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On the First Reliable Record of the Ichthyosaur *Ophthalmosaurus icenicus* Seeley in the Oxfordian–Kimmeridgian Beds of European Russia

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Abstract—An incomplete skeleton of the ichthyosaur *Ophthalmosaurus icenicus* Seeley, 1874 excavated in the Oxfordian–Kimmeridgian beds south of the town of Syzran (Samara Region) is described. Members of the genus *Ophthalmosaurus* are characterized by a unique combination of characters, most of which are well-pronounced in the specimen described here: the extracondylar area of the basioccipital is reduced, but still visible beyond the occipital condyle and has a well-pronounced ventral notch; the scapular shaft is mediolaterelly flattened; the humerus has three distal facets: the anterior facet is the smallest; the facet for the accessory preaxial element has a sharpened anterior margin; the facet for the radius faces distally; the facet for the ulna faces posterodistally; the posterior margin of the ulna is concave and sharpened, involved in the perichondral ossification; the intermedium is rhomboid, with two distal facets equal in size for the second and third distal carpals; the epipodial and autopodial elements are round and thickened, loosely arranged in the fin. This specimen is the first reliable evidence of the presence of *Ophthalmosaurus* in the Oxfordian–Kimmeridgian of Russia. The previously described remains of a Kimmeridgian ichthyosaur referred to as *O. undorensis* Efimov, 1991 should be identified as Ophthalmosauridae indet.

Keywords: Ophthalmosaurus icenicus, ichthyosaur, Oxfordian, Kimmeridgian, Upper Cretaceous, Russia
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INTRODUCTION

Bones of Late Jurassic ichthyosaurs are frequently recorded in European Russia. They are usually represented by isolated vertebral centra and rib fragments, less often, by cranial remains, limb, and girdle bones, which allow taxonomic identification. At the same time, not all stratigraphic levels of the upper series of the Jurassic System are rather completely characterized by ichthyosaurs (Efimov, 2001). Only the Middle and Upper Volgian beds contain frequent fossils of this reptiles (Efimov, 1991, 1998, 1999a, 2001; Arkhangelsk, 1997, 1998, 2000, 2001; Arkhangelsky and Zverkov, 2014; Zverkov et al., 2015a, 2015b). The Oxfordian and Kimmeridgian beds as well as the Lower Volgian have yielded considerably fewer ichthyosaurian remains (Efimov, 2001).

At present, the only reliable *Ophthalmosaurus* sp. in Russia is known from the Upper Volgian of Nenets Autonomous Region (Zverkov et al., 2015a). Thereby, an incomplete ichthyosaur skeleton found in 2007 by A.V. Evgrafov, a worker of the Syzran Regional Museum (SKM), during a survey of the Mesozoic sections on the bank of the Volga River near the village of Elizarovo (Syzransky District, Samara Region) is particularly important. At present, this specimen is stored in SKM (SKM, no. OF 242/1-19).

Unfortunately, the precise stratigraphic level of the specimen has not been identified. However, the properties of enclosing rock (established by light gray clayey matter remaining on the bones) and a number of certain features of preservation of the bone matter (such as yellowish brown color, increased ferrugination, gypseous crusts, and limonite on the surface of some bones) are evidence that the specimen comes from the Oxfordian–Kimmeridgian beds. Light gray calcareous clay preserved on the bone surfaces forms

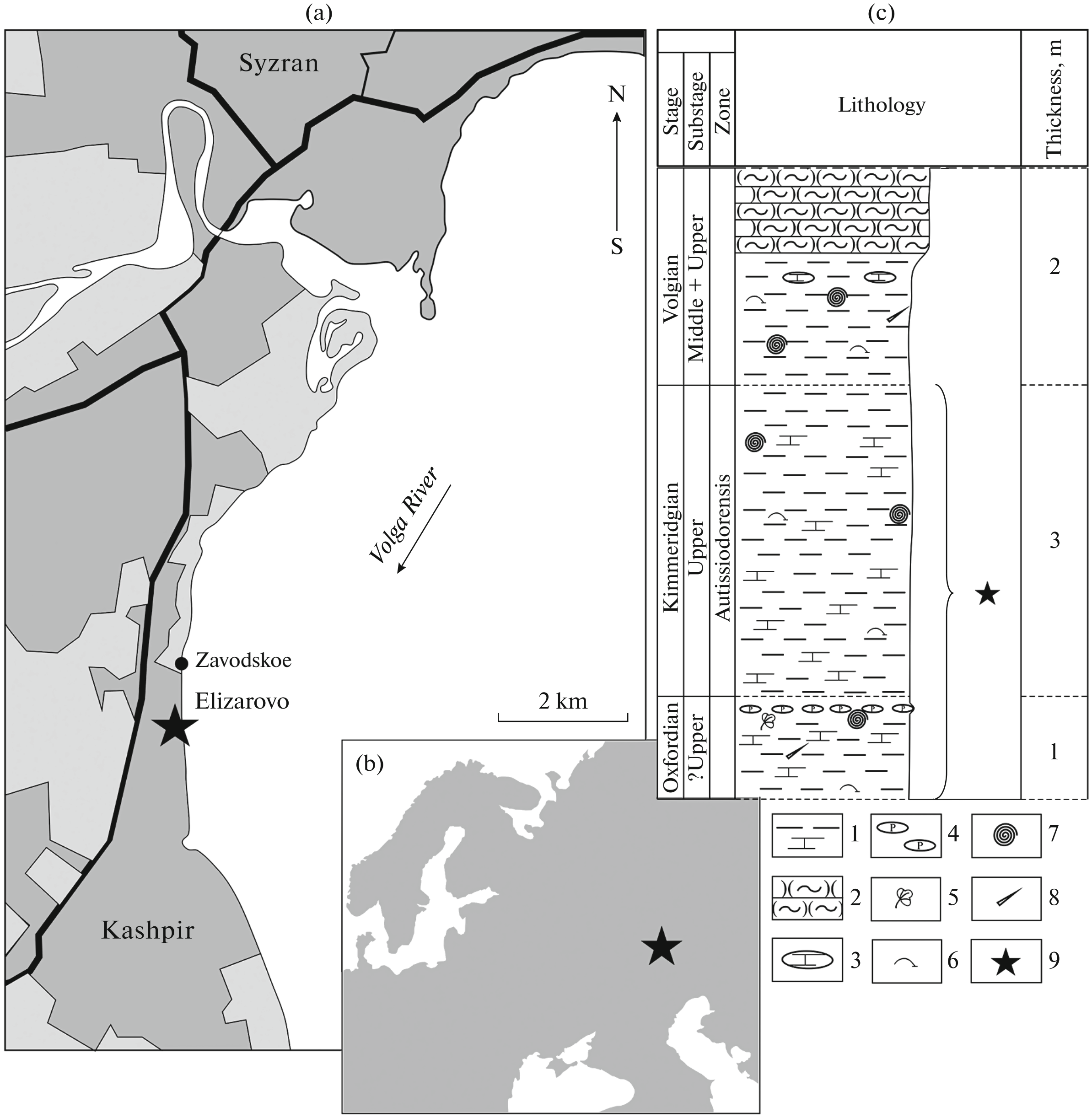

Fig. 1. Geographical position of (a, b) Elizarovo and Zavodskoe localities and also (c) geological section of the Upper Jurassic (after Morov and Kuchera, 2012). Designations: (1) calcareous clay, (2) siltstone, (3) marl concretions, (4) phosphorite pebble, (5) wood remains, (6) bivalves, (7) ammonites, (8) belemnites, (9) locality and presumable level of finding specimen SKM, no. OF 242/1-19.

in this region the section of the Oxfordian–Kimmeridgian (M.A. Rogov, Geological Institute of the Russian Academy of Sciences (GIN), personal communication).

According to published data, near the point where the ichthyosaur skeleton was found, Oxfordian, Kimmeridgian, and Volgian deposits outcrop (Morov and Kuchera, 2012) (Fig. 1c). Along the bank of the Volga River, the bedrock is well exposed in landslide cirques; small outputs in bank steeps are less often. According to the description of a neighboring section (Zavodskoe), the Oxfordian beds are composed of light gray schistose calcareous clays about 1 m of exposed thickness and immersed under the level of the reservoir (Morov and Kuchera, 2012). At the top, there is a horizon of phosphorite concretions with fragments of phosphatized wood, phosphatized fragments of unidentifiable ammonite molds, and abundant gryphaeid bivalves. The shells sometimes bear calciferous serpulid tubes, which are particularly typical for Middle–Upper Oxfordian assemblages (Morov and Kuchera, 2012). The Kimmeridgian beds overlie with unconformity the Oxfordian calcareous clays and are only represented by the upper substage (basal

Autissiodorensis Zone, biohorizon aff. *rebholzi:* Rogov, 2010) (Morov and Kuchera, 2012). The material collected by the amateur paleontologist I. S''edugin (Syzran) in the Zavodskoe outcrop additionally includes ammonites characteristic of the upper part of the *Eudoxus* Zone (*Aulacostephanus yo* (d'Orbigny), identified by Rogov), although they only occur in phosphorite pebbles. By analogy with the Upper Jurassic section at the Samara Bend exposed by a quarry near the village of Valy, Rogov proposed that, at this point, the *Autissiodorensis* Zone overlies with erosion the Oxfordian–basal Kimmeridgian (?) beds, and ammonites of the *Eudoxus* Zone only occur in the phosphorite horizon at the base of the *Autissiodorensis* Zone. In general appearance, the Kimmeridgian beds are difficult to distinguish from the Oxfordian. These strata are composed of light gray calcareous shale. The upper boundary is everywhere overlain by landslips or turf-covered. Remains of invertebrates are only observed in the lower interval of the section (about 1 m from the base), mostly in a crushed condition, and represented by the following taxa: ammonites (*Sutneria* aff. *rebholzi* Berckhemer, *Aulacostephanus kirghisensis* (d'Orb.), *A. volgensis* (Vischniakoff), *Aspidoceras* cf. *catalaunicum* (Loriol), *Nannocardioceras* sp., ?*Neochetoceras* sp.), scaphopods (*Laevidentalium* sp.), bivalves (*Nuculoma* cf. *variabilis* (Sow.), *Liostrea plastica* (Trautschold), ?*Inoceramus* sp.), gastropods (*Dicroloma cohleata* (Quenstedt)) and polychaetes (?*Nogrobs (Tetraserpula)* sp.). Occasionally, molds of bivalves and gastropods are pyritized. The strata reach 3 m of visible thickness.

In the region considered here, the Volgian Regional Stage is represented by the middle and upper substages (Morov and Kuchera, 2012). Outputs of the middle substage are only observed in landslips and represented by clays, in places, bituminous. They enclose shells of *Inoceramus* cf. *pseudoretrorsus* Gerasimov. Combustible shales have not been recorded. The landslip surfaces and alluvium occasionally display thin marl concretions with the ammonite *Epivirgatites nikitini* (Michalsky) and bivalve *Buchia* cf. *piochii* (Gabb). The lower part of the Upper Volgian Substage is composed of straw-colored friable laminate opoka-like siltstones. These rocks of the Volgian Regional Stage are rarely observed in intact condition; they reach 2 m of visible thickness. The lower boundary of the Volgian beds is turf-covered. The strata enclose the following invertebrates: ammonite molds (*Kachpurites fulgens* (Trautschold), *Craspedites mosquensis* Gerasimov, *C. kaschpuricus* (Trautschold), *C. parakaschpuricus* Gerasimov, *Garniericeras* sp.); belemnites (*Acroteuthis mosquensis* (Pavlov)), and bivalves (*Anopaea sphenoidea* Gerasimov, *Buchia terebratuloides* (Lahusen)).

It has previously been indicated that the Kimmeridgian Stage of the East European Plate is poorly understood with reference to both stratigraphy and paleontology (Rogov and Kiselev, 2007; Morov and Kuchera, 2012). The presence in the Oxfordian–Kimmeridgian section in the vicinity of Syzran of well-preserved fossils of invertebrates and vertebrates confirms the necessity of detailed examination of this stratigraphic interval.

It is noteworthy that the identification of Upper Jurassic ichthyosaurs was for a long time complicated because paleontologists did not establish the synapomorphies of the genus *Ophthalmosaurus* Seeley, 1874, which is well-known from the Middle–Upper Jurassic beds of Western Europe. In this connection, remains of the majority of Jurassic and even some Cretaceous ichthyosaurs with three distal facets on the humerus were referred to it (see, e.g., Bogolyubov, 1910; Efimov, 1991; Russell, 1993). To date, it has been established that humeri of almost all Middle and Upper Jurassic ichthyosaurs have three distal articular surfaces for the radius, ulna, and accessory preaxial element. It is shown that members of the genus *Ophthalmosaurus* have a unique combination of skeletal characters (Andrews, 1910; Applebey, 1956; Kirton, 1983; McGowan and Motani, 2003; original data): the teeth are weakly fixed in alveolar grooves, their roots are round in cross section; the orbits are large (orbital ratio >0.20); the sclerotic ring occupies most of the orbit; the postorbital region is narrow; the squamosal is retained, triangular in shape; the basioccipital has a flat anterior surface; it is reduced, but projects beyond the condyle and has a well-pronounced ventral notch; the extracondylar area is limited laterally by a pair of large facets for the stapes; the basioccipital peg is reduced; the scapular shaft is flattened in cross section; the humerus has three distal facets: the anterior facet is the smallest; the facet for the preaxial accessory element has a sharpened anterior margin; the facet for the radius is turned distally; the facet for the ulna faces posterodistally; the posterior margin of the radius is concave and sharpened, included in the perichondral bone; the intermedium is rhomboid, with two proportional distal facets for the second and third distal carpals; the epipodial and autopodial elements are round and thickened, loosely arranged in the fin; the longest digit includes about 20 elements; the ischiopubis is flattened, with a closed obturator foramen; the femur has two distal facets, the anterior one is larger. At present, the genus *Ophthalmosaurus* includes two species, *O. icenicus* and *O. natans* (Marsh, 1879) (McGowan and Motani, 2003); however, North American *O. natans* possibly belongs to a separate genus, *Baptanodon* Marsh, 1880 (Fischer et al., 2012).

Most of the above listed characters of *Ophthalmosaurus* are observed in the specimen considered; therefore, it is assigned to *O. icenicus* Seeley, 1874, the type species of ophthalmosaurs, which has previously been recorded only in the Middle–Upper Jurassic of Western Europe (Seeley, 1874; Andrews, 1910; Appleby, 1956; Kirton, 1983; McGowan and Motani, 2003). This specimen is of great interest, expanding the data on the geographical and stratigraphic ranges of *O. icenicus*.

The material described in the present paper is stored in the Syzran Regional Museum (specimen SKM, no. OF 242/1-19); it is an incomplete skeleton, including the basioccipital, left stapes, left quadrate, articular, a large part of the angular of the left lower jaw ramus; two fused anterior vertebrae (altas and axis), three anterior dorsal vertebral centra, many rib fragments, right coracoid, two incomplete scapulae, right humerus, left and right ulnae, elements of the mesopodium and autopodium, and a number of unidentifiable bone fragments.

DESCRIPTION AND COMPARISON OF MATERIALS

Skull. The basioccipital (specimen SKM, no. OF 242/1) (Pl. 8, fig. 1) is a massive subspherical bone, with a convex occipital condyle. The extracondylar area of the bone is slightly reduced and projects laterally and ventrally in the posterior plane beyond the condyle; it has a well-pronounced ventral notch (Pl. 8, fig. 1a). The notochordal pit is located slightly above the midheight of spherical occipital condyle. The facets for the exoccipitals are large, oval, extended anteroposteriorly, separated by a narrow projection of the neural canal, which does not form an anterior peg (Pl. 8, fig. 1b). The facets for the stapes are large, subtriangular, located on the anterolateral surfaces of the basioccipital (Pl. 8, figs. 1c, 1d). The facet for the opisthotic is considerably smaller than the facet for the stapes (the ratio is 1 : 3), oval in shape, and located in the dorsal part of the anterolateral surfaces (Pl. 8, figs. 1c, 1d). The anteroventral facet for the basisphenoid is pentagonal in outline and divided by a medial groove (Pl. 8, fig. 1c).

The stapes (specimen SKM, no. OF 242/2) (Pl. 8, fig. 2) has a large medial head characteristic of all members of the family Ophthalmosauridae Baur, 1887 (Fischer et al., 2012) and laterally directed process adjoining the quadrate. The medial head is higher than wide, differentiated into three facets (Pl. 8, fig. 2e): large, anteromedially directed facet for the basisphenoid; smaller posterodistally directed facet for the basioccipital; and relatively small and poorly pronounced facet for the opisthotic located on the dorsal surface of the medial stapedial head. The distal part of the stapedial shaft is slightly widened and has an oval facet for the quadrate (Pl. 8, figs. 2a–2d). The ventral margin of the stapes forms an outgrowth for contact with the medial plate of the pterygoid. The hyoid process is poorly developed (Pl. 8, fig. 2b).

The left quadrate (specimen SKM, no. OF 242/3) (Pl. 8, fig. 4) is a massive C-shaped bone with an extensive posterodistal incisure (quadrate foramen) (Pl. 8, figs. 4a–4c). The occipital lamella is well developed, overhanging the quadrate foramen; its surface is positioned at an angle of 100° to the pterygoid lamella. The facet for the stapes is slightly concave, located in the center of the bone medial surface (Pl. 8, figs. 4b, 4c). The anterior margin of the pterygoid lamella is slightly concave (Pl. 8, figs. 4a–4c). The condyles for articulation with the mandible are well developed and separated by a smooth groove (Pl. 8, figs. 4c, 4d). The boss for the articular bone is more massive and more projecting ventrally compared to the boss for the surangular (Pl. 8, fig. 4c).

The articular (specimen SKM, no. OF 242/4) is subtrapezoid; its corners are rounded (Pl. 8, fig. 3). The articular, along with the surangular, formed the articular surface of the lower jaw. The lateral surface of the bone is flat and the medial surface is convex.

The lower jaw fragment is represented by the posterior third of the left angular, the region located under the orbit (specimen SKM, no. OF 242/5). In the anterior part of the fragment, the ventral surface has a facet for the splenial. The dorsal surface has a groove for the surangular and coronoid.

Axial skeleton. The atlas and axis (epistropheus) (Fig. 2) (specimen SKM, no. OF 242/6) are fused without a trace of a suture. The vertebral centra are extended somewhat and narrowed ventrally (Figs. 2a, 2c). Their ventral surface is rounded and rough; the axis has an extensive facet for the intercenter (Figs. 2c, 2e). The diapophyses and parapophyses of the atlas are fused with each other and with the anterior margin of the vertebra (Fig. 2b). The diapophyses of the axis are fused with the facets of the neural arches and directed obliquely anteroventrally; the parapophyses of the axis are small, round (Fig. 2b).

Two anterior dorsal vertebrae (specimen SKM, no. OF 242/7, 8) taper ventrally. The diapophyses are fused with the areas for neural arches, but separated from the anterior margin of the centrum. The para-

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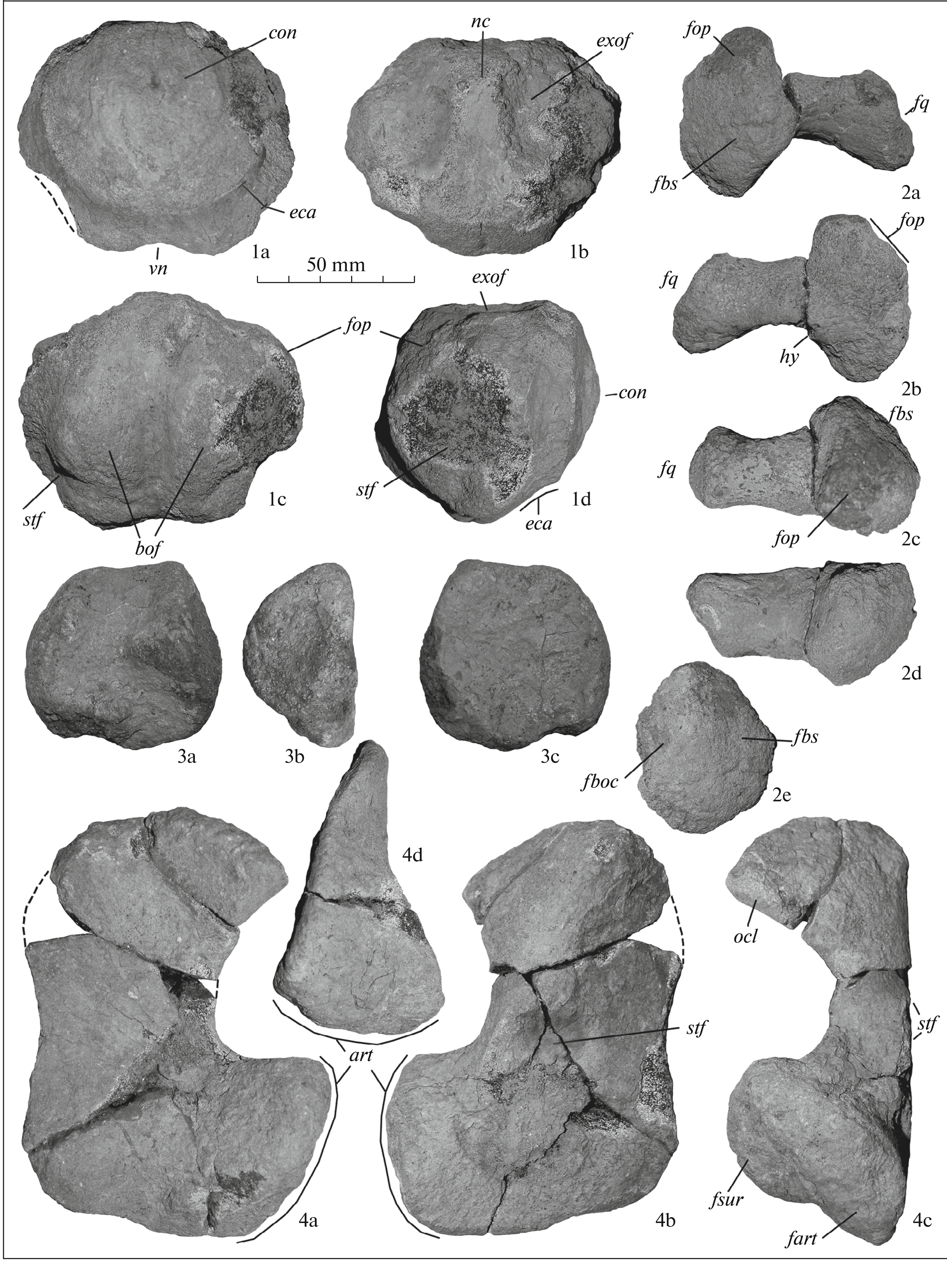
Explanation of Plate 8

Figs. 1–4. *Ophthalmosaurus icenicus* Seeley, 1874, specimen SKM, no. OF 242, cranial elements; Elizarovo locality, Samara Region, Russia; Upper Jurassic, Oxfordian–Kimmeridgian: (1) specimen SKM, no. OF 242/1, basioccipital: (1a) posterior, (1b) dorsal, (1c) ventral, and (1d) lateral views; (2) specimen SKM, no. OF 242/2, stapes: (2a) anterior, (2b) posterior, (2c) dorsal, (2d) ventral, and (2e) medial surface views; (3) specimen SKM, no. OF 242/4, articulare: (3a) medial surface, (3b) anterior, and (3c) lateral surface views; (4) specimen SKM, no. OF 242/3, quadratum: (4a) lateral, (4b) medial surface, (4c) posterior, and (4d) ventral views. Designations: (*art*) articular surface, (*bof*) facets for the basioccipital, (*con*) occipital condyle, (*eca*) extracondylar area, (*exof*) facet for the exoccipital, (*hy*) hyoid process, (*fart*) facet for the articular, (*fboc*) facet for the basioccipitale, (*fbs*) facet for the basisphenoid, (*fop*) facet for the opisthotic, (*fq*) facet for the quadrate, (*fsur*) facet for the surangular, (*nc*) neural canal, (*ocl*) occipital lamella, (*stf*) facet for the stapes, (*vn*) ventral notch.

Plate 8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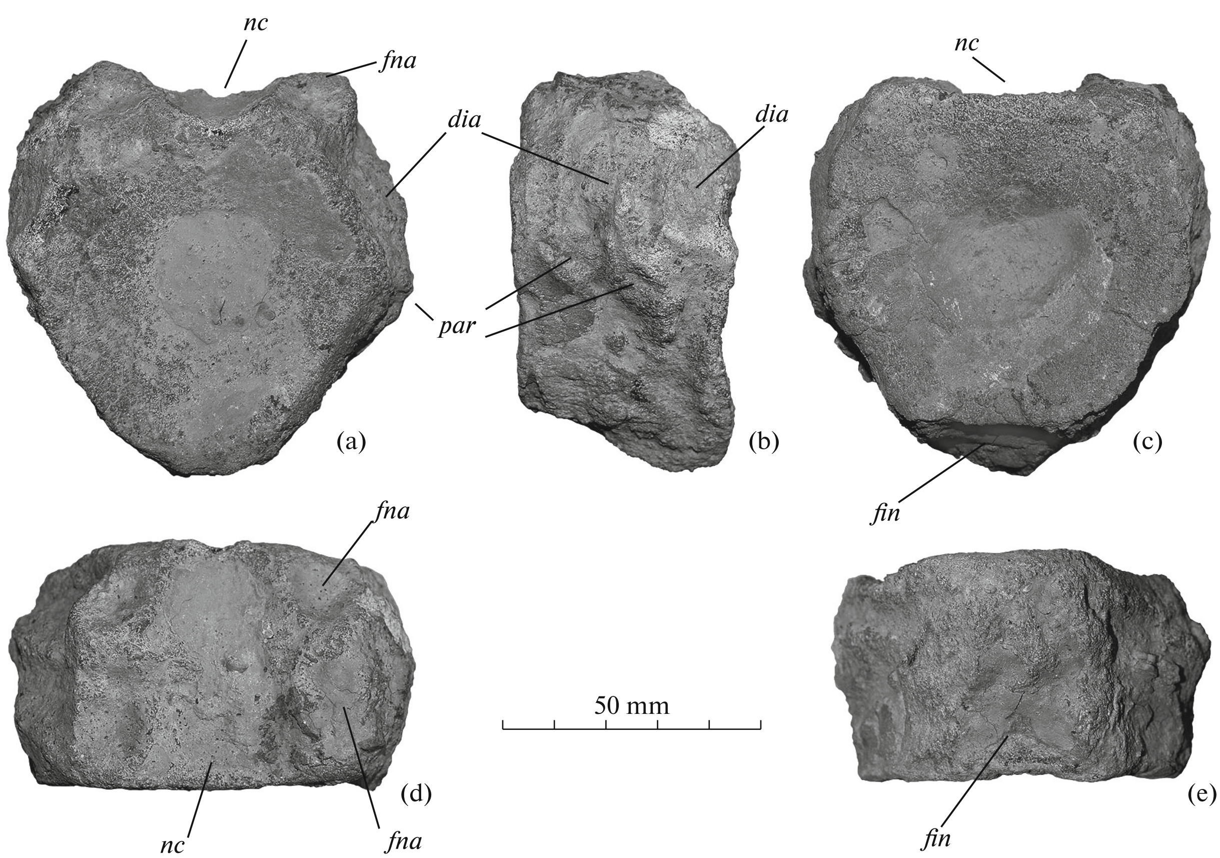


Fig. 2. Atlas and axis of *Ophthalmosaurus icenicus* Seeley, 1874, specimen SKM, no. OF 242/6: (a) anterior, (b) lateral, (c) rear, (d) dorsal, and (e) ventral views; Elizarovo locality, Samara Region, Russia; Upper Jurassic, Oxfordian–Kimmeridgian. Designations: (*dia*) diapophyses, (*fin*) facet for intercenter axis, (*fna*) facets for neural arches, (*nc*) neural canal, (*par*) parapophyses.

pophyses are irregularly oval, directed subvertically, not fused with the anterior margin of the centrum, located at the midheight of the vertebra.

One more anterior dorsal vertebra (specimen SKM, no. OF 242/9) is rounded ventrally. It is characterized by fusion of the diapophyses with both the areas for the neural arches and anterior margin of the vertebral centrum. The parapophysis is irregularly oval, positioned at the midheight of the centrum, and separated from its anterior margin.

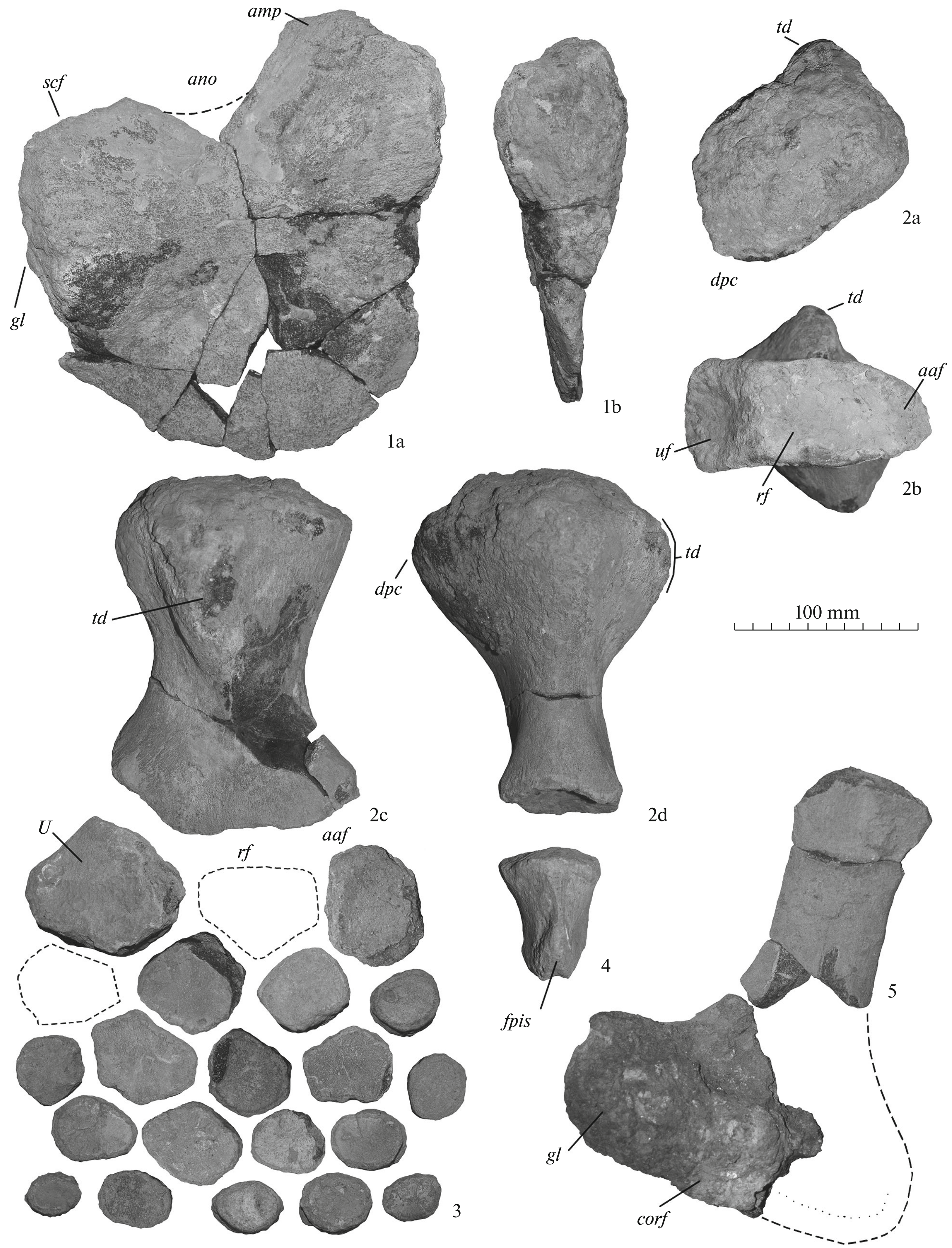
In locality has yielded many rib fragments (specimen SKM, no. OF 242/10), some fragments are up to 35–40 cm long. All of them are oval in cross section at the midlength.

Bones of girdles and free limbs. The pectoral girdle is represented by the right coracoid and incomplete scapulae. The coracoid (specimen SKM, no. OF 242/11) (Pl. 9, fig. 1) is preserved completely (however, the bone margins are crumbled in places), typical for *Ophthalmosaurus* in its round shape (Kirton, 1983). The bone is large, has an extensive anterior notch (Pl. 9, fig. 1a). The medial facet is lenticular in cross section, shifted to the anterior margin, where it is widest (Pl. 9, fig. 1b). The ventral surface of the coracoid is saddle-shaped; the shaft extends from the anteromedial margin to glenoid fossa. The angle between the scapular and glenoid facets is 90°. The glenoid facet is teardrop-shaped in cross section, tapering posteriorly. The facet for the scapula is directed anteriorly. The

Explanation of Plate 9

Figs. 1–4. *Ophthalmosaurus icenicus* Seeley, 1874, specimen SKM, no. OF 242, bones of postcranial skeleton; Elizarovo locality, Samara Region, Russia; Upper Jurassic, Oxfordian–Kimmeridgian: (1) specimen SKM, no. OF 242/11, coracoid: (1a) ventral view and (1b) medial surface; (2) specimen SKM, no. OF 242/14, humerus: (2a) proximal surface, (2b) distal surface, (2c) dorsal surface, and (2d) rear view; (3) specimen SKM, no. OF 242/15-19, epipodial and autopodial elements, dorsal view; (4) specimen SKM, no. OF 242/15, ulna, rear view; (5) specimen SKM, no. OF 242/12, scapula, dorsal view. Designations: (*aaf*) facet for the anterior accessory element, (*amp*) anteromedial process of the coracoid, (*ano*) anterior notch, (*corf*) facet for the coracoid, (*dpc*) deltopectoral crest, (*fpis*) facet for the pisiform bone, (*gl*) glenoid, (*rf*) facet for the radius, (*scf*) facet for the scapula, (*td*) dorsal process, (*U*) ulna, (*uf*) facet for the ulna.

Plate 9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anteromedial process of the coracoid is relatively small. The posterior margin of the coracoid is strongly flattened.

Both scapulae (specimen SKM, no. OF 242/12, 13) are strongly damaged because of expansion of gypsum crystals. The right scapula is better preserved (Pl. 9, fig. 5). The bone expands strongly proximally, has a completed ossification between the acromion and facet for the coracoid. The facet is drop-shaped, tapering anteriorly. The glenoid facet is massive. The diaphysis of the scapular shaft is flattened mediolaterally. The diaphysis is approximately as wide as the distal margin of the element.

The right humerus (specimen SKM, no. OF 242/14) is preserved almost completely (Pl. 9, fig. 2). The proximal end is widened, trapezoid in cross section (Pl. 9, fig. 2a). The angle of torsion of the long axes of the distal and proximal ends is 85°. The dorsal surface has a rather massive dorsal crest extending obliquely towards the facet for the radius. The ventral surface has a wide and flattened deltopectoral crest (Pl. 9, fig. 2d). The distal end has three facets: for the preaxial accessory element, radius, and ulna (Pl. 9, fig. 2b). The facet for the preaxial accessory element is concave, subtriangular in outline. The facets for the radius and ulna are slightly concave, rounded oval in outline. The angles between the facets for the ulna, radius, and preaxial accessory element are 50° and 45°, respectively (Pl. 9, fig. 2c). The facet for the radius is wider than the facet for the ulna.

The material includes two ulnae (specimen SKM, no. OF 242/15, 16), preaxial accessory element (specimen SKM, no. OF 242/17), intermedium (specimen SKM, no. OF 242/18), and disarticulated elements of the mesopodium and autopodium (specimen SKM, no. OF 242/19) (Pl. 9, fig. 3).

The ulna is large, anteriorly comes in contact with the radius and anteroventrally the intermedium, has a ventral facet for the ulnare and a posteroventral facet for the pisiform. The posterior margin of the ulna is sharpened and involved in perichondral ossification typical for all ophthalmosaurines (sensu Fischer et al., 2012; Pl. 9, fig. 4). The proximal surface is slightly convex. The preaxial accessory element is circular in outline and has a slightly convex dorsal facet for the humerus. Posteriorly, this bone came in contact with the radius and, posteroventrally, with the radiale. The anterior margin of the bone is sharpened, but is not involved in perichondral ossification. The intermedium rhomboid in shape; both distal facets for the second and third distal carpals are similar in size. All available elements of the autopodium are thickened and have rounded corners or rounded outline (Pl. 9, fig. 3).

Comparison. The specimens described here resemble *O. icenicus* in both cranial and postcranial skeletal elements. Among the ophthalmosaurs from the Oxford Clay Formation of England described by C.W. Andrews, specimen SKM, no. OF 242/1–19 is most similar to the specimen housed in the Museum of Natural History of London, specimen NHMUK R 2160 (Andrews, 1910). This specimen, like our ophthalmosaur, differs from the others in a number of features: the occipital condyle is less convex than in the majority of other specimens; the posterior margin of the quadrate is concave (in the majority of others, it is convex or straight); the coracoid is longer than wide; and the facet for the ulna is wider than the facet of the radius. Andrews (1910) proposed that specimen NHMUK R 2160 could possibly be used as a type specimen of a new species of *Ophthalmosaurus*; however, later researchers have not adhered to this point of view.

The ichthyosaur *Ophthalmosaurus undorensis* Efimov previously described based on a humerus and vertebrae from the Kimmeridgian of the Volga Region was referred by Efimov to *Ophthalmosaurus* based on the presence of three distal facets of the humerus (Efimov, 1991). However, as mentioned above, this is not a distinctive character of *Ophthalmosaurus* (Fischer et al., 2012; Zverkov et al., 2015a). In opinion of Efimov, the only character distinguishing the new species from *O. icenicus* is the relative greater thickness of "the carpal part of the fin" (Efimov, 1991, p. 114). However, this is also typical for other ophthalmosaurids with similar humeral morphology, i.e., Oxfordian–Volgian *Arthropterygius* Maxwell, 2010 and Volgian *Undorosaurus* Efimov, 1999 (Efimov, 1999b; Maxwell, 2010; original data of N.G. Zverkov). Therefore, in our opinion, *O. undorensis* should be regarded as nomen dubium. This material should be referred to as Ophthalmosauridae indet.

CONCLUSIONS

The new ichthyosaur remains described from the town of Syzran provide the first reliable data on the presence of *O. icenicus* in the Oxfordian–Kimmeridgian beds of Russia. Along with the ophthalmosaur from the Nenets Autonomous Region, the new skeleton shows the similarity of Late Jurassic ichthyosaur faunas of the Middle Russian Sea and basin of Western Europe.

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