic of some representatives of the genera *Anas* s.s. (*A. acuta*, Mallards) and *Spatula* (*S. querquedula*), but is normally absent from the closely sized *S. clypeata* and the species of the genus *Mareca*. The presence of such an excavation is however a primitive feature, which is also found in *Aythya* and other basal taxa.

The crista acrocoracoidea (see Elzanowski et al. 2012) is short and thin in dorsal view and is subparallel to the long axis of the bone (Fig. 5). In all extant ducks (especially in *Mareca*), this crest is notably more strongly inclined medially, but it is more parallel to the long axis of the bone in *A. acuta* and *A. platyrhynchos*. Importantly, this crest is always very thick and long in the recent dabbling ducks (Fig. 5), while it is thin and unusually short in *A. kurochkini*. The thickness of the crest seems to be uncorrelated with the occurrence of the excavation just medial to this crest because, for example, in *A. querquedula*, the excavation is always well developed, but the crest is wide as in other extant species of *Anas*.

In *A. kurochkini,* the facies articularis humeralis is short and has a very wide cranial angle. All extant dabbling ducks have longer facies with a more acute cranial angle (Fig. 5e). A somewhat similar morphology is present in some mallards (*A. platyrhynchos, A. undulata, A. poecilorhyncha)* as an individual variation.

Remarks A good number of Neogene species have been described within the genus *Anas*, but all Early and most Middle Miocene taxa apparently represent fossil genera, while Late Pliocene and Pleistocene taxa most probably should be synonymized with extant species. Representatives of the genus *Anas* s.l. are present in the fossil record starting from the middle Miocene (Zelenkov 2012a), and in the Late Miocene of Europe, ducks of two size classes have been repeatedly reported. Small teals, similar in size to the modern *A. crecca* and *A. querquedula*, are represented by *A. albae* Jánossy 1979 and *A. eppelsheimensis* Lambrecht, 1933. The latter species was described based on non-diagnostic material (see Mlíkovský 2002) and thus should be considered to be a nomen dubium. Mlíkovský (2002) considered *A. albae* as Anatidae genus incertae sedis, but Kessler (2009a) confirmed its taxonomic status. It is reasonable to ascribe all latest Miocene (MN 11-13) small ducks from the Central and Eastern Paratethys to *A. albae* Jánossy 1979, including finds of *A.* cf. *crecca* and *A.* cf. *querquedula* from the biozones MN 11-13 of Ukraine (Voinstvensky 1967; Sobolev 2004). A similarly sized duck is known from the latest Miocene (MN 13) of Eastern Mongolia (Zelenkov 2012b), and *A. pullulans* Brodkorb 1961 has been described from the roughly contemporary deposits of North America (Brodkorb 1961). It is possible that all of these finds may represent a single species, or at least they can be treated as a single species for convenience (if so, *A. pullulans* has taxonomic priority).

There are also finds of a larger duck, the size of *A. clypeata* or *A. penelope,* in the Late Miocene of Eastern Europe. No valid Late Miocene species are known for this size class, as the only named taxon, *Anas isarensis* Lambrecht, 1933, must be considered a nomen dubium because it has been established based on a scapula (now lost), which is an extremely poorly diagnostic marker in Anatidae and cannot be used to separate similarly sized species of dabbling ducks. "*Anas* cf. *clypeata"* and "*A.* cf. *penelope"* have been reported from the biozones MN11-13 of Ukraine (Voinstvensky 1967; Sobolev 2004), and *Anas clypeata* was recently found in the Late Miocene (MN 13) of Hungary (Kessler 2009a). Interestingly, the holotype of *A. kurochkini* was also preliminary identified by one of us as "*A.* cf. *clypeata"* (Panteleyev 2005). All of these finds likely refer to a single duck species (*A. kurochkini*) that was widespread in the Eastern Paratethys region in the Late Miocene.

Order CHARADRIIFORMES Huxley, 1867
Family SCOLOPACIDAE Vigors, 1825
Genus ***Gallinago*** Brisson, 1760
Gallinago azovica sp. nov.

Etymology After the Sea of Azov.

Holotype ZIN PO 7299, cranial fragment of right coracoid (Fig. 6a, f, i).

Referred material ZIN PO 7303, fragment of left coracoid.

Type locality and horizon Locality Morskaya-2 near Morskaya railroad station, Rostov Oblast, northeastern Sea of Azov region; Russia. Greenish clay member, Middle Turolian (late MN 12 –early MN 13).

Occurrence Type locality only.

Measurements (mm) Length of cranial end 8.3, minimal shaft width 2.8, mid-height of facies articularis humeralis 2.9.

Differential diagnosis The size of extant *Tringa nebularia* or *Calidris pygnax*; larger than any other extant and extinct snipes except *G. nobilis*. Differs from all genera of Scolopacidae except *Gallinago* in the following set of characters: procoracoid process with wide base; caudal margin of the procoracoid process forms an abrupt connection with the shaft; tuberculum brachiale is craniocaudally narrow.

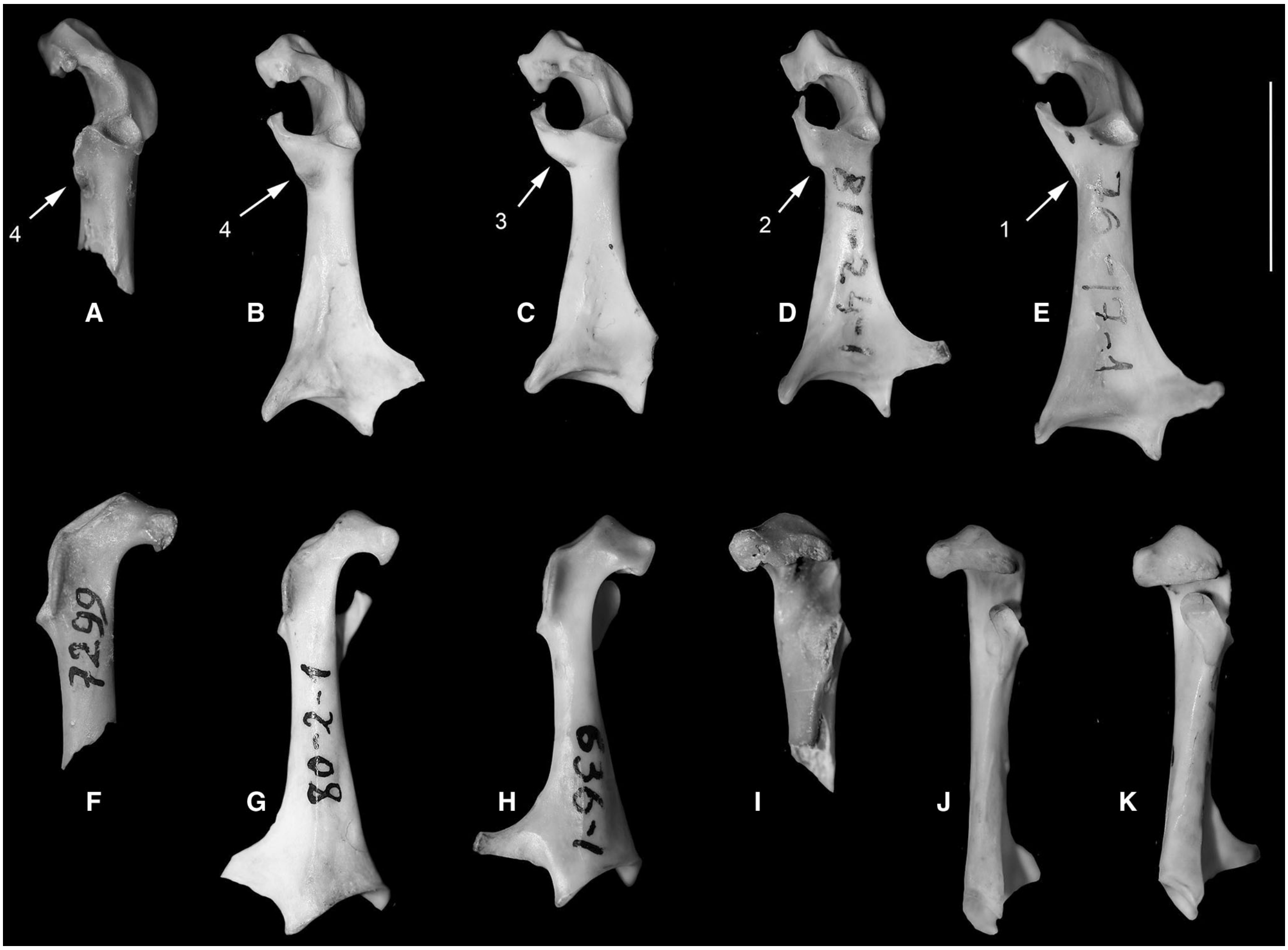

Fig. 6 *Gallinago azovica* sp. nov. from the Late Miocene of Morskaya-2 (Southern Russia) compared with extant waders. **a**, **f**, **i** *Gallinago azovicus* sp. nov., holotype right coracoid ZIN PO 7299, dorsal (**a**), ventral (**f**) and medial (**i**) views. **b**, **g**, **j** *Gallinago solitaria*, extant, right coracoid PIN 80-2-1, dorsal (**b**), ventral (**g**) and medial (**j**) views. **c** *Limnodromus scolopaceus*, extant, right coracoid PIN 80-19-2, dorsal view. **d**, **h**, **k** *Calidris pugnax*, extant, right coracoid PIN 81-24-1, dorsal (**d**), ventral (**h**) and medial (**k**) views. **e** *Tringa nebularia*, extant, right coracoid PIN 76-17-1, dorsal view. Designations: *1* procoracoid process continuous with the shaft; *2* abrupt connection of the procoracoid process with the shaft; *3* abrupt connection with a characteristic scar; *4* abrupt connection, scar present, procoracoid process wide at its base. *Scale bar* 1 cm

Description and comparisons The holotype coracoid can be referred to Scolopacidae and differs from other charadriiform families in the following characters: foramen n. supracoracoidei absent, facies articularis humeralis protrudes notably beyond the ventral margin of the bone, and the acrocoracoid is strongly curved. Among Scolopacidae, the fossil is similar to Calidrinae as well as the genera *Limnodromus* and *Gallinago* in the morphology of the processus procoracoideus. In the rest of the Scolopacidae (including *Coenocorypha*, *Scolopax* and *Lymnocryptes*), the caudal margin of the procoracoid process is smoothly continuous with the shaft (exemplified by *Tringa nebularia*, Fig. 6e). In Calidrinae, *Limnodromus* and *Gallinago*, the process forms an abrupt connection with the shaft, with a characteristic scar (Fig. 6b–d), which is well visible in the fossil (Fig. 6a). This scar allows distinguishing Calidrinae + *Limnodromus* + *Gallinago* from all other waders. Calidrinae can be distinguished from *Limnodromus* and *Gallinago* by the morphology of the processus acrocoracoideus in ventral view. In snipes and allies (including the fossil species), the process is notably narrower than in Calidrinae (Fig. 3f–h). Moreover, the tuberculum brachiale is craniocaudally higher in Calidrinae (Fig. 3i–k). The genera *Limnodromus* and *Gallinago* differ from one another in the shape of the processus procoracoideus: in *Gallinago*, the process has a wide base and tapers distally, while in *Limnodromus* the process is considerably narrower. Hence, the mentioned scar is positioned closely to the cotyla scapularis (Fig. 5b, c). The fossil coracoid agrees with *Gallinago* in these features; the caudal margin of the procoracoid process does not extend subperpendicular to the bone shaft, as in *Limnodromus*.

Remarks The living South American giant snipe *G. nobilis* is larger than other extant species of the genus and is thus comparable in size to *G. azovica*. However, affinities of the new species with the giant snipe seem unlikely for geographic reasons. Furthermore, no connection between extant South American and Neogene European bird faunas has been demonstrated or proposed. Additionally, so far no modern species of birds has been unambiguously reported from the Late Miocene.

Gallinago veterior Jánossy 1979 from the Pliocene (biozone MN 15) of Hungary (Jánossy 1979) was intermediate in size between extant *G. gallinago* and *G. media* and thus was notably smaller than *G. azovica*. *Gallinago veterior* was recently (Kessler 2009b) documented from the middle Miocene, Late Miocene and Late Pliocene of Hungary (biozones MN 6, MN 13, MN 16). The oldest find, from the locality Mátraszőlős 1, is especially dubious, but all of these finds were not illustrated and thus require confirmation.

Discussion

Only a few bird taxa were previously known from the latest Miocene or Early Pliocene of Ukraine and Moldova (reviewed in Mlíkovský 2002), but their identifications were largely based on a limited number of extant taxa (fossil species from other territories were disregarded). More Late Miocene bird taxa were reported from the Central Paratethys (Hungary) by Jánossy (1991, 1993) and recently by Kessler (Kessler 2009a, b; Kessler and János 2012a, b), but these were also insufficiently described and illustrated, and extensive comparisons based on phylogenetically important characters were lacking. It is noteworthy that no common species of birds was reported from the Late Miocene of the Black Sea region and Eastern Europe, possibly because of methodological flaws (limited geographical and taxonomical comparisons). As a result, there is no clear understanding of what the Late Miocene Eastern European avian faunas looked like. Thus, the three bird species reported in this work constitute a significant addition to the present knowledge of the Miocene birds of Europe.

One of our conclusions is that the Late Miocene small quail from Morskaya is different from *P. ponticus*, which was reported from the Pliocene of Eurasia (Kurochkin 1985; Bocheński and Kurochkin 1987; Zelenkov and Kurochkin 2009). This find is in agreement with the observation that the Eastern European mammalian faunas of the latest Miocene (so called "Pikermian fauna") generally did not cross the Miocene-Pliocene boundary (Eronen et al. 2009). The small quail from Morskaya is assigned to *Palaeocryptonyx hungaricus*, which was previously known from the similarly-aged sediments of Hungary (Jánossy 1991). Both the specimens from Morskaya and the type material of *Palaeocryptonyx hungaricus* from Hungary show characteristic features of the genus *Plioperdix*. Thus, a new combination is proposed here, *Plioperdix hungarica*. The new find in Morskaya shows that the genus *Plioperdix* was widespread in Eastern Europe during the Late Miocene. The occurrence of the genus *Plioperdix* in the Late Miocene of Eastern Europe coincides with the spread of open semi-arid landscapes (e.g., van Dam 2006; Syabryaj et al. 2007). There is further no evidence that the genus *Palaeocryptonyx* was present in the Late Miocene or Pliocene of Eastern Europe.

The middle-sized duck from Morskaya is here described as a new species, *Anas kurochkini*. We suppose that this species was previously reported from the Late Miocene of Eastern Europe as *Anas clypeata* or *Anas* cf. *clypeata* by various authors (Voinstvensky 1967; Sobolev 2004; Kessler 2009b). Although *A. kurochkini* is indeed similar to *Spatula clypeata* in size, it shows clear differences from all modern species. This fact supports a taxonomic identity of the fossil species, given the uniform morphology of the coracoid in extant ducks. Some of the characteristic features mentioned in the diagnosis are sometimes present as individual variations in Mallards. These morphological traits do not occur in the other species of *Anas* s.s. (at least *A. crecca* and *A. acuta*, for which a representative sample was available), thus indicating that the fossil species most probably belongs to the lineage of Mallards. *Anas kurochkini* is however much smaller than all extant and Pleistocene mallards, indicating that size increase in this lineage may be a recent evolutionary event.

The two species discussed above are also present in the Late Miocene of Hungary. These data represent the first evidence that at least a part of the avian faunas of that time were probably similar across the Paratethys. The third species described here is a large snipe, which in contrast has never been reported elsewhere.

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Appendix

List of extant ingroup taxa examined for comparative purposes (number of examined specimens).

Phasianidae (Phasianinae, Rollulinae): *Rollulus rouloul*; *Arborophila brunneopectus*; *Ammoperdix griseogularis* (6); *Tetraogallus altaicus*; *T. himalayensis*; *Alectoris graeca* (3); *Pternistis erckelii*; *P. bicalcaratus*; *Francolinus francolinus* (2); *Perdix perdix* (3); *P. dauuricae* (3); *Coturnix coturnix* (2); *C. japonica*; *Synoicus sinensis* (4); *Ptolipachus petrosus*; *Bambusicola thoracica*; *Galloperdix lunulata*; *Ithaginus cruentus*; *Tragopan satyra*; *Pucrasia macrolopha* (2); *Lophophorus impejanus*; *Gallus gallus* (wild) (2); *Lophura leucomelanos* (2); *L. nycthemera*; *L. edwardsi (2)*; *L. swinhoii* (2); *Crossoptilon crossoptilon*; *C. mantchuricum* (2); *Catreus wallichii* (2); *Syrmaticus ellioti* (2); *S. humiae* (2); *S. mikado* (2); *S. reevesii* (2); *Phasianus colchicus* (7); *Chrysolophus pictus* (2); *Polyplectron emphanum*; *Argusianus argus* (3); *Pavo cristatus*.

Anatinae: *Mareca penelope* (20); *M. americana*; *M. sibilatrix* (2); *M. falcata* (5); *M. strepera* (12); *Spatula versicolor*; *S. hottentota* (2); *S. querquedula* (12); *S. discors* (2); *S. cyanoptera*; *S. rhynchotis* (2); *S. clypeata* (14); *Sibirionetta formosa* (2); *Anas crecca* (19); *A. platyrhynchos* (41); *A. laysanensis*; *A. undulata* (2); *A. poecilorhyncha* (2); *A. acuta* (13); *A. bahamensis*.

Scolopacidae: *Limosa limosa* (2); *L. lapponica* (2); *Numenius minutus* (2); *N. phaeopus* (4); *N. arcuata* (2); *N. madagascariensis* (3); *Bartramia longicauda*; *Tringa erythropus* (2); *T. totanus* (4); *T. stagnatilis*; *T. nebularia* (10); *T. flavipes*; *T. ochropus* (3); *T. solitaria*; *T. glareola* (2); *Catoptrophorus semipalmatus*; *Xenus cinereus*; *Actitis hypoleucos* (3); *A. macularia*; *Heteroscelus brevipes* (3); *H. incanus*; *Arenaria interpres* (3); *Steganops tricolor*; *Phalaropus fulicaria (2)*; *Ph. lobatus (3)*; *Scolopax rusticola* (7); *S. minor*; *Gallinago solitaria*; *G. megala* (2); *G. stenura* (2)*;* *G. media*; *G. gallinago* (4); *Lymnocryptus minimus* (2); *Limnodromus griseus*; *L. scolopaceus* (3); *Calidris canutus* (2); *C. tenuirostris*; *C. alba* (4); *C. pusilla*; *C. mauri* (2); *C. ruficollis* (2); *C. minuta* (2); *C. temminckii*; *C. subminuta*; *C. minutilla*; *C. bairdii*; *C. melanotos* (2); *C. acuminata*; *C. maritima* (2); *C. ptilocnemis*; *C. alpina*; *C. ferruginea* (2); *C. pygmea*; *C. falcinellus*; *C. himantopus*; *C. pugnax* (5).

References

Ballmann, P. 1969. Die Vögel aus der althurgidalen spaltenfüllung von wintershof (West) bei Eichstätt in Bayern. *Zitteliana* 1: 5–60.

Baumel, J.J., and L.M. Witmer. 1993. Osteologia. In Handbook of Avian Anatomy: Nomina Anatomica Avium.2nd edn, ed. Baumel, J.J, 45–132. Cambridge: Publications of the Nuttall Ornithological Club 23

Bedetti, C., and M. Pavia. 2013. Early Pleistocene birds from Pirro Nord (Puglia, Southern Italy). *Palaeontographica Abt A* 298: 31–53.

Bernor, R.L., V. Fahlbusch, P. Andrews, H. de Bruijn, M. Fortelius, F. Rögl, F.F. Steininger, and L. Werdelin. 1996. The evolution of Western Eurasian Neogene mammal faunas: a chronologic, systematic, biogeographic, and paleoenvironmental synthesis. In *The evolution of Western Eurasian Neogene mammal faunas*, ed. R.L. Bernor, V. Fahlbusch, and H.-W. Mittmann, 419–470. New York: Columbia University Press.

Bocheński, Z., and E.N. Kurochkin. 1987. New data on Pliocene phasianids (Aves: Phasianidae) of Moldavia and S. Ukraine. *Acta zoologica cracoviensia* 30: 81–96.

Boev, Z.N. 1997. *Chauvireria balcanica* gen. n., sp. n. (Phasianidae — Galliformes) from the Middle Villafranchian of Western Bulgaria. *Geologica Balcanica* 27: 69–78.

Brodkorb, P. 1961. Birds from the Pliocene of Juntura, Oregon. *Quarterly Journal of the Florida Academy of Sciences* 24: 169–184.

Butendieck, E. 1980. *Die Benennung des Skeletts beim Truthuhn (Meleagris gallopavo) unter Berücksichtigung der Nomina Anatomica Avium 1979*. Hochschule: Inaug Diss Tierärtzl.

De Pietri, V.L., L. Costeur, M. Güntert, and G. Mayr. 2011. A revision of Lari (Aves, Charadriiformes) from the early Miocene of Saint-Gérand-le-Puy. *Journal of Vertebrate Paleontology* 31: 812–828.

De Pietri, V.L., and G. Mayr. 2012. An assessment of the diversity of early Miocene Scolopaci (Aves, Charadriiformes) from Saint-Gérand-le-Puy (Allier, France). *Palaeontology* 55: 1177–1197.

Dickinson, E.C. and J.V. Remsen Jr. 2013. The howard and moore complete checklist of the birds of the world, Vol. 1 of Non-passerines. (Eastbourne: Aves Press)

Elzanowski, A., M. Bieńkowska-Wasiluk, R. Chodyń, and W. Bogdanowicz. 2012. Anatomy of the coracoid and diversity of the Procellariiformes (Aves) in the Oligocene of Europe. *Palaeontology* 55: 1199–1221.

Eronen, J.T., M.M. Ataabadi, A. Micheels, A. Karme, R.L. Bernor, and M. Fortelius. 2009. Distribution history and climatic controls of the Late Miocene Pikermian chronofauna. *Proceedings of the National Academy of Sciences* 106: 11867–11871.

Fortelius, M., L. Werdelin, P. Andrews, R.L. Bernor, A.W. Gentry, L. Humphrey, H.-W. Mittmann, and S. Viranta. 1996. Provinciality, diversity, turnover, and paleoecology in land mammal faunas of the Later Miocene of Western Eurasia. In *The evolution of Western Eurasian Neogene mammal faunas*, ed. R.L. Bernor, V. Fahlbusch, and H.-W. Mittmann, 414–448. New York: Columbia University Press.

Göhlich, U.B., and C. Mourer-Chauviré. 2005. Revision of the phasianids (Aves: Galliformes) from the Lower Miocene of Saint-Gérand-Le-Puy (Allier, France). *Palaeontology* 48: 1331–1350.

Gonzalez, J., H. Düttman, and M. Wink. 2009. Phylogenetic relationships based on two mitochondrial genes and hybridization patterns in Anatidae. *Journal of Zoology* 279: 310–318.

Kessler, E. 2009a. New results with regard to the Neogene and Quaternary Avifauna of the Carpathian Basin, Part I. *Földtani Közlöny* 139: 445–468.

Kessler, E. 2009b. New results with regard to the Neogene and Quaternary Avifauna of the Carpathian Basin. Part II. *Földtani Közlöny* 139: 251–271.

Kessler, E., and H. János. 2012a. The avifauna in North Hungary during the Miocene. Part I. *Földtani Közlöny* 142: 67–78.

Kessler, E., and H. János. 2012b. The avifauna in North Hungary during the Miocene. Part II. *Földtani Közlöny* 142: 149–168.

Kurochkin, E.N. 1985. Birds of the Central Asia in Pliocene. *Transaction of the Joint Soviet-Mongolian Paleontological Expedition* 26: 1–120. (in Russian).

Kurochkin, E.N. and I.M. Ganea, 1972. Birds from the late sarmatian of Moldavia. *Vertebrates of the Neogene and Pleistocene of Moldavia*. Shtiintsa, Chişinău, 45–70 (in Russian).

Jánossy, D. 1979. Plio-Pleistocene bird remains from the Carpathian basin. IV. Anseriformes, Gruiformes, Charadriiformes, Passeriformes. *Aquila* 85: 11–39.

Jánossy, D. 1991. Late Miocene bird remains from Polgardi (W-Hungary). *Aquila* 98: 13–35.

Jánossy, D. 1993. Bird remains from the upper Miocene (MN 9) of Rudabánya (N-Hungary). *Aquila* 100: 53–70.

Manegold, A. 2008. Earliest fossil record of the Certhioidea (treecreepers and allies) from the early Miocene of Germany. *Journal of Ornithology* 149: 223–228.

Manegold, A., G. Mayr, and C. Mourer-Chauviré. 2004. Miocene songbirds and the composition of the European passeriform avifauna. *Auk* 121: 1155–1160.

Mayr, G., M. Poschman, and M. Wuttke. 2006. A nearly complete skeleton of the fossil galliform bird *Palaeortyx* from the late Oligocene of Germany. *Acta Ornithologica* 41: 129–135.

Mlíkovský, J. 2002. Cenozoic birds of the world. Part 1: Europe. Praha: Ninox press.

Mourer-Chauviré, C. 1992. The galliformes (Aves) from the phosphorites du Quercy (France): systematics and biostratigraphy. *Natural History Museum of Los Angeles County, Science Series* 36: 67–95.

Mourer-Chauviré, C., and D. Geraads. 2010. The upper Pliocene avifauna of Ahl al Oughlam, Morocco. Systematics and biogeography. *Records of the Australian Museum* 62: 157–184.

Mourer-Chauviré, C., J.-B. Peyrouse and M. Hugueney. 2013. A new roller (Aves: Coraciiformes s. s.: Coraciidae) from the Early Miocene of the Saint-Gérand-le-Puy area, Allier, France. In *Paleornithological Research 2013. Proceeding of 8th International. Meeting Society of Avian Paleontology and Evolution,* ed. U.B. Göhlich and A. Kroh, 81–92. Wien: Verlag Naturhistorisches Museum Wien.

Panteleyev, A.V. 2005. Izuchenie miocenovykh ptits Evropeiskoi Rossii [The study of Miocene birds of Southern European Russia], Rostov-on-Don: Problems of paleontology and archaeology of Southern Russian and adjacent territories, 73–74 (in Russian).

Pavia, M., U.B. Göhlich, and C. Mourer-Chauviré. 2012. Description of the type-series of *Palaeocryptonyx donnezani* Depéret, 1892 (Aves: Phasianidae) with the selection of a lectotype. *Comptes Rendus Palevol* 11: 257–263.

Sánchez Marco, A. 2009. New Iberian galliformes and reappraisal of some Pliocene and Pleistocene Eurasian taxa. *Journal of Vertebrate Paleontology* 29: 1148–1161.

Sobolev, D.V., and I.V. Marisova. 2011. Novye vidy miotsenovykh kanyukov (Falconiformes, Accipitridae) [New species of the Miocene buzzards (Falconiformes, Accipitridae)]. In *Modern ecological problems of the Ukranian polissya and adjacent areas*, ed. G.G. Senchenko, and I.V. Smalya, 158–163. Nezhin: PP Lysenko M.

Sobolev, D.V. 2004. Vodoplavuyushie ptitsy pozdnego neogena Ukrainy [Aquatic birds of the late neogene of Ukraine], Prirodnichi nauki na mezhi stolit (do 70-richchya prirodnichogeographichnogo fakulteta NDPU), Nezhin, 83–84 (in Russian).

Syabryaj, S., T. Utescher, S. Molchanoff, and A.A. Bruch. 2007. Vegetation and palaeoclimate in the Miocene of Ukraine. *Palaeogeography, Palaeoclimatology, Palaeoecology* 253: 153–168.

Sych, V.F. 1985. *Morphology of the flight apparatus of tetraonid and phasianid birds: Musculature and its extra- and intraorgan innervation*. Kiev: Naukova Dumka. (in Russian).

Titov, V.V., and A.S. Tesakov. 2013. Late Miocene (Turolian) vertebrate faunas from Southern European Russia. In *Fossil mammals of Asia. Neogene biostratigraphy and chronology,* ed. X. Wang, L.J. Flynn and M. Fortelius, 538–545. New York: Columbia University Press.

Titov, V.V., A.S. Tesakov, I.G. Danilov, G.A. Danukalova, E.N. Mashchenko, A.V. Panteleev, M.V. Sotnikova, and E.K. Sychevskaya. 2006. The first representative vertebrate fauna from the Late Miocene of Southern European Russia. *Doklady Biological Sciences* 411: 508–509.

Umanskaya, A.S. 1979. Miotsenovye ptitsy zapodnogo prichernomorya USSR [Miocene birds of the Western Black sea area]. *Vestnik zoologii* 15: 40–45. (in Russian).

Umanskaya, A.S. 1981. Miotsenovye ptitsy zapodnogo prichernomorya USSR. Soobschenie II [Miocene birds from the Western Black Sea Region of USSR. Communication II]. *Vestnik zoologii*, 17-21 (in Russian).

van Dam, J.A. 2006. Geographic and temporal patterns in the late Neogene (12–3 Ma) aridification of Europe: The use of small mammals as paleoprecipitation proxies. *Palaeogeography, Palaeoclimatology, Palaeoecology* 238: 190–218.

Voinstvensky, M.A. 1967. Iskopaemaya ornitofauna Ukrainy [Fossil ornithofauna of Ukraine]. *Prirodnaya obstanovka i fauny proshlogo*, 3-76 (in Russian).

Wang, N., R.T. Kimball, E.L. Braun, B. Liang, and Z. Zhang. 2013. Assessing phylogenetic relationships among Galliformes: a multigene phylogeny with expanded taxon sampling in Phasianidae. *PLoS ONE* 8: e64312.

Zelenkov, N.V. 2012a. A new duck from the middle Miocene of Mongolia, with comments on Miocene evolution of ducks. *Paleontological Journal* 46: 520–530.

Zelenkov, N.V. 2012b. Neogene Geese and Ducks (Aves: Anatidae) from localities of the great lakes depression, Western Mongolia. *Paleontological Journal* 46: 607–619.

Zelenkov, N.V., and E.N. Kurochkin. 2009. Neogene Phasianids (Aves: Phasianidae) of Central Asia: 2. Genera *Perdix*, *Plioperdix*, and *Bantamyx*. *Paleontological Journal* 43: 318–325.