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Vertebrates from the Pontian of the Shkodova Gora Locality (Northwestern Black Sea Region, Upper Miocene)

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Abstract—Remains of fishes, turtles, birds, and mammals are described from the Upper Miocene (MN13) Shkodova Gora locality (Ukraine, Odessa Region), the only representative locality of Pontian large vertebrates in the northwestern Black Sea Region. Asiatic fish and avian taxa are recorded for the first time in the Upper Miocene of Europe. The Shkodova Gora ichthyofauna includes eight freshwater fish species (belonging to Acipenseridae, Cyprinidae, Siluridae, and Percidae). Taxa that have previously been recorded only in Western Siberia (*Abramis bliccoides, Perca lepidopoma*), eastern Kazakhstan, and the Altai Mountain (*Rutilus tungurukensis*) are revealed. *Acipenser gueldenstaedtii* is recorded for the first time in the Upper Miocene of Eastern Europe. The occurrence of the genus *Ctenopharyngodon,* a member of the Chinese plain faunal assemblage is of great interest. The Shkodova Gora avifauna (seven taxa) is mostly composed of waterfowl, including *Phalacrocorax mongoliensis*, which has previously been known only from the Lower Pliocene of Mongolia. The finding of *Proanser major* is the youngest record of this species in the fossil record. Mammals of the Shkodova Gora association include a hare resembling *Trischizolagus dumitrescuae*, *Palaeoryx* cf. *pallasi,* and *Hipparion* cf. *moldavicum,* which have not been mentioned among Pontian taxa of the northern Black Sea Region. Pontian paleolandscapes in the area of the Shkodova Gora locality are reconstructed.

Keywords: Vertebrata, Late Miocene, Pontian, paleoenvironments, Black Sea

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INTRODUCTION

The data on the vertebrate fauna from the Pontian Stage (Upper Miocene) of the northwestern Black Sea Region are rather fragmentary and restricted to individual finds of freshwater fishes, birds, reptiles, and mammals. A representative microtheriofauna is known from the 16th station locality of the Bol'shoi Fountain (Odessa, Pontian lectostratotype: Nesin, 2013); however, rich localities of large vertebrates of that time have not been found in the region in question; the most interesting faunal assemblage is only known from Shkodova Gora (a hill presently situated inside Odessa). At the end of the 19th century, Wildhalm (1886) described fossil remains of vertebrates from Pontian limestones in the vicinity of Odessa, but without allocation to a certain locality. Among other things, he recognized new taxa of fishes (*Acipenser euhuso* Widhalm, 1886, *Scardinius nordmanni* Widhalm, 1886, *Silurus glanis fossilis* Widhalm, 1886) and birds (*Pelecanus odessanus* Widhalm, 1886, *Haliaetus fossilis* var. *odessana* Widhalm, 1886). Andrusov (1917), Bogatchev (1958), and Tarashchuk (1962) reported that the Pontian beds near Odessa (also without mentioning the point of collecting) yielded bones of *Leuciscus* sp., *Rutilus frisii, Pelecus* sp., *Cyprinus carpio, Tinca* sp., *Cobitis* sp., *Esox lucius, Perca* sp., and *Lates* sp. In 1957, fossil vertebrates dated Pontian, were found by T.G. Gritsai in a limestone mine on Shkodova Gora (Dubrovo and Kapelist, 1979). The results of studying these specimens were partially reported by Pidoplichko and Tarashchuk (1960), Tarashchuk (1962), Korotkevich (1988), and Logvinenko (2008). These studies provided approximate data on the composition of the vertebrate fauna (fishes, reptiles, large mammals) and paleogeography of the region in the Pontian. Korotkevich (1988) established the Tavrida assemblage of terrestrial verte-

brates and regarded the Shkodova Gora fauna as the type of this complex.

At the same time, a significant part of specimens from Shkodova Gora have neither been described nor figured; this is the basis for the present study.

In the literature, there is certain confusion on the names of localities on Shkodova Gora. In the figure captions of cormorant bones, Wildhalm (1886) indicated that they come from "limestone quarries of Novaya Slobodka near Odessa" and the locality of a pelican is "Odessa limestones." This suggests that pelican and cormorant remains are probably of different origin; nevertheless, they come from the same region, as follows from the title and text of the publication (Wildhalm, 1886). Tugarinov (1940) described the cormorant *Pliocarbo longipes* from "Pontian limestones" in the vicinity of the village of Slobodka near Odessa (collected by Romanov). He assigned the material of Wildhalm to the same taxon, but did not identify whether or not they come from the same locality. Tarashchuk (1962) did not mention Novaya Slobodka; however, all (both new and Wildhalm's) specimens are referred to the Shkodova Gora locality (Pidoplichko and Tarashchuk, 1960). Voinstvensky (1967) believed that all Wildhalm's specimens come from stone quarries of Novaya Slobodka, and the material described by Tugarinov is considered to come from "karstic caves of Odessa." Dubrovo and Kapelist (1979; see also Zelenkov and Kurochkin, 2015) proposed a different treatment, distinguishing between Novaya Slobodka and Shkodova Gora localities; they indicated that only *Pliocarbo longipes* (for the first time!) and *Phalacrocorax* come from Shkodova Gora, while the birds described by Wildhalm are attributed to the Novaya Slobodka locality. These authors associated bone remains of other vertebrates only with Shkodova Gora.

Since Shkodova Gora is situated in the area of Slobodka (presently inside Odessa) and other localities of Neogene vertebrates are unknown in this region, it is plausible that the type material of *Pliocarbo longipes* comes from Shkodova Gora (Dubrovo and Kapelist, 1979; Zelenkov and Kurochkin, 2015). This hill is situated close to the Novaya Slobodka locality (a part of Slobodka); therefore, all fossil specimens probably come from the same beds. The chronological framework of the Pontian Regional Stage of the Eastern Paratethys are ambiguously determined by different authors (for example, Pevzner et al., 2003), but according to available information, the lower boundary of the Pontian is rather reliably dated 6.04 Ma and the upper boundary is estimated from 5.5 to 4.7 Ma (Krijgsman et al., 2010; Hilgen et al., 2012). The chronological interval 6.04–5.5 Ma suggests that the vertebrate fauna from Shkodova Gora corresponds to Biozone MN13. At the same time, the possible Pliocene age of the Late Pontian beds could have explained

Fig. 1. Geographical position of the Shkodova Gora locality (Ukraine, Odessa Region; Upper Miocene, Lower Pontian; marked by asterisk).

that some authors referred Pontian faunas to Biozone MN14 (Topachevsky et al., 1997).

The material of the present study is represented by fish, reptile, bird, small and large mammal remains from the Shkodova Gora locality (Fig. 1), which are stored mostly in the Department of Paleontology of the National Museum of Natural History of the National Academy of Sciences of Ukraine (NMNHU-P). The anatomical nomenclature follows Lepiksaar (1994) for fishes and *Nomina Anatomica Avium* (Baumel et al., 1993) for birds. The measurements follow the standard technique for fishes (Morales and Rosenlund, 1979) and birds (Driesch, 1976).

SYSTEMATIC PALEONTOLOGY

CLASS ACTINOPTERYGII

Order Acipenseriformes

Family Acipenseridae Bonaparte, 1831

Genus *Acipenser* Linnaeus, 1758

***Acipenser gueldenstaedtii* Brandt et Ratzeburg, 1833**

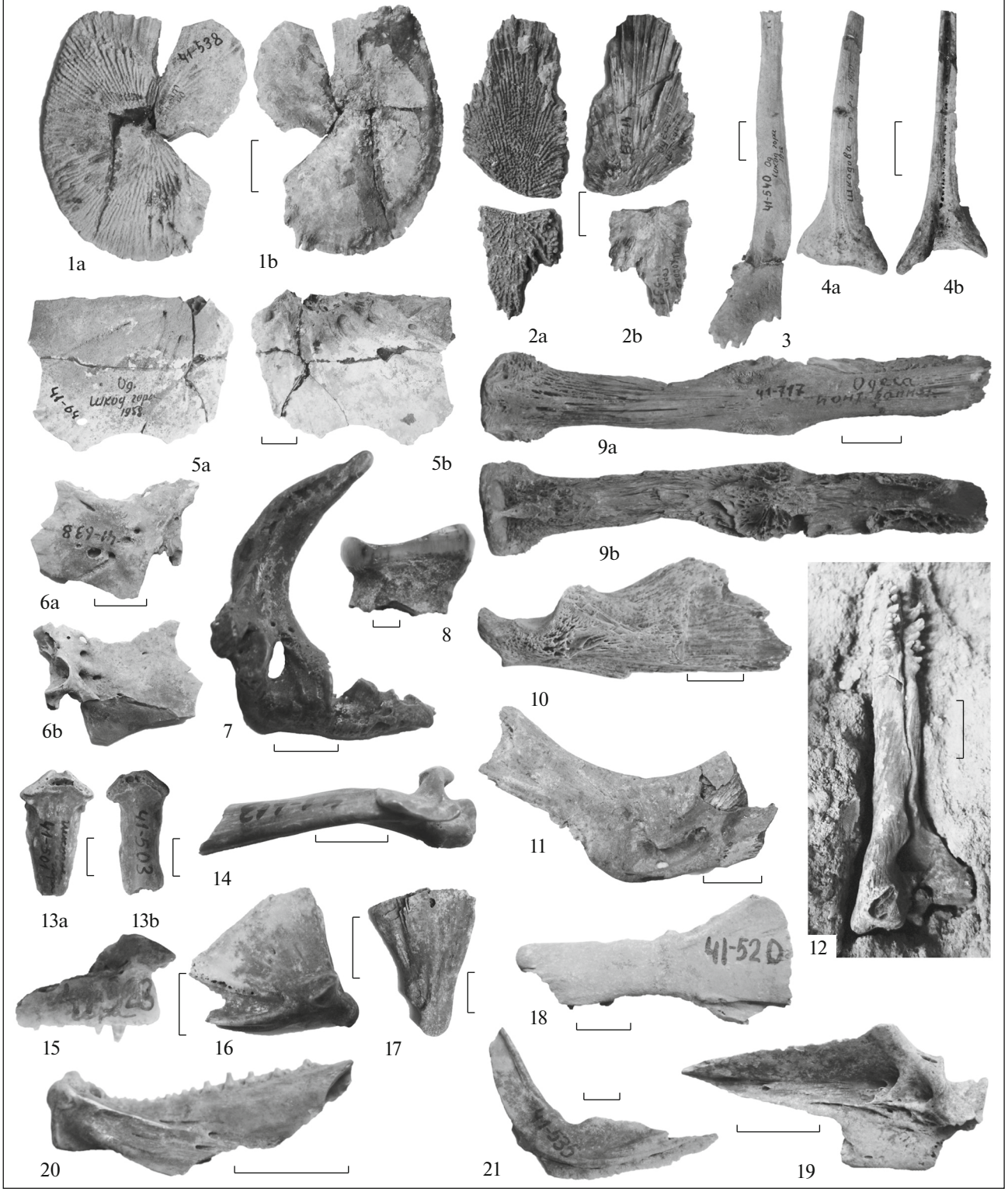
Plate 8, figs. 1–4

Acipenser güldenstädtii: Lebedev, 1960, p. 221, text-figs. 64, 82, and 92.

Holotype. Not designated (extant species).

Description. The subopercle (specimen NMNHU-P, no. 41/538) is wide, elongated ovoid,

Plate 8


1a
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with rounded margins. The parietal (specimen NMNHU-P, no. 41/539) has a distinctive ornamentation composed of noncontinuous ridges. The internal surface of the parietal is ridged, ornamented with distinct narrow ridges, particularly in the anterior part. Pinna pectoralis I (specimen NMNHU-P, nos. 41/540, 41/541) has an expanded base. The pectoral spine is smooth, slightly curved; distally, it gradually becomes thinner.

Measurements in mm. Subopercle: height, 124; width, 89; diagonal length, 134. Parietal: length, 123. Pinna pectoralis I: specimen NMNHU-P, no. 41/540: length, 145; width, 65; specimen NMNHU-P, no. 41/541: length, 92; width, 32.

Comparison. *Acipenser gueldenstaedtii* differs from the other Acipenseridae in the massive elongated and more convex subopercle, the large parietal with distinctive ornamentation. *A. stellatus* Pallas, 1771 is characterized by a flat subopercle with an arched upper margin and teeth on the lower margin. *A. ruthenus* L., 1758 and *A. stellatus* are similar to *A. gueldenstaedtii* in the extent of curvature of the shaft of pinna pectoralis I (Radu, 2005), but differ in the considerably smaller size.

Remarks. The subopercle of *A. gueldenstaedtii* is wider than that of *Huso huso* (L., 1758) and has less notched margins (Bartosiewicz and Takács, 1997). Pinna pectoralis I of *A. gueldenstaedtii* is comparable in size to that of *Huso huso*, but differs in the less curved shaft and the absence of distinct longitudinal ridges near the base (see Bartosiewicz and Takács, 1997).

Material. Subopercle (specimen NMNHU-P, no. 41/538), parietale (specimen NMNHU-P, no. 41/539), pinna pectoralis I (specimen NMNHU-P, nos. 41/540, 41/541); Ukraine, Odessa Region, Shkodova Gora locality; Upper Miocene, Pontian.

Order Cypriniformes

Family Cyprinidae Fleming, 1822

Genus *Rutilus* Rafinesque, 1820

***Rutilus tungurukensis* Sytchevskaya, 1989**

Plate 8, fig. 7

Rutilus rutilus: Lebedev, 1959, pp. 40–41, text-fig. 13; Sytchevskaya and Devyatkin, 1962, p. 174.

Rutilus cf. *rutilus:* Sytchevskaya, 1980a, p. 50.

Rutilus tungurukensis: Sytchevskaya, 1989, pp. 24–26, pl. 2, figs. 4 and 5, text-fig. 9.

Holotype. PIN, no. 3875/800, right pharyngeal bone with three teeth; Kazakhstan, Aktyubinsk Region, Shalkarskii District, Tunguruk Sor locality; Lower Miocene, Aral Formation.

Description. The ceratobranchial (specimen NMNHU-P, no. 41/547) is short and massive. The pharyngeal teeth are arranged in a single row, from them preserved only the bases. The first pharyngeal tooth was positioned at the level of the anterior branch of the ceratobranchial. The cavernous surface is wide, begins from the level of the anterior angle of the bone and consists of three cavities. Anterior to the cavernous surface, the bone plane has small foramina arranged in a row and repeating in approximately every 2 mm.

Measurements in mm. Ceratobranchial length, 19.4; width, 7.1; dental row length, 12.3.

Comparison. The ceratobranchiale of *Rutilus tungurukensis* differs from that of *R. rutilus* (L., 1758) in the smooth ventral edge, the less pronounced anterior angle, and in the narrower and longer posterior toothless process. It differs from that of *R. frisii* (Nordmann, 1840) in the longer dental row, from *R. robustus* Kovalchuk, 2014 in the less stout and lower bone and also in the narrower septa between the cavernous surfaces.

Explanation of Plate 8

Fish bones from the Upper Miocene of the Shkodova Gora locality (Ukraine, Odessa Region).

Figs. 1–4. *Acipenser gueldenstaedtii* Brandt et Ratzeburg, 1833: (1) specimen NMNHU-P, no. 41/538, right subopercle: (1a) external and (1b) internal views; (2) specimen NMNHU-P 41/539, right parietal: (2a) external and (2b) internal views; (3) specimen NMNHU-P, no. 41/540, pinna pectoralis I, frontal view; (4) specimen NMNHU-P, no. 41/541, pinna pectoralis I: (4a) frontal and (4b) posterior views.

Figs. 5 and 6. *Ctenopharyngodon* sp.: (5) specimen NMNHU-P, no. 41/640, opercle: (5a) external and (5b) internal views; (6) specimen NMNHU-P, no. 41/638, opercle fragment: (6a) external and (6b) internal views.

Fig. 7. *Rutilus tungurukensis* Sytchevskaya, 1989, specimen NMNHU-P, no. 41/547, ceratobranchial.

Fig. 8. *Rutilus robustus* Kovalchuk, 2014, specimen NMNHU-P, no. 41/497, pharyngeal tooth.

Figs. 9–12. *Silurus glanis* L., 1758: (9) specimen NMNHU-P, no. 41/717, parasphenoid: (9a) ventral and (9b) dorsal views; (10) specimen NMNHU-P, no. 41/626, articular; (11) specimen NMNHU-P, no. 41/615, cleithrum; (12) specimen NMNHU-P, no. 41/620, pinna pectoralis I.

Figs. 13–21. *Sander lucioperca* (L., 1758): (13) vomer: (13a) specimen NMNHU-P, no. 41/501 and (13b) NMNHU-P, no. 41/503; (14) specimen NMNHU-P, no. 41/413, maxilla; (15) specimen NMNHU-P, no. 41/528, palatine; (16) specimen NMNHU-P 41/498, quadrate; (17) specimen NMNHU-P, no. 41/518, epihyal; (18) specimen NMNHU-P, no. 41/520, ceratohyal; (19) specimen NMNHU-P, no. 41/603, articular; (20) specimen NMNHU-P, no. 41/515, dentary; (21) specimen NMNHU-P, no. 41/535, preopercle.

Scale bars: (1–4, 11, 19) 20 mm; (5, 6, 12–18, 20, 21) 10 mm; (7, 9–10) 5 mm; (8) 2 mm.

Material. Ceratobranchial (specimen NMNHU-P, no. 41/547); Ukraine, Odessa Region, Shkodova Gora locality; Upper Miocene, Pontian.

***Rutilus robustus* Kovalchuk, 2014**

Plate 8, fig. 8

Rutilus frisii?: Lebedev, 1959, p. 41, text-fig. 14; Sytchevskaya and Devyatkin, 1962, p. 174.

Rutilus cf. *frisii:* Sytchevskaya, 1980a, p. 50, text-fig. 22; 1989, p. 26, text-fig. 10.

Rutilus robustus: Kovalchuk, 2014, p. 413, text-fig. 2; Kovalchuk, 2015a, p. 136, pl. V, figs. 1 and 2.

Holotype. Geological and Paleontological Museum of the Transnistrian State University, no. Prz 10-1/12, complete right pharyngeal bone with one tooth; Moldova, Slobodzeiskii District; Priozernoe locality; Lower Pliocene, Upper Ruscinian (MN15).

Description. An isolated pharyngeal tooth (specimen NMNHU-P, no. 41/497) with a wide fungoid, laterally compressed crown and a distinct constriction near the tooth neck. A convex tooth belly rises at a small angle to the gently sloping apex.

The grinding surface is smooth, slightly oblique in the direction of the belly. The latter is round, lacking a keel. The pedicle is short, oval in cross section.

Measurements in mm. Crown height, 7.8; crown width, 11.7.

Comparison. The pharyngeal tooth differs from that of *R. rutilus* in the large size and greater robustness, from *R. frisii* in the less oblique grinding surface and well-pronounced constriction near the neck.

Remarks. The pharyngeal tooth from Shkodova Gora is identical in morphology to that of *R. robustus* from the type locality, but it is larger. Pharyngeal teeth, described as *Rutilus* cf. *frisii* (Sytchevskaya, 1989) from the Miocene of the Zaisan Depression and Altai possibly also belong to *R. robustus*.

Material. An isolated pharyngeal tooth (specimen NMNHU-P, no. 41/497); Ukraine, Odessa Region, Shkodova Gora locality; Upper Miocene, Pontian.

Genus *Abramis* Cuvier, 1816

***Abramis bliccoides* Schtylko, 1934**

Plate 9, fig. 1

Abramis bliccoides: Shtylko, 1934, p. 4, pl. 6, figs. 38, 39, pl. 7, figs. 40–44; Yakovlev, 1960, p. 104; Sytchevskaya, 1980a, p. 59, pl. 9, fig. 12, text-fig. 28.

Abramis ponticus: Bogatchev, 1958, p. 729, text-fig. 1.

Abramis brama: Lebedev, 1959, p. 55, text-fig. 30.

Holotype. TsNIGR Museum (Chernyshev Central Research Geological Museum, St. Petersburg), no. 53/3242; Russia, Omsk Region, Gor'kovskii District, Serebryanoe locality; Upper Miocene (MN12–MN13), Pavlodar Formation.

Description. Specimen NMNHU-P, no. 41/2543 is an imprint of an incomplete skeleton. The body is deep; the head is about half the maximum body depth and more than 0.2 of its length. The number of vertebrae is 40, including 19 dorsal (with 16 pairs of ribs) and 21 caudal vertebrae. The dorsal fin begins posterior to the vertical of the origin of the abdominal fin and contains 13 rays. The origin of the anal fin is on the vertical of the fifth caudal vertebra. The number of its rays is probably at most 25. The caudal peduncle is short and deep.

Measurements in mm. Body height, ~ 90; body length up to the hypuralia end, 230.

Comparison. *Abramis bliccoides* differs from *A. ponticus* Bogatchev, 1958 in the division of vertebrae into regions of the vertebral column, the number of rib pairs and rays in the anal fin, and also in the considerably smaller size (the body of *A. ponticus* is 1.5 times as long). It differs from *A. brama* (L., 1758) in the fewer vertebrae and greater number of rays in the anal fin.

Material. Incomplete skeleton imprint (specimen NMNHU-P, no. 41/2543); Ukraine, Odessa Region, Shkodova Gora locality; Upper Miocene, Pontian.

Order Siluriformes

Family Siluridae Cuvier, 1816

Genus *Silurus* Linnaeus, 1758

***Silurus glanis* Linnaeus, 1758**

Plate 8, fig. 9–12

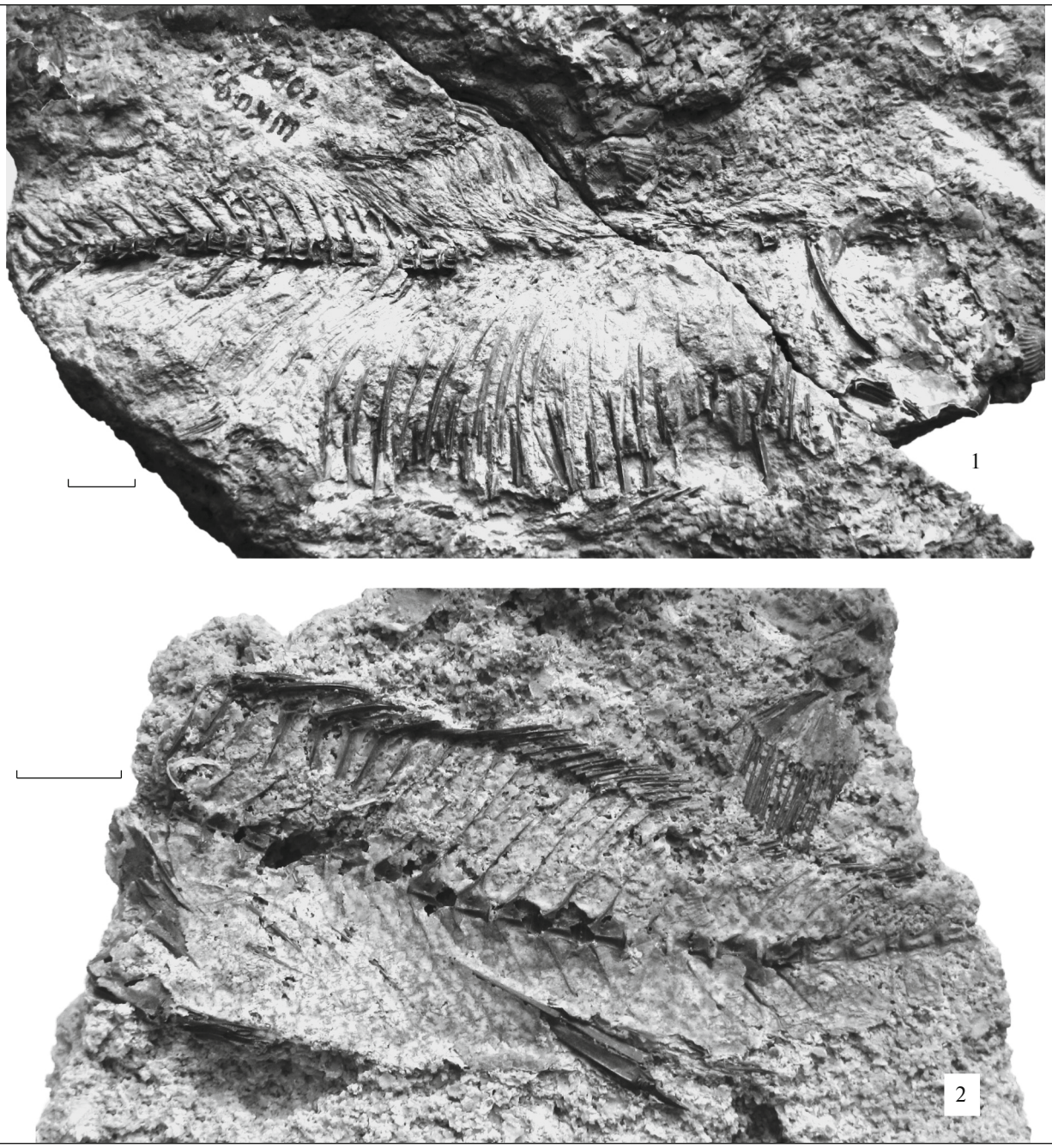
Silurus glanis: Lebedev, 1960, p. 46, text-figs. 6, 42, 49; Kobayakawa, 1989, p. 158, text-fig. 4d; Kovalchuk and Ferraris, 2016, p. 10, text-fig. 6.

Holotype. Not designated (extant species).

Description. The parasphenoid (specimen NMNHU-P, no. 41/717) is wide, trapezoid in cross section. The articular (specimen NMNHU-P, no. 41/626) has an expanded anterior and rounded posterior part of the oval articular facet. The cleithra (specimen NMNHU-P, no. 41/615) have a high and massive ascending process and posterodorsally inclined vertical ramus. Pinna pectoralis I (specimen NMNHU-P, no. 41/620) is straight, oval in cross section, with an expanded and dorsoventrally compressed base. The shaft of the pectoral spine has long fused denticles. The dorsal process of the pectoral spine has a narrow edge; the ventral process is relatively small; and the anterior margin is wide and flattened.

Comparison. *Silurus glanis* differs from other species of the genus *Silurus* in the presence of long fused denticles on the medial edge of pinna pectoralis I and the posteriorly expanded glenoid fossa on the cleithra. In addition, *S. glanis* 1977 differs from *S. aristotelis* Garman, 1890, *S. cochinchinensis* Valenciennes,

Plate 9



Explanation of Plate 9

Imprints of bony fish skeletons from the Upper Miocene of the Shkodova Gora locality (Ukraine, Odessa Region).

Fig. 1. *Abramis bliccoides* Schtylko, 1934, specimen NMNHU-P, no. 41/2543; scale bar, 20 mm.

Fig. 2. *Perca lepidopoma* (Schtylko, 1934), specimen NMNHU-P, no. 41/2544; scale bar, 10 mm.

1840, and *S. meridionalis* Chen, 1977 in the wider parasphenoid and the long shaft of the cleithra. *S. soldatovi* Nikolsky et Soin, 1948 differs from *S. glanis* in the low articular wall, the wide crista articularis, and the presence of small nonfused denticles on the medial and lateral edges of pinna pectoralis I.

M a t e r i a l. Parasphenoid (specimen NMNHU-P, no. 41/717); articular (specimen NMNHU-P,

no. 41/626); cleithrum (specimen NMNHU-P, no. 41/615); pinna pectoralis I (specimen NMNHU-P, no. 41/620); Ukraine, Odessa Region, Shkodova Gora locality; Upper Miocene, Pontian.

Order Perciformes

Family Percidae Bleeker, 1859

Genus *Perca* Linnaeus, 1758

***Perca lepidopoma* (Schtylko, 1934)**

Plate 9, fig. 2

Acerina lepidopoma: Shtylko, 1934, pl. 8, figs. 52–54; pl. 9, figs. 55 and 56.

Perca fluviatilis: Lebedev, 1959, p. 59, text-fig. 33.

Perca fluviatilis lepidopoma: Yakovlev, 1960, p. 105.

Perca lepidopoma: Sytchevskaya, 1980b, p. 123, pl. 10, fig. 12; pl. 13, fig. 9.

Holotype. TsNIGR Museum, no. 90/3242; Russia, Omsk Region, Gor'kovskii District, Serebryanoe locality; Upper Miocene (MN12–MN13), Pavlodar Formation.

Description. The skeleton imprint (specimen NMNHU-P, no. 41/2544) is incomplete, without a head and end of the caudal peduncle. The vertebral column retains at less 22 vertebrae (the total number could have been 35, including 15 abdominal and 20 caudal vertebrae). The caudal peduncle is short, approximately 0.2 of the body length. The first dorsal fin originates from the vertical of the pectoral fin, consists of 16 spiny rays; the second dorsal fin has two spiny and 12 branched rays. The preservation of the anal and pectoral fins prevents the determination of the number of rays in them.

Measurements in mm. Total body length, 80; body depth, 14 (minimum) and 35 (maximum).

Comparison. *Perca lepidopoma* differs from *P. fluviatilis* L., 1758 in the fewer vertebrae and rays in the first dorsal fin; from *P. schrenkii* Kessler, 1874 in the position of the first dorsal fin; from *P. skobloi* Sytchevskaya, 1989 in the presence of a constriction of the caudal peduncle, the greater number of caudal vertebrae and rays in the second dorsal fin.

Material. Incomplete skeleton imprint (specimen NMNHU-P, no. 41/2544); Ukraine, Odessa Region, Shkodova Gora locality; Upper Miocene, Pontian.

Genus *Sander* Oken, 1817

***Sander lucioperca* (Linnaeus, 1758)**

Plate 8, figs. 13–21

Lucioperca lucioperca: Lebedev, 1960, p. 55, text-figs. 9, 47, and 77; Tarashchuk, 1965, p. 90, text-fig. 4; Sytchevskaya, 1980b, p. 121.

Sander lucioperca: Kovalchuk and Murray, 2016, p. 7, text-fig. 4.

Holotype. Not designated (extant species).

Description. The vomer has a narrow shaft and relatively small and low head; the arched dental field is wide, has two large caniniform teeth located medially. The teeth on the premaxilla are identical in diameter and length. The maxilla is characterized by the presence of a wide head. The palatine is large, with two caniniform teeth in the anterior part. The articular is high, with a wide and deep glenoid fossa and a wide costa superior. The dentary is low and narrow, with the ventral edge curved medially. The symphyseal end expands and has two caniniform teeth. The labial wall of the dentary is convex; the symphyseal margin is oblique. The preopercle (specimen NMNHU-P, no. 41/535) is equipped with teeth on the horizontal ramus.

Measurements in mm. Vomer (n = 14): caput vomeri width, 12.8–19.3 (mean = 15.2); dental row width, 1.3–1.9 (mean = 1.6); crown diameter, 0.9–1.5 (mean = 1.2). Maxilla (n = 4): caput maxillary width, 7.8–11.7 (mean = 9.9). Palatine (n = 2): crown diameter, 3.3 and 4.1. Quadrate (n = 5): articular angle, 60°–68° (mean = 65°); facet articularis length, 10.4–12.7 (mean = 11.8); facet articularis width, 5.1–5.8 (mean = 5.3). Dentary (n = 2): symphyseal height, 7.4 and 13.7; symphyseal width, 3.3 and 6.8; tooth crown diameter, 1.9 and 2.2; dental row width, 1.8 and 1.9.

Comparison. *Sander lucioperca* differs from *S. volgensis* (Gmelin, 1789) in the well-developed caniniform teeth in the dentary and palatine and also in the larger size. It differs from *S. svetovidovi* Kovalchuk, 2015 in the smaller angle between the axis and quadrate plane, the round and somewhat smaller condylus lateralis, and in the presence of a double ridge on the anteroventral margin.

Material. Vomer (specimen NMNHU-P, nos. 41/501-514); maxilla (specimen NMNHU-P, nos. 41/413, 41/611-613), palatine (specimen NMNHU-P, no. 41/528, no. 41/609); quadrate (specimen NMNHU-P, nos. 41/498-500, 41/604, 41/605); dentary (NMNHU-P, nos. 41/515, 41/516); epihyal (specimen NMNHU-P, nos. 41/518, 41/519, 41/522); ceratohyal (specimen NMNHU-P, no. 41/520); Ukraine, Odessa Region, Shkodova Gora locality; Upper Miocene, Pontian.

CLASS AVES

Order Anseriformes

Family Anatidae Leach, 1819

Genus *Proanser* Umanskaya, 1979

***Proanser major* Umanskaya, 1979**

Cygnus sp.: Voinstvensky, 1967, p. 11; Mlíkovský, 2002, p. 115.

Proanser major: Umanskaya, 1979, p. 42, text-figs. 2–5; Zelenkov and Kurochkin, 2015, p. 167, pl. XIV, figs. 27–30.

Holotype. NMNHU-P, no. 25/1682, proximal fragment of right carpometacarpus; Ukraine, Odessa Region, Grebeniki locality; Upper Miocene (MN 11), Upper Sarmatian.

Description (Figs. 2n–2p). The incisura tendinosa is distinct; the apices of the condylus ventralis and condylus dorsalis of the ulna subparallel.

Measurements in mm. Greatest width of the distal end of the ulna, 15.5; anteroposterior diameter of the condylus dorsalis, 13.3; least width of bone shaft, 8.6.

Comparison. The genus *Proanser* is monotypic.

Remarks. The characters mentioned in the description are evidence that the ulna from Shkodova Gora belongs to *Proanser major*, which has previously been recorded only in more ancient deposits (MN11) of southern Ukraine (Umanskaya, 1979). The remarks on the taxonomic status of *Proanser* (including differences from the extant genus *Alopochen*) were provided previously (Zelenkov and Kurochkin, 2015).

Material. Distal fragment of right ulna (specimen NMNHU-P, no. Av-230); Ukraine, Odessa Region, Shkodova Gora locality; Upper Miocene, Pontian.

Order Pelecaniformes

Family Pelecanidae Vigors, 1825

Genus *Pelecanus* Linnaeus, 1758

***Pelecanus odessanus* Widhalm, 1886**

Pelecanus odessanus: Wildhalm, 1886, p. 6, pl. 5, figs. 1–4; Mlíkovský, 2002, p. 87; Zelenkov and Kurochkin, 2015, p. 201, text-fig. 65.

Pelecanus odessanus fossilis: Voinstvensky, 1967, p. 697.

Lectotype. Not numbered, depository not known, right tarsometatarsus (figured in Wildhalm, 1886, pl. 5, figs. 1–3; Zelenkov and Kurochkin, 2015, text-fig. 65); designated by Mlíkovský (2002); Ukraine, Odessa Region, Shkodova Gora locality ("Novaya Slobodka"); Upper Miocene, Pontian.

Description (Fig. 2u). A coracoid fragment (paralectotype NMNHU-P, no. Av-224) is mostly represented by the shaft and partly broken extremitas sternalis. The foramen n. supracoracoidei is small, round. The dorsal surface of the extremitas sternalis is indistinctly concave; the angulus medialis is gracile.

Comparison. See in (Zelenkov and Kurochkin, 2015).

Remarks. In the collection of NMNHU, we have found the paralectotype of this species, the depository of which had previously been considered unknown (Tarashchuk, 1962; Zelenkov and Kurochkin, 2015). The bone is identical in outline to that figured by Wildhalm (1886, pl. 5), although it is not separated from limestone matrix, which is not shown in the original publication.

Material. Paralectotype from the type locality.

Family Phalacrocoracidae Bonaparte, 1854

Genus *Phalacrocorax* Brisson, 1760

***Phalacrocorax longipes* (Tugarinov, 1940)**

Pliocarbo longipes: Tugarinov, 1940, p. 205, text-figs. 1 and 2; Voinstvensky, 1967, p. 14.

Phalacrocorax longipes: Mlíkovský, 2002, p. 87; Zelenkov and Kurochkin, 2015, p. 205, pl. XXI, figs. 12 and 13.

Lectotype. PIN, no. 228/2, right tarsometatarsus; Ukraine, Odessa Region, Shkodova Gora locality; Upper Miocene, Pontian.

Description (Figs. 2a–2d, 2t, 2u). See in (Tugarinov, 1940) and (Zelenkov and Kurochkin, 2015).

Comparison. *Phalacrocorax longipes* is somewhat larger, but more gracile than *Ph. carbo* (L., 1761).

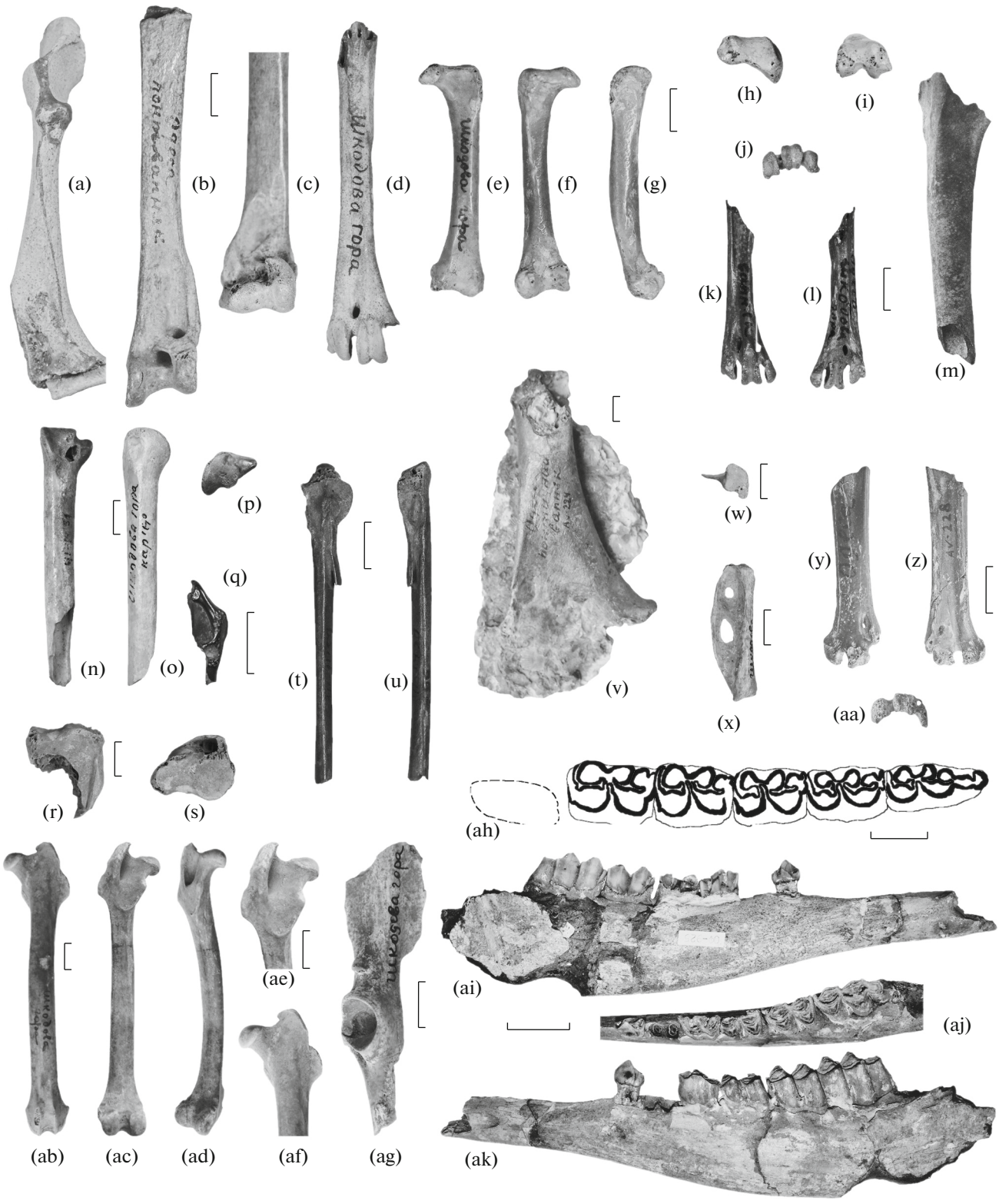
Remarks. The overwhelming majority of avian bone remains from Shkodova Gora belong to this large cormorant (Figs. 2a–2d, 2t, 2u). Previously, only a tarsometatarsus of *Ph. longipes* was described and a femur was tentatively assigned to this species (Tugarinov, 1940). New specimens of various skeletal elements confirm the hypothesis of the previous authors (Voinstvensky, 1967; Zelenkov and Kurochkin, 2015) about the similarity of this species to extant large cormorants (for the diagnosis of this species, see Zelenkov and Kurochkin, 2015). In addition to the large size and some slenderness, the only known structural difference of *Ph. longipes* from all living species is the absence of a fossa on the dorsal surface of trochlea metatarsi III (Zelenkov and Kurochkin, 2015). However, among new specimens, there is a tarsometatarsus (specimen NMNHU-P, no. 41/1447), which has this fossa; this is evidence of individual variation in this character. The low processus extensorius distinguishing the carpometacarpus of *Ph. longipes* is not characteristic of extant cormorants, except for *Ph. auritus* (Lesson, 1831).

Material. Fragmentary maxilla (specimen NMNHU-P, no. 41/3), coracoids (specimens NMNHU-P, nos. 41/704, 41/705, 41/710, 41/1457), humeri (specimens NMNHU-P, nos. 41/2, 41/703, 41/1453, 41/1455, 41/1456, 41/1458, 41/1463), carpometacarpi (specimen NMNHU-P, nos. 41/1454, 41/1759), femur (specimen PIN, no. 228/1), tibiotarsi (specimens NMNHU-P, nos. 41/1448-1450, 41/1460, 41/1462), tarsometatarsi (lectotype of PIN, no. 228/2; specimens NMNHU-P, nos. 41/1445–1447, 41/1452) from the type locality.

***Phalacrocorax mongoliensis* Kurochkin, 1971**

Phalacrocorax mongoliensis: Kurochkin, 1971, p. 59, text-fig. 1; 1985, p. 22, text-fig. 5, pl. I, figs. 5 and 6; Zelenkov and Kurochkin, 2015, p. 206, pl. XXI, figs. 15 and 16.

Holotype. PIN, no. 2614/29, distal fragment of the left femur; Mongolia, Kobdos aimag, Chono-Khariakh locality; Lower Pliocene, upper subformation of the Khirgis Nur Formation.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D e s c r i p t i o n (Figs. 2e–2m). The femoral shaft (specimen NMNHU-P, no. Av-231) is very slightly curved in lateral view; in the proximal end, the caudal margin of the trochanter is positioned in line with the caudal side of the femoral head; the facies articularis antitrochanterica and the cranial part of the trochanter gently pass into each other without an incisure; the sulcus fibularis is shallow; the trochlea fibularis and crista tibiofibularis are directed subperpendicular to each other. In the tarsometatarsus, trochlea metatarsi II projects more distally than trochlea metatarsi III; the incisura intertrochlearis lateralis is considerably deeper than the incisura intertrochlearis medialis; the dorsal aperture of the foramen vasculare distale is large.

M e a s u r e m e n t s i n m m. Specimen NMNHU-P, no. Av-231: maximum length of femur, 52.6; length along medial margin, 51.2; greatest height of proximal end, 7.4; greatest width of preserved part of proximal end, 13.4; greatest width of distal end, 14.3; greatest height of distal end, 8.7; least width of shaft, 5.8. Specimen NMNHU-P, no. Av-233: greatest width of proximal end of tarsometatarsus, 12.7; width of trochlea metatarsi III, 4.8; least width of shaft, 5.5.

C o m p a r i s o n. *Phalacrocorax mongoliensis* differs from *Ph. longipes* in the significantly smaller size [somewhat smaller than extant *Ph. aristotelis* (L., 1761)]. The femur differs from that of all extant cormorants in the shallower sulcus fibularis and in the fact that the trochlea fibularis and crista tibiofibularis are positioned almost perpendicular to each other. The poorly pronounced dorsoventral curvature of the shaft also distinguishes the femur of *Ph. mongoliensis* from all living *Phalacrocorax,* except for *Ph. auritus*. At the same time, *Ph. mongoliensis* has a narrower distal end of the femur than in *Ph. auritus*. The tarsometatarsus is distinguished from that of living species of *Phalacrocorax* by the trochlea metatarsi II extending beyond trochlea metatarsi III and by the significantly deeper incisura intertrochlearis lateralis than the incisura intertrochlearis medialis (in extant cormorants, they proximally terminate at the same level).

R e m a r k s. The femur from Shkodova Gora is identical in size and very similar in morphology to the holotype of *Ph. mongoliensis* from the Lower Pliocene of the Chono-Khariakh locality in Mongolia (Kurochkin, 1985; Zelenkov and Kurochkin, 2015) and, based on this, referred to the same species. This taxon differs from *Microcarbo* in the expanded complex of the condylus lateralis+trochlea fibularis in distal view (in *Microcarbo,* this part of the distal end is significantly narrowed).

M a t e r i a l. The Shkodova Gora locality has yielded a left femur (specimen NMNHU-P, no. Av-231), fragmentary left tarsometatarsus (specimen NMNHU-P, no. Av-233), a proximal humeral fragment (specimen NMNHU-P, no. Av-227; from "Pontian limestones of Odessa").

OTHER VERTEBRATES

***Ctenopharyngodon* sp. (Actinopterygii: Cypriniformes, Cyprinidae)**. The collection from Shkodova Gora contains two fragments of wide, massive, and slightly convex opercles (specimens NMNHU-P, nos. 41/638, 41/640; Pl. 8, figs. 5, 6). The bone is 65–70 mm wide. The shape and size of the fovea articularis, the presence of an openwork structure in the articular region on the internal bone surface, and the absence of ornamentation on the external surface suggest that these remains belong to the genus *Ctenopharyngodon*. The opercle is somewhat similar to that of *Cyprinus* and differs from it in the more notched dorsal edge and considerably less developed ornamentation on the external bone surface.

Testudines (Reptilia). The material of turtles from the Shkodova Gora locality includes a cranial fragment (specimen NMNHU-P, no. 42/1; Figs. 3a–3c) described as *Macrocephalochelys pontica* Pidoplichko et Tarashchuk, 1960, an isolated maxilla (possibly

Fig. 2. Remains of birds and mammals from the Upper Miocene of the Shkodova Gora locality (Ukraine, Odessa Region): (a–d, t, u) *Phalacrocorax longipes* (Tugarinov, 1940): (a) specimen NMNHU-P, no. 41/1457, left coracoid, dorsal view; (b) specimen NMNHU-P, no. 41/1449, left tibiotarsus fragment, cranial view; (c) specimen NMNHU-P, no. 41/2, left humeral fragment, cranial view; (d) specimen NMNHU-P, no. 41/1447, right tarsometatarsus, dorsal view; (t, u) specimen NMNHU-P, no. 41/1759, right carpometacarpus fragment: (t) ventral and (u) caudal views; (e–m) *Phalacrocorax mongoliensis* Kurochkin, 1971: (e–i) specimen NMNHU-P, no. Av-231, left femur: (e) dorsal, (f) ventral, (g) lateral, (h) proximal, and (i) distal views; (j–l) specimen NMNHU-P, no. Av-233, distal part of left tarsometatarsus: (j) distal, (k) dorsal, and (l) plantar views; (m) specimen NMNHU-P, no. Av-227, left humeral fragment, caudal view; (n–p) *Proanser major* Umanskaya, 1979, specimen NMNHU-P, no. Av-230, right ulnar fragment: (n) ventrocaudal, (o) caudal, and (p) distal views; (q) Anatidae gen. indet., specimen NMNHU-P, no. Av-229, left coracoid fragment, dorsal view; (r, s, w, x) Aves indet.: (r, s) specimen NMNHU-P, no. Av-225, right ulnar fragment: (r) cranial and (s) proximal views; (w, x) specimen NMNHU-P, no. Av-232, phalanx of digit 1 of right wing: (w) proximal and (x) dorsal views; (v) *Pelecanus odessanus* Widhalm, 1886, specimen NMNHU-P, no. Av-224, left coracoid, dorsal view; (y–aa) Strigidae gen. indet., specimen NMNHU-P, no. Av-229, right tarsometatarsus: (y) dorsal, (z) plantar, and (aa) distal views; (ab–ag) cf. *Trischizolagus dumitrescuae* Radulesco et Samson, 1967: (ab–af) specimen NMNHU-P, no. 41/706, left femur: (ab) frontal, (ac) rear, and (ad) lateral views; (ae, af) proximal epiphysis: (ae) rear and (af) frontal views; (ag) specimen NMNHU-P, no. 41/707, left innominate bone, lateral view; (ah) *Hipparion* cf. *moldavicum* Gromova, 1952, specimen NMNHU-P, no. 41/36, teeth P_3–M_3 of the left half of the lower jaw, grinding surface; (ai–ak) *Palaeoryx* cf. *pallasi* (Wagner, 1857), specimen NMNHU-P, no. OF-925, left lower jaw ramus with P_2, P_4–M_3: (ai) lingual, (aj) dorsal, and (ak) labial views. Scale bars: (a–ag) 10 and (ah–ak) 30 mm.

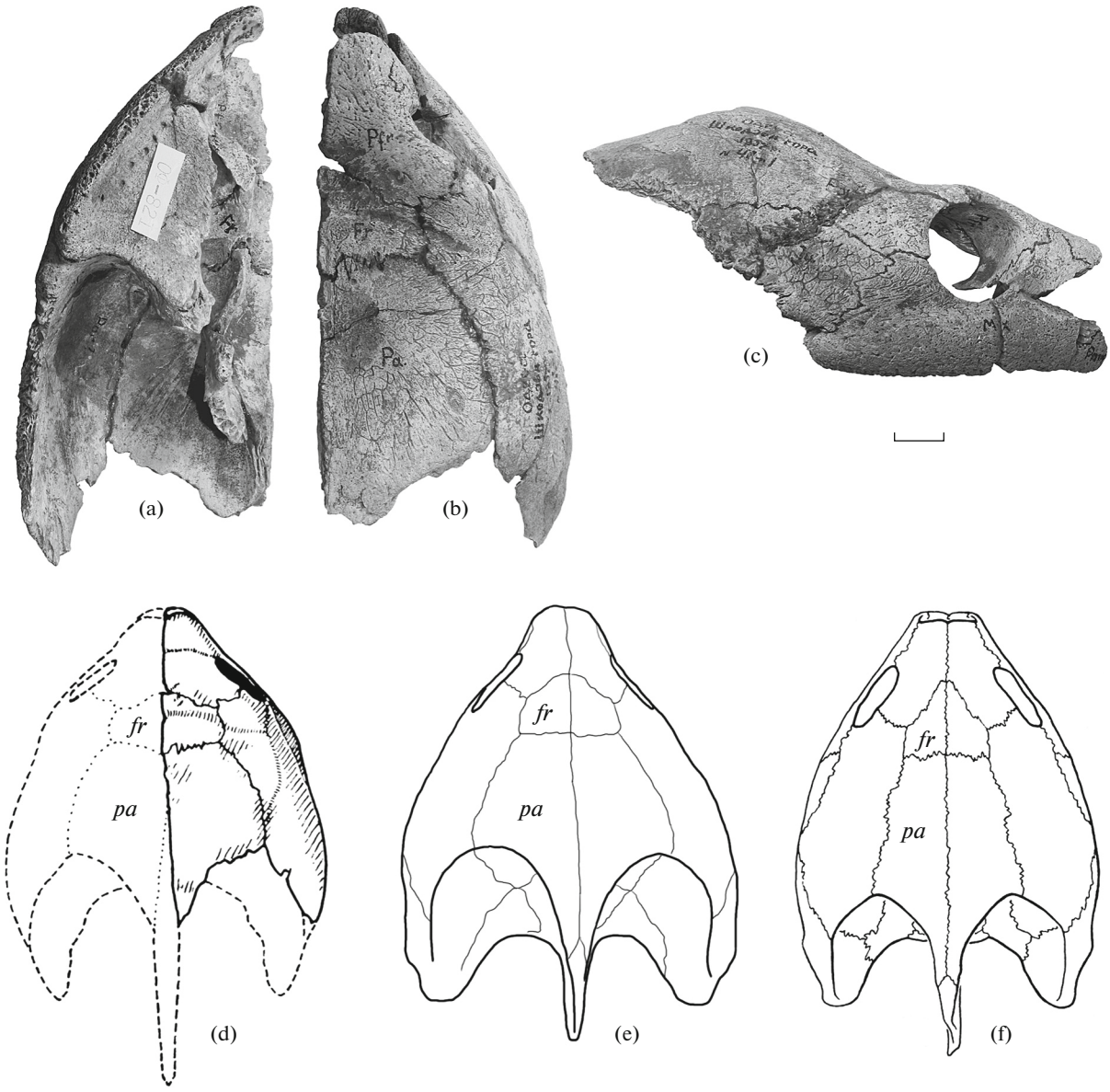

Fig. 3. Skulls of members of the genus *Chelydropsis* (Chelonia): (a–e) *Ch. pontica* (Pidoplichko et Tarashchuk, 1960): (a–c) specimen NMNHU-P, no. 42/1, skull fragment from the Upper Miocene of the Shkodova Gora locality (Ukraine, Odessa Region): (a) ventral, (b) dorsal, and (c) lateral views; (d) skull reconstructed based on the holotype, dorsal view (Pidoplichko and Tarashchuk, 1960); (e) specimen KPKGU (Department of Paleontology, Kiev State University), no. 1711, Kuturskoe locality (Crimea; Upper Miocene), dorsal view (after Tarashchuk, 1971); (f) reconstructed skull of *Ch. murchisoni* (Bell, 1831), dorsal view (after Gaffney and Schleich, 1994). Designations: (*fr*) frontal, (*pa*) parietal. Scale bar, 10 mm.

from the same individual), and uncertain remains identified as *Testudo* sp. (Pidoplichko and Tarashchuk, 1960). *Macrocephalochelys pontica* was originally referred to the family Platysternidae (Pidoplichko and Tarashchuk, 1960; Tarashchuk, 1971), but later transferred to the genus *Chelydropsis* Peters, 1868 of the family Chelydridae (Chkhikvadze, 1971, 1973), which were accepted by Joyce (2016). Subsequently, Chkhikvadze (1982, 1983) identified this species as *Trionyx nopcsai* Szalai, 1934, which was described based on a lower jaw symphysis from the Pliocene of Romania (Szalai, 1934; Młynarski, 1966), and attributed to it a series of cranial specimens from the Pliocene of Ukraine, Moldova, Slovakia, Germany, and Romania. Khozatsky and Redkozubov (1986, 1989) recorded both *Ch. nopcsai* (shell fragments) and *M. pontica* (dentaries) in the Pliocene of Moldova. In our opinion, the holotype of *Trionyx nopcsai* may belong to *Chelydropsis*, although it is too fragmentary to identify it to a separate species and, the more so, to corroborate that it is identical to *M. pontica*, which is only known from skulls without lower jaws. The ques-

tion of the assignment of lower jaw fragments from the Pliocene of Moldova to *M. pontica* (Khozatsky and Redkozubov, 1986, 1989) also requires additional examination (see Chkhikvadze, 1989). It seems more correct to regard *Trionyx nopcsai* as a nomen dubium and, following a number of researchers (Młynarski, 1980, 1981; Lapparent de Broin, 2000), the valid name for Late Miocene and Pliocene *Chelydropsis* of Eastern Europe is *Chelydropsis pontica*. The assignment to this species of fragmentary shell specimens from Pliocene localities of Eastern Europe (Chkhikvadze, 1982, 1983; Khozatsky and Redkozubov, 1989) also requires additional substantiation. Joyce (2016) referred all members of the genus *Chelydropsis* from the Neogene of Europe to one species, *Ch. murchisoni* (Bell), based on the assumption that European Chelydridae were represented by one evolutionary lineage (*Ch. decheni*–*Ch. murchisoni*), which did not undergo further diversification. However, *Ch. pontica* considerably differs from *Ch. murchisoni* (Figs. 3d–3f) in the following characters of the skull structure: (1) the skull is more expanded in the posterior part; (2) the cheek emargination is deepest in the anterior part; (3) the frontals are short and only slightly wedge in between the prefrontals; (4) the parietals are wide, expand significantly posteriorly. Taking into account these distinctions, the idea of synonymy of *Ch. pontica* and *Ch. murchisoni* looks baseless.

Remains of *Testudo* sp. (Testudinidae) from Shkodova Gora were mentioned without data on the material; its depository is not known; therefore, their presence in the assemblage of the locality requires confirmation. Since some specimens from Neogene localities of Eastern Europe originally referred to the genus *Testudo* turned out to belong to *Chelydropsis* (see Joyce, 2016), it is not improbable that *Testudo* sp. from Shkodova Gora actually belongs to the latter genus.

Anatidae gen. indet. (Aves: *Anas* sensu lato). A fragment of poorly preserved and strongly rounded cranial end of a right coracoid (specimen NMNHU-P, no. Av-229; Fig. 2q) belongs to a relatively small duck, most similar in size and morphology to extant *Sibirionetta formosa* (Georgi).

Measurements of this specimen in mm: cranial end length from the caudal margin of the cotyla scapularis, 12.5; bone depth at the level of the facies articularis humeralis, 4. A characteristic feature of this specimen is the presence of a well-pronounced depression occupying a significant part of the sulcus m. supracoracoidei (as in *S. formosa* and members of the genus *Spatula*). This fragment belonged to a smaller bird than *Anas kurochkini* Zelenkov et Panteleyev from the Upper Miocene of the Azov Region (Zelenkov and Panteleyev, 2015); this is the first record of a nondiving duck of this size class in the Upper Miocene of Eastern Europe. A duck similar in size has been described from the Upper Miocene–Lower Pliocene of Mongolia (*Anas* sp. 2; Zelenkov, 2012), although it represents a separate taxon. The incisure in the sulcus m. supracoracoidei of specimen PIN, no. 3378/121 from the Lower Pliocene Chono-Khariakh locality is less extended ventrally. In addition, in the Mongolian duck, the cranial margin of the cotyla scapularis is positioned subperpendicular to the long bone axis, while in specimen NMNHU-P, no. Av-229, this margin is positioned at a blunt angle to the long bone axis is dorsal view (this is apparently a primitive feature of the Anatidae, which is observed in *Dendrocygna,* Oxyurini, and Mergini).

Strigidae gen. indet. (Aves). A fragmentary right tarsometatarsus (specimen NMNHU-P, no. Av-228; Figs. 2x–2aa) belonged to an medium-sized owl. The bone is relatively massive (the ratio of the distal end width to the least diaphysis width is approximately 2 : 3, whereas in the majority of living members of the family, this ratio is about 1 : 2). The incisura intertrochlearis medialis is wide. The dorsal aperture of the foramen vasculare distale and the distal aperture of the canalis interosseus distalis are located at a significant distance (twice greater than their diameters), as in extant *Bubo bubo* (L., 1758) and unlike that of the majority of others owls. The poor preservation of the bone prevents precise determination of the taxonomic position of this taxon, but the similarity to extant *Bubo* suggests that the owl from Shkodova Gora probably belongs to Striginae. This bird differs from Late Miocene eagle owls (*B. perpasta* Ballmann, 1976 and *B. longaevus* Umanskaya, 1979) primarily in the smaller size (in mm): the maximum width of the preserved part of the distal end is 11.3; the width of the preserved part of trochlea metatarsi III is 4.4; the width of the incisura intertrochlearis medialis is 2.25; and the least width of the shaft is 7.2.

Aves indet. A proximal phalanx of the first digit of the right wing (specimen NMNHU-P, no. Av-232; Figs. 2w, 2x) and a fragment of a right ulna (specimen NMNHU-P, no. Av-225; Figs. 2r, 2s) belonged to a large bird of uncertain taxonomic position; it was of the same size class as extant *Balearica pavonina* (L., 1758).

Measurements of specimen NMNHU-P, no. Av-232 in mm: greatest length, 38.1; least width of the bone body in the cranial part, 4.3. The height of the proximal end of specimen NMNHU-P, no. Av-225 is 23.2 mm.

cf. *Trischizolagus dumitrescuae* Radulesco et Samson, 1967 (Mammalia: Lagomorpha, Leporidae). This species is represented by a left femur (specimen NMNHU-P, no. 41/706; Figs. 2ab–2af) and a left pelvic bone fragment (specimen NMNHU-P, no. 41/707; Fig. 2ag), which apparently belonged to one adult individual. The differences from typical *Trischizolagus dumitrescuae* are the somewhat larger femur with closer positioned apices of trochanters. *Hypolagus igromovi* Gureev was somewhat smaller. *H. beremendensis* (Kormos) differs from *Trischizolagus*

in the position of the trochanter minor significantly closer to the bone head and in the less developed distal part of the epicondylus medialis (Fostowicz-Frelik, 2007). *Oryctolagus, Hypolagus, Pentalagus,* and *Sylvilagus* differ from *Trischizolagus* and *Lepus* in the smaller size (see Fostowicz-Frelik, 2007; De Marfà, 2009).

The pelvic fragment is similar in morphology to the type specimens of *Trischizolagus dumitrescuae*, differing in the better developed spina iliaca posteriori inferior for the attachment of the m. recti femoris. This character and development of linea glutei media on the lateral side of the iliac wing are also characteristic of *H. beremendensis* (Fostowicz-Frelik, 2007). In the specimen described, this crest reaches the acetabulum, while in *Hypolagus* it terminates at the spina iliaca.

***Hipparion* cf. *moldavicum* Gromova, 1952 (Mammalia: Perissodactyla, Equidae)**. A medium-sized hipparion is represented by the left lower jaw with teeth P_3–P_4, M_1–M_3 and the alveolus of P_2 (specimen NMNHU-P, no. OF-41-36; Fig. 2ah). The dental row (along the alveoli) is 148 mm long. The molar–premolar index is approximately 100. The double knot is slightly asymmetrical; the metaconid and metastylid are subround (significantly differ in shape in M_1). The ectoflexid already enters the neck of the double knot in moderately worn premolars and almost adjoins the groove of the double knot in M_1 and M_2 (type IV after Gromova, 1952). The enamel is weakly plicate. The protostylid and ectostylid are absent. The size and simple structure of teeth suggest that the specimen described is close to *H. moldavicum* known from the Middle Turolian of Europe (Krakhmalnaya, 1996; Forsten and Krakhmalnaya, 1997; Vlachou and Koufos, 2009).

***Palaeoryx* cf. *pallasi* (Wagner, 1857) (Mammalia: Artiodactyla, Bovidae)** is represented by an incomplete left lower jaw with P_2, P_4, M_1–M_3 and a relatively low and narrow horizontal ramus (specimen NMNHU-P, no. OF-925; Figs. 2ai, 2ak). The presence on moderately worn P_4 of open first three valleys and flattened T-shaped metaconid combined with well-developed parastylids and entostylids and also the presence of rudimentary pillars between the protoconids and hypoconids in mesohypsodont M_2–M_3 suggest that the specimen in question should be assigned to Hippotraginae. The general measurements (dental row P_2–M_3 reaches 124 mm of length) and proportion of the dental row (premolars compose 38% of dental row length, the index of the premolar row length is 60.6%) are similar to that of members of the genus *Palaeoryx*. The relatively large size and great relative length of lower premolars from Shkodova Gora are evidence that this taxon is close to *P. pallasi* (Wagner, 1857) and differs somewhat from *P. majori* Schlosser, 1904 (Kostopoulos and Bernor, 2011). It should be noted that, until recently, representatives of the genus *Palaeoryx* have only been known from the Early Maeotian of the northern Black Sea Region (Korotkevich and Krakhmalnaya, 1984).

DISCUSSION

The study of vertebrates from the Shkodova Gora locality has shown that they are represented by eight fish species, seven avian taxa, one or two turtle species, and three mammal species. In the previous studies, mammals from the Shkodova Gora locality were only represented by Cervidae and Giraffidae of uncertain genera (Dubrovo and Kapelist, 1979) and birds were only *Phalacrocorax longipes* (Zelenkov and Kurochkin, 2015). Our data essentially supplement the Pontian vertebrate fauna of the Eastern Paratethys.

The finds of *Palaeoryx* and a hare resembling *Trischizolagus* are the first for the Pontian of the northwestern Black Sea Region. Previously, the hare genus *Trischizolagus* in this region has only been recorded in the Pliocene (MN14–MN16: Averianov and Tesakov, 1997); however, more ancient specimens have been described from almost contemporaneous Late Miocene (MN13) beds of Western Europe, Mongolia, and Afghanistan (López Martínez, 1989; Averianov and Tesakov, 1997). The antelope genus *Palaeoryx* is common in Middle Turolian faunas (MN12) of Greece, Bulgaria, Turkey, Ukraine, Moldova, Iran, and China (Gentry, 1971; Krakhmalnaya, 1996; Kostopoulos, 2006, 2009; Kostopoulos and Bernor, 2011), but also occurs in Late Turolian (MN 13) localities of Greece (Bouvrain and Bonis, 2007). The anseriform bird *Proanser major* was only known from more ancient deposits of Ukraine (MN11: Umanskaya, 1979) and the cormorant *Phalacrocorax mongoliensis* has previously been described from the Early Pliocene of Mongolia (Kurochkin, 1985). Thus, the occurrence of *Palaeoryx* in Shkodova Gora is evidence of wide distribution of this genus in the terminal Miocene and coexistence of *Proanser major* and *Phalacrocorax mongoliensis* confirms the hypothesis of the similarity and wide distribution of Late Miocene and Early Pliocene waterfowl faunas, as was previously proposed based on the study of materials from Mongolia (Zelenkov, 2013, 2016).

A rather rich fish fauna of Shkodova Gora also significantly expands the previously known Pontian ichthyofauna of the Eastern Paratethys (Kovalchuk, 2015a), which presently includes 22 species. The occurrences of *Abramis bliccoides* and *Perca lepidopoma* (previously known from the Upper Miocene–Middle Pliocene of Western Siberia), *Rutilus tungurukensis* (Lower–Upper Miocene of eastern Kazakhstan and the Altai Mountains), *Ctenopharyngodon* sp. (Upper Miocene–Lower Pliocene of China) are of particular interest. The presence of these taxa in Shkodova Gora confirms the idea of Sytchevskaya (1983, 1989) about the existence of a uniform Neogene Euro-Siberian ichthyofauna. *Rutilus robustus* found in Shkodova Gora has previously been recorded in the Upper

Miocene of the Pontian lectostratotype (Ukraine) and the Pliocene of the Priozernoe locality in Moldova (Kovalchuk, 2014). The geographical range of this species was apparently wider than was previously believed (Kovalchuk, 2015a) and reached eastern Kazakhstan. Bones of *Acipenser gueldenstaedtii* is the earliest reliable record of this species in Eastern Europe. The absence of pikes in the Shkodova Gora ichthyofauna has engaged our attention, although it may be accounted for by the insufficient sample size.

The fish assemblage from Shkodova Gora apparently existed in the delta of a relatively large river which was located in the area of the Dniester–Southern Bug interfluve and flew into the Pontian Sea. This is evidenced by the presence of anadromous (*Acipenser gueldenstaedtii*) and semi-anadromous fishes (*Rutilus robustus* and *Abramis bliccoides,* ecological analogues of *R. frisii* and *A. brama*) and also species capable of dwelling in brackish-water conditions (*Ctenopharyngodon* sp., *Silurus glanis, Sander lucioperca*). The majority of these fishes were confined to the bottom water layers rich in oxygen in the sites with rapid or slow currents and sandy–oozy or pebbly floor. The presence of phytophiles (*Rutilus, Abramis, Perca, Silurus*) and pelagophile (*Ctenopharyngodon*) is evidence of significant development of underwater vegetation. The above-water vegetation could also be well developed; the reed and cattail thickets could be inhabited by pelicans, cormorants, and anseriforms (*Proanser, Anas*). The presence in the Shkodova Gora Assemblage of large freshwater Chelydridae (*Chelydropsis*) is evidence of a stagnant pond (probably former riverbed) and also of a rather warm climate with positive minimum temperatures. Turtles of the genus *Chelydropsis* apparently fed on mollusks, as follows from the expanded alveolar surfaces of their jaws (Joyce, 2016).

Terrestrial landscapes in the deltaic area were probably represented by weakly humid open spaces (steppes or forest–steppes), as follows from the presence of the antelope genus *Palaeoryx* (see also Korotkevich, 1988). Paleobotanic data (Molyavko, 1960; Syabryaj et al., 2007) also suggest that, in the northern Black Sea Region of that time, grassy associations were widespread, replacing in the Pontian the previously prevailing meadows rich in Chenopodiaceae. Although certain data suggest that, in the Pontian, valley forests were widespread (Syabryaj et al., 2007), the Shkodova Gora fauna lacks typical forest taxa.

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