



УДК 568.152

## ON A NEW ICHTHYOSAUR OF THE GENUS *UNDOROSAURUS*

M.S. Arkhangelsky<sup>1, 2\*</sup> and N.G. Zverkov<sup>3</sup>

<sup>1</sup>Saratov State Technical University, Politekhnikeskaya St. 77, 410054 Saratov, Russia

<sup>2</sup>Saratov State University, Astrakhanskaya St. 83, 410012 Saratov, Russia, e-mail: paleozoo@gmail.com

<sup>3</sup>Lomonosov Moscow State University, Leninskie Gory 1, 119991 Moscow, Russia; e-mail: zverkovnik@rambler.ru

### ABSTRACT

A new species of ichthyosaur genus *Undorosaurus* from the Volgian stage of Moscow is described based on an incomplete forelimb. It differs from congeners basically in the form and position of pisiforme. With the application of cladistic method the phylogenetic position of two genera *Undorosaurus* and *Paraophthalmosaurus* in the system of Ichthyosauridae is defined. Both taxa are referred to the clade Ophthalmosaurinae.

**Key words:** ichthyosaurs, Jurassic, phylogeny, *Undorosaurus*

## О НОВОМ ПРЕДСТАВИТЕЛЕ ИХТИОЗАВРОВ РОДА *UNDOROSAURUS*

М.С. Архангельский<sup>1, 2\*</sup> и Н.Г. Зверьков<sup>3</sup>

<sup>1</sup>Саратовский государственный технический университет, ул. Политехническая 77, 410054 Саратов, Россия

<sup>2</sup>Саратовский государственный университет, ул. Астраханская 83, 410012 Саратов, Россия; e-mail: paleozoo@gmail.com

<sup>3</sup>Московский государственный университет, Ленинские горы 1, 119991 Москва, Россия; e-mail: zverkovnik@rambler.ru

### РЕЗЮМЕ

По неполной передней конечности описан новый вид ихтиозавра рода *Undorosaurus* из волжских отложений г. Москвы. Он отличается от других представителей рода, главным образом, формой и расположением гороховидной кости. С применением кладистических методов определено филогенетическое положение родов *Undorosaurus* и *Paraophthalmosaurus* в системе ихтиозаврид. Оба рода отнесены к кладе Ophthalmosaurinae.

**Ключевые слова:** ихтиозавры, юра, филогения, *Undorosaurus*

## INTRODUCTION

During the last decade a number of new genera and species of ichthyosaurs based on a nearly complete materials were described from the Upper Jurassic and Cretaceous deposits of the European countries and the Americas (Druckenmiller and Maxwell 2010; Druckenmiller et al. 2012; Fisher et al. 2012). In Russia remains of ichthyosaurs are also widely

known, but are usually represented by isolated bones and tooth crowns. Such fragmentary material makes it difficult to propose accurate taxonomic identification and morphological study. This fact makes important to pay very close attention to any, even relatively complete ichthyosaur remains originating from the Upper Jurassic of Russia.

In autumn 2013, the authors have revised remains of the Mesozoic marine reptiles stored in the Geological State Museum RAS named after V.I. Vernadsky (hereinafter GSM). There are materials there,

\*Corresponding author/Автор-корреспондент

collected and described by the outstanding Russian geologist and paleontologist – Hermann Gustav Heinrich Ludwig Trautschold (1817–1902). One of the most interesting specimens – a left ichthyosaur forelimb, was discovered by H. Trautschold in 1878 in the Upper Jurassic black clayey glauconite sands near the village Mnevniky, situated on the left bank of the Moskva River (Trautschold, 1879). Currently, this area is located in the Moscow city territory. According to Trautschold in the material was also presented fragmented skull bones, fragments of mandibular ramus and ribs. All of these fossil remains, except fin, were severely weathered and, unfortunately, to date, destroyed. Trautschold described the limb, but did not refer it to any genus or species of ichthyosaurs (Trautschold 1879).

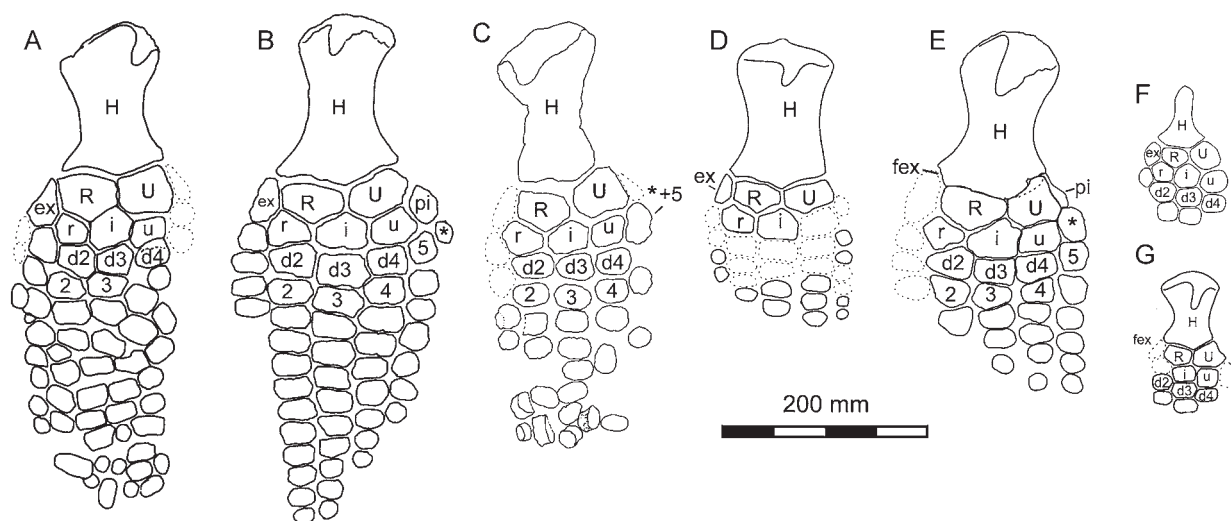
According to Trautschold (1879), the bones occur in the Kimmeridgian sands. The study of the Upper Jurassic deposits of Mnevniky vicinity carried out by M.A. Rogov (Geological Institute RAS) showed that they belong to the Volgian (Tithonian) age. The bones, in his opinion, come from black glauconite sands of stratigraphic interval *Epivirgatites nikitini* – *Kachpurites fulgens* (M.A. Rogov pers. comm.).

Characteristic proportions and structure allow to refer the limb to the genus *Undorosaurus* Efimov, 1999, erected by V.M. Efimov (1999b) from the Volgian Stage of the Middle Volga and Moscow regions. The humerus length equals 152 mm in type species (*U. gorodischensis* Efimov, 1999) and 150 mm in the described species, width of proximal and distal ends of the humerus is respectively 100 mm and 98 mm in type species and 100 mm and 110 mm in the described species. The described forelimb shares some characteristic features with the type species of the genus *Undorosaurus*: the posterodistally deflected ulnar facet and distally facing radial facet, distal contact of the intermedium with distale carpale 3, and antero-distal contact with distale carpale 2, rounded anterior edge of the humerus and small semicircular facet for extrazeugopodial element, straight posterior surface of the ulna nearly as thick as the rest of the element and some other.

Representatives of the genus *Undorosaurus* are characterized by the presence of three distal facets on humerus; extrazeugopodial element of the accessory preaxial digit contacts with anterior distal facet of the humerus, having a small size, as in most ophthalmosaurids. Preaxial digit is well developed; its length and the number of phalanges were comparable

with those in the main digits. In this, *Undorosaurus* differs from *Ophthalmosaurus* Seeley, 1874. In *Ophthalmosaurus* preaxial accessory digit was almost two times shorter than the others (pers. obs. of authors). The fifth digit extends from the postero-distal edge of ulnare. Large pisiforme has an extensive contact with the ulna. Distal edge of intermedium is flat and has a wide distal contact with distale carpale 3, and antero-distal contact with distale carpale 2. Among ophthalmosaurids this character is observed in *Undorosaurus*, *Cryopterygius* Druckenmiller et al., 2012, *Paraophthalmosaurus* Arkhangelsky, 1997 (Arkhangelsky 1997, 1998; Efimov 1999a; Fig. 1). This character is less expressed in some species of the genus *Platypterygius* Huene, 1922 (Arkhangelsky 1998a; Efimov 1999a,b; Druckenmiller et al. 2012; Maxwell and Kear 2010; Zammit et al. 2010). Intermedium of *Ophthalmosaurus* contacts with distale carpale 3 and distale carpale 4 (Motani 1999). Forefin of *Undorosaurus*, generally, relates to “longipinnate” type of forefin architecture.

The forelimb stored in the collection of GSM has certain morphological differences from previously described undorosaurus (Efimov 1999): pisiform bone is strongly narrowed and not completely separated from ulna, in several places they are fused completely. It is directly in contact with humerus. From the humerus originates a large rounded first element of postaxial accessory digit, which has not received sufficient development (phalanges are not developed in this digit). Pisiforme contacts anteriorly with ulnare, distally – with metacarpal 5. This significant difference is used as a basis for the erection of a new species, despite the incompleteness of the available material. New data will complement the diagnosis of the genus *Undorosaurus* in general. It should be noted that previously, due to inaccurate illustration given by Trautschold (Trautschold 1879: Taf.V) in his publication, this limb was incorrectly defined by Arkhangelsky (1998a; Fig. 1) as *Paraophthalmosaurus* sp., whose limbs have similar architecture. *Paraophthalmosaurus* differs by its smaller size, the biggest known humerus UPM EP-II-16(1202) (see below for this and other institutional abbreviations) is 90 mm in length and belongs to an adult specimen (Efimov 1997). The deltopectoral crest in this genus is more prominent, posterior surface of ulna is concave with a thin tapered margin, and ulnare is more isometric, square in shape (Arkhangelsky 1997; Efimov 1997, 1999a).



**Fig. 1.** Forefins of the Late Jurassic ophthalmosaurines: A – *Cryopterygius kristiansenae*, left, dorsal surface (Druckenmiller et al. 2012); B – *Undorosaurus gorodischensis*, UPM EP-N-24(785), right, dorsal surface (Efimov 1999b, with changes); C – *Undorosaurus* sp., YKM 44028-7, left, ventral surface; D – *Undorosaurus gorodischensis*, UPM EP-N-23(744), left, dorsal surface (Efimov 1999b); E – *Undorosaurus trautscholdi* sp. nov., GSM 1503, left, dorsal surface; F – *Ophthalmosaurus* sp. (Fernández 2000); G – *Paraophthalmosaurus kabanovi*, UPM EP-N-8(1076) left, dorsal surface (Efimov 1999a). Images on figures B, C and F were reversed for easier comparison. **Abbreviations:** 2–5 – metacarpals; d2–d4 – distal carpals; dp – dorsal process; dpc – deltopectoral crest; ex – extrazeugopodial element; fpe – facet of humerus for the extrazeugopodial element; H – humerus; I – intermedium; nd – avascular necrosis depression; pi – pisiforme, basal element of posterior supernumerary digit; R – radius; r – radiale; U – ulna; u – ulnare; \* – first element of posterior supernumerary digit.

Until recently *Undorosaurus* was considered as a junior synonym of *Ophthalmosaurus*, however, a number of authors previously removed it from this synonymy, due to its strong teeth with a subquadratic section of the root (synapomorphy of Platypterygiinae; see Fischer et al., 2012), developed pelvic girdle, with medially unfused ischium and pubis, as well as the presence of the “longipinnate” type of the forefin (McGowan and Motani 2003). These features differentiate *Undorosaurus* from *Ophthalmosaurus*.

Previously, Russian researchers used traditional approach (without applying of cladistic analysis) to the study of the phylogeny of the ichthyosaurs (Efimov 1997; Arkhangelsky 1998), which led to a series of controversial hypotheses and conclusions. Perhaps for this reason other researchers were skeptical of the determination of new ichthyosaur taxa from Russia and attempted to bring them in synonymy with the already known forms (Maisch and Matzke 2000; McGowan and Motani 2003). Inaccessibility of Russian materials for foreign colleagues and fairly brief descriptions prevented their inclusion in the phylogenetic reconstructions. Below the authors are making the first attempt to determine the phylogenetic position of several genera of ichthyosaurs described for the first time from the territory of Russia.

**Institutional abbreviations.** GSM, Geological State Museum of the Russian Academy of Sciences named after V.I. Vernadsky (Moscow, Russia); GIN, Geological Institute of the Russian Academy of Sciences (Moscow, Russia); MOZ, Museo Prof. J. Ol-sacher, Dirección Provincial de Minería (Zapala, Argentina); YKM, Ulyanovsk Regional Museum of Local Lore named after I.A. Goncharov (Ulyanovsk, Russia); UPM, Undory Paleontological Museum (Undory Village, Ulyanovsk region, Russia).

## SYSTEMATICS

### Order Ichthyosauria Blainville, 1835

### Family Ophthalmosauridae Baur, 1887

### Subfamily Ophthalmosaurinae Baur, 1887 (sensu Fischer et al. 2012)

### Genus *Undorosaurus* Efimov, 1999

**Type species.:** *Undorosaurus gorodischensis* Efimov, 1999.

**Distribution.** Middle Volga and Moscow regions, Russia.

**Stratigraphic range.** Upper Jurassic, middle to upper Volgian.

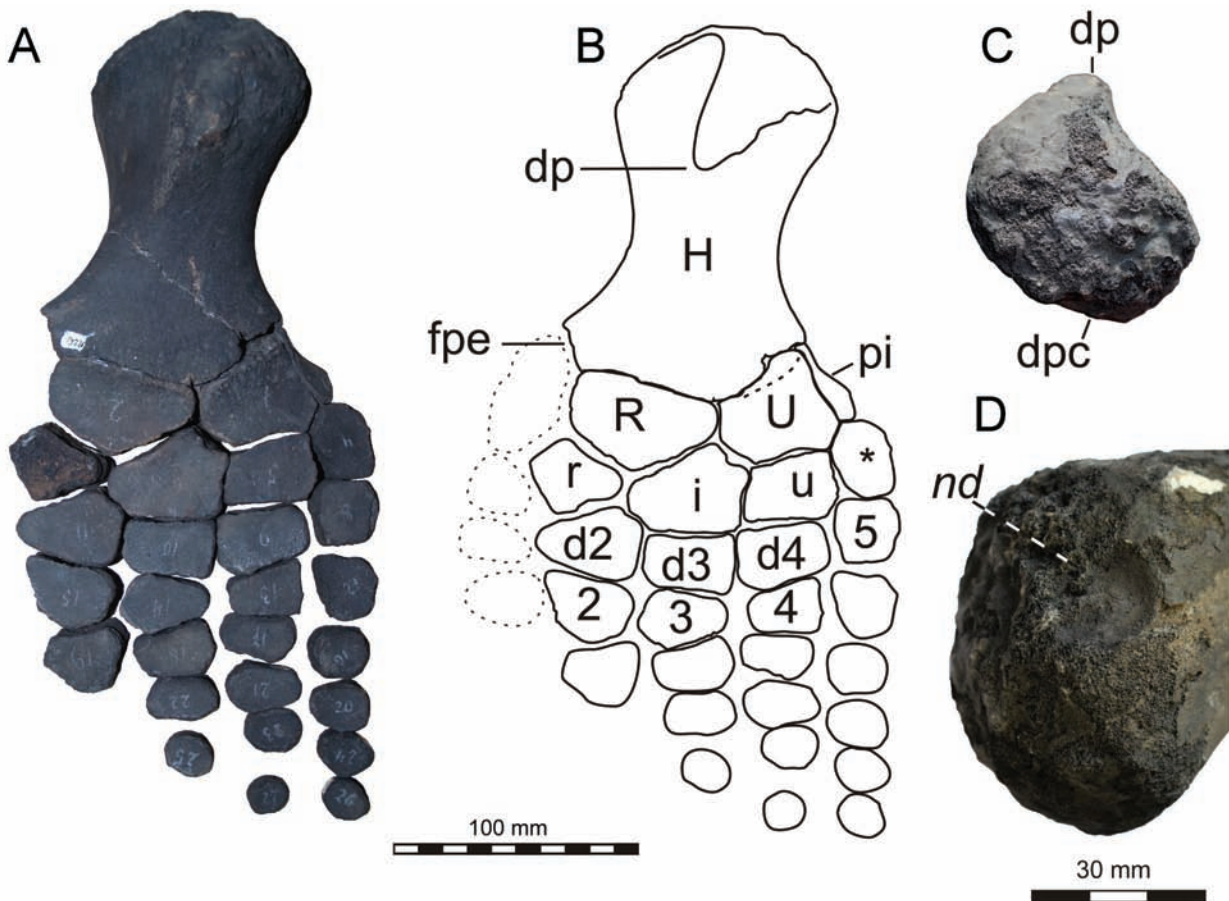
**Diagnosis** (after Efimov 1999b, with changes of the authors). A large ichthyosaur nearly 4–6 m long. Sagittal eminence is slightly developed. Teeth large (60 mm), with stout roots squared in cross-section. Vertebrae massive. Ribs thick and stout, 8-shaped in cross section. Coracoids oval and plate-shaped with a prominent rounded anterior notch. Ventral part of the scapula is slightly anteroposteriorly expanded, acromion process of the scapula is slightly developed, acromion is not separated from the coracoid facet of the scapula. Humerus with three main distal facets, the anterior one for the articulation of a preaxial accessory element is semicircular in outlines. The small fourth distal facet for pisiforme can present posterior to the ulna. Ulnar facet is posterodistally deflected, radial facet – distally. Deltopectoral crest extremely

reduced. Humeral torsion is approximately 50°. Forefin of “longipinnate” architecture. Preaxial accessory digit is well developed, as long as other digits. Metacarpal 5 lies posterodistal to the ulnare. Distal edge of the intermedium flattened has extensive contact with distale carpale 3 and slight anterodistal contact with distale carpale 2. Pisiforme originates from the posterodistal or posterior edge of the ulna and can possess small associated facet on humerus. Ischiopubis flattened, unfused distally; femur with two distal facets; phalanges polygonal-rounded.

***Undorosaurus trautscholdi* sp. nov.**  
(Fig. 2)

**Holotype.** GSM 1503, partial left forefin.

**Locality and horizon.** Mnevniki, Moscow, Russia; Upper Jurassic, upper Volgian (Trautschold, 1878).



**Fig. 2.** Left forefin of *Undorosaurus trautscholdi* sp. nov.: A – dorsal surface; B – interpretation of the elements of the limb; C – surface of the proximal epiphysis; D – avascular necrosis depression. For abbreviations see Fig. 1.



**Etymology.** The species is named in honor of outstanding geologist H. Trautschold, who collected the remains of the describing specimen and made the original description.

**Diagnosis.** Humeral distal facets concave, proximal surfaces of radius and ulna are slightly convex; Pisiforme has contact with humerus, it is strongly narrowed anteroposteriorly and not yet fully separated from ulna. The small fourth distal facet for pisiforme can be present posterior to the ulna. From the pisiform bone originates prominent rounded first element of postaxial accessory digit.

## DESCRIPTION

The available left forefin is well preserved. The epipodial bones are in the natural articulation (Fig. 2 A–C). Humerus length 150 mm. Width of proximal end – 100 mm, distal – 110 mm. The angle formed by the comparison of the long axes of the proximal and distal ends of the humerus (humeral torsion) is approximately 50°. The proximal end of humerus has rectangular outlines (Fig. 2C). In anteroventral surface located a poorly developed deltopectoral crest. Well developed dorsal process extends obliquely forward toward the front edge of radial facet. Its length is 60 mm, height – near 32 mm. Distal end of humerus bears three oval facets for extrazeugopodial element, radius and ulna. The length of the facets is respectively: 20 mm, 60 mm, 45 mm. In this facet for the anterior accessory element is located at a prominent angle in relation to the facet radius (50°). Ulnar facet is posterodistally deflected, radial facet – distally.

Radius is roughly pentagonal in outlines. Anteriorly it contacts the extrazeugopodium of the anterior accessory digit, anterodistally with the radiale, posterodistally with the intermedium, medially with the ulna. The radiale articulates anteroproximally with the extrazeugopodial element, posterproximally with the radius, posterodistally with distal carpal 2, medially it contacts the intermedium. Distal carpal 3 has proximal contact only with the intermedium, distal carpal 4 – with the ulnare. The pisiforme originates from the posterior surface of the ulna and has contact with the humerus, it is strongly narrowed anteroposteriorly and not yet fully separate from ulna. From the pisiform bone originates prominent rounded first element of postaxial accessory digit. It contacts proximoanteriorly with the ulna, anteriorly

with the ulnare distally with metacarpal 5. The fifth digit is slightly shifted postaxially. Metacarpal 5 has small proximoanterior contact with the ulnare and wide anterior contact with distal carpal 4. Distal carpal 2 has wide proximal contact with radiale and in a less degree with intermedium.

Proximal autopodial elements are polygonal with rounded angles, distal elements are rounded. Despite the fact that there is no sudden decrease in height of phalanges, it is clear that the flipper is incomplete distally. The most complete digit (digit 5) comprises only five phalanges. The real shape of the flipper appears to be close to the other best known representatives of the genus.

**Remarks.** Of considerable interest is a forefin stored in Ulyanovsk Regional Museum (YKM 44028-7; Fig. 1C). It is likely that this specimen can be referred to the same genus. Unfortunately the pisiforme is missed in this specimen, however ulnar posterior surface in this specimen is pitted and very like that in life it was in wide contact with pisiform. The feature of this specimen is large elongated element, located posteriorly than ulnare. It is most likely, that it represents fused first element of postaxial accessory digit and metacarpal five: fusion of some limb elements is sometimes occur in ichthyosaurs, particularly in thoroughly investigated *Stenopterygius* Jaekel, 1904 (Johnson 1979; Maxwell 2012) and in *Ophthalmosaurus* (Knight 1903). Preaxial accessory digit in YKM 44028-7, as in GSM-1503 is missing, making it difficult to compare them with other representatives of the genus and with *Cryopterygius kristiansenae* Druckenmiller et al., 2012, which has a similar architecture of the forefin (Druckenmiller et al. 2012). However, the character of the posterior edge of the ulna in *Cryopterygius* is similar to that in YKM 44028-7, and probably, it was in wide contact with pisiform, subsequently lost during fossilisation.

**Paleoecological observations.** There is wide (near 2 cm in diameter) depression on the proximal epiphysis of the described *humerus*, closer to the ventral side, near the deltopectoral crest (Fig. 2D). Similar defects have been interpreted by Rothschild et al. (2012), as avascular necrosis. According to the aforementioned author, avascular necrosis was observed in over 15% of the Late – Middle Jurassic to Cretaceous ichthyosaurs with the highest occurrence (18%) in the Early Cretaceous (Rothschild et al. 2012). These data support the hypothesis that some ichthyosaurs, notably Ophthalmosaurinae, could be deep-sea div-

ers (Fischer et al. 2013; Motani et al. 1999). In the light of new data can be to suggest that *Undorosaurus* could also dive to great depths.

## PHYLOGENETIC ANALYSIS

To assess the phylogenetic position of the genus *Undorosaurus* Efimov, 1999 we used matrix developed by Fischer et al. (2012) with the addition of *Leninia stellans* Fischer et al. 2013, described a year later (Fischer et al. 2013). Three new characters and four ophthalmosaurian genera were added: Volgian ichthyosaurs of the Volga Region – *Undorosaurus gorodischensis* Efimov, 1999, *Paraophthalmosaurus saveljeviensis* Arkhangelsky, 1997 and *P. kabanovi* (Efimov, 1999), and the recently described from the Volgian deposits of Spitsbergen *Cryopterygius kristiansenae* (Arkhangelsky 1997, 1998b; Efimov 1997, 1999a, b; Druckenmiller et al. 2012; see Appendices 1–5). The forms above in major part are fragmentary and could only be coded for respectively 66.6%, 42.6%, 42.6% and 74%. The new characters were coded from the literature (McGowan and Motani 2003; Johnson 1979; Andrews 1910; Kirton 1983; Gilmore 1905; Fernández 1994, 1997, 1999, 2001; Maxwell 2010; Bardet and Fernández 2000; Zammit et al. 2010; Kolb and Sander 2009; Druckenmiller and Maxwell 2010; Maxwell and Caldwell 2006; Fischer et al. 2011, 2012). The data matrix was analyzed in TNT ver.1.1. (Goloboff et al. 2010).

The following new characters were added to the matrix:

52. Medial facet for the scapula on coracoid: 0 – absent, 1 – present and well prominent. The appearance of the medial facet for the scapula in the coracoid is caused by the strong growth of acromion and a concurrent anterolateral shift in of the front edge of the coracoid, it leads to locking of scapular-coracoid foramen. This configuration is currently known only for some representatives of the two ichthyosaur genera: *Stenopterygius* and *Paraophthalmosaurus* (Johnson 1979; Efimov 1999a).

53. Coracoid shape in adults: 0 – rounded (length to width ratio less than 1,3, and often is close to 1); 1 – elongated (length to width ratio greater than or equal to 1,5). Most representatives of the clade Thunnosauria Motani, 1999 are characterized by rounded shape of the coracoid. Elongated, or how it was characterized by Efimov (1999b) plowshare-shaped coracoids possess forms belonging to genera:

*Stenopterygius* Jaekel, 1904, *Paraophthalmosaurus* and *Nannopterygius* Huene, 1922 (according to Kirton 1983). This character was used by Efimov to assign '*Yasykovia*' to the family Stenopterygiidae Kuhn, 1934 (Efimov 1999a).

54. Intermedium/distal carpal 2 contact: 0 – absent; 1 – present. Anterodistal contact of intermedium with distale carpale 2 among ophthalmosaurids can be observed in *Undorosaurus*, *Cryopterygius*, *Paraophthalmosaurus* and in less pronounced degree in some species of the genus *Platypterygius* (Arkhangelsky 1998a; Efimov 1999a, b; Druckenmiller et al. 2012; Maxwell and Kear, 2010; Zammit et al. 2010)

Two most parsimonious trees with a length of 115 steps were recovered from the analysis. The strict consensus tree (Fig. 3) has a length of 122 steps, a consistency index (CI) of 0.48 and a retention index (RI) of 0.62. A strict consensus resulted in two monophyletic groups Platypteryginae and Ophthalmosaurinae as in Fischer et al. (2012). All forms which were added in the analysis are considered to be part of the clade Ophthalmosaurinae. Most Ophthalmosaurinae species (*Ophthalmosaurus icenicus*, *O. natans*, *Acamptonectes densus*, *Undorosaurus gorodischensis*, *Cryopterygius kristiansenae*, *Paraophthalmosaurus saveljeviensis* and *P. kabanovi*) form a polytomic clade, probably, because the added taxa are known from fragmentary remains (some have more than 50% of missing data).

*Paraophthalmosaurus saveljeviensis* and *P. kabanovi* (originally described as *Yasykovia kabanovi* (Efimov 1999a)) form a clade. This topology was quite expected: the question of the synonymy of *Paraophthalmosaurus* and '*Yasykovia*' has been repeatedly raised (Pervushov et al. 1999; Storrs et al. 2000; Arkhangelsky 2008).

## DISCUSSION

To date, the question of development of pre- and postaxial digits in ichthyosaurs is not well understood. In *Undorosaurus*, concurrently with well-developed preaxial digit, there is a slightly developed additional postaxial digit. However, in more ancient ichthyosaurs such as *Mixosaurus*, *Stenopterygius* and *Ichthyosaurus*, there is a marked row of ossicles posterior to the fifth digit (Maxwell 2012; Motani 1999). In most ophthalmosaurids the postaxial digit is quite developed and in some members of the genus *Platypterygius* there are several additional postaxial digits (Motani 1999; Zammit et al. 2010). The pres-

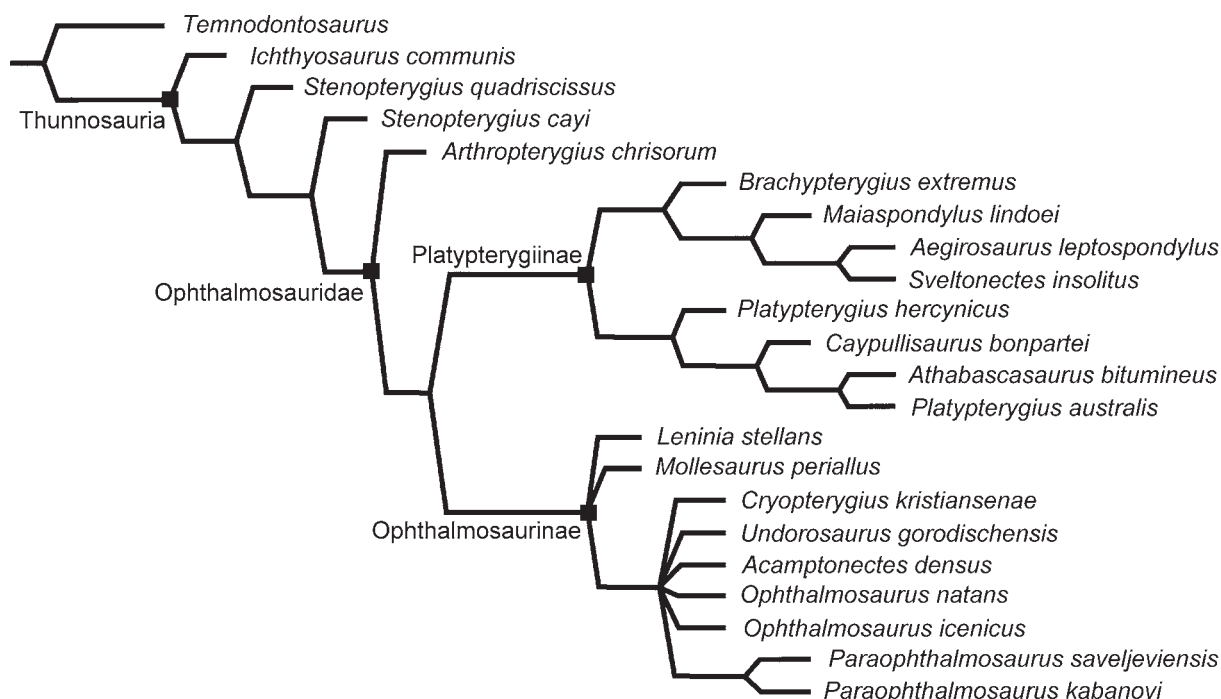


Fig. 3. Strict consensus of two most parsimonious trees. See text for description.

ence of only a few elements in the postaxial digit and often only basal element – pisiforme is one of the characteristic features of the Late Jurassic ichthyosaurs such as *Undorosaurus* and ‘*Otschevia*’ (Efimov 1998–1999b). Another interesting feature of the anatomy of the forefin of ichthyosaurs is contact of *pisiforme* with the *humerus* that took place mainly in the Cretaceous platypterygiines (Adams and Fiorillo 2010; Kolb and Sander 2009; Maxwell and Kear 2010; McGowan 1972). Presently among the Late Jurassic ichthyosaurs such contact is known in three forms: *Undorosaurus trautscholdi* sp. nov., *Otschevia alekseevi* Arkhangelsky, 2001 and an ophthalmosaurid from the Tithonian of Argentina MOZ-P – 1854 (Arkhangelsky 2000; Fernández 2007; Gasparini 1988). According to modern phylogenetic hypotheses, this feature evolved independently in the family Ophthalmosauridae.

In our interpretation of the limb elements of *Cryopterygius*, we accepted the view, which Druckenmiller et al. (2012) and others considered less satisfactory. If we take our point of view, the architecture of the limbs of *Cryopterygius* practically does not differ from that of *Undorosaurus* (Fig. 1) and *Paraophthalmosaurus*. This forefin architecture is found in many

forms of the Late Jurassic ichthyosaurs of the Northern Hemisphere. However, such architecture of the forefin was present in some ichthyosaurs of the Southern Hemisphere as well (Fig. 1F) (Fernández 2000).

Taxonomic validity of the genera *Undorosaurus* and *Paraophthalmosaurus*, in our opinion is beyond doubt; both forms differ from each other and from other ophthalmosaurinae in a number of characters (see Appendices 1–5). There is some kind of uncertainty about the validity of *Cryopterygius*. This uncertainty is due to missing data on these genera, notably on the structure of its basicranium and skull roof. Describing a new form from Spitsbergen, researchers noted, that *Cryopterygius* is most similar to *Undorosaurus*. However, given other morphological differences between the two taxa, that the skull of *Undorosaurus* is largely unknown, and in light of questions regarding the taxonomic validity of *Undorosaurus*, PMO 214.578 was referred to the new taxon *Cryopterygius* pending the availability of new data (Druckenmiller et al. 2012). This genus shares some diagnostic features of *Undorosaurus* (see Appendices 1–5). The unique characters of *Cryopterygius kristiansenae*: prominent acromion process of the scapula and presence of the second preaxial accessory digit.

It is also important to note that there is potential for a different interpretation of some elements of the limb of *Undorosaurus trautscholdi* sp. nov., in which the element defined by the authors as pisiforme may be a neomorph, and the first element of the additional postaxial digit in this case can be pisiforme that had not changed its position.

## CONCLUSIONS

The authors described a new species of the genus *Undorosaurus* (*U. trautscholdi*). Anatomy of its forelimb differs from previously known species of the genus: contact of pisiform bone with the humerus, its shape and size; smaller size of radiale. In the course of phylogenetic analysis, it was found that the genera *Undorosaurus* and *Paraophthalmosaurus* is part of the clade Ophthalmosaurinae (sensu Fischer et al. 2012) and they may be considered as valid. The presence on the proximal epiphysis of the humerus depression from avascular necrosis of decompression syndrome indicates the ability that *Undorosaurus* and closely-related forms to dive to great depths.

## ACKNOWLEDGEMENTS

The authors appreciate to V. Fischer (University of Liège and Royal Belgian Institute of Natural Sciences, Belgium) for his linguistic corrections and comments on the manuscript, I.A. Starodubtseva, G.N. Kurbatova (GSM), M.A. Rogov (GIN) and I.M. Stenshin (YKM) for their help in writing of this paper. We thank two anonymous reviewers for their helpful comments and for improving the manuscript.

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**Appendix 1. Coding of new characters 52–54.**

Abbreviation: A = 0/1

<i>Temnodontosaurus</i>	000
<i>Ichthyosaurus communis</i>	000
<i>Stenopterygius quadricissus</i>	1A0
<i>Ophthalmosaurus icenicus</i>	000
<i>Ophthalmosaurus natans</i>	000
<i>Chacaicosaurus cayi</i>	??0
<i>Brachypterygius extremus</i>	??0
<i>Arthropterygius chrisorum</i>	00?
<i>Mollesaurus periallus</i>	???
<i>Caypullisaurus bonapartei</i>	000
<i>Aegirosaurus leptospondylus</i>	000
<i>Platypterygius australis</i>	001
<i>Platypterygius hercynicus</i>	000
<i>Maiaspondylus lindoei</i>	???
<i>Athabascasaurus bitumineus</i>	???
<i>Sveltonectes insolitus</i>	000
<i>Acamptonectes densus</i>	00?
<i>Leninia stellans</i>	???

**Appendix 2. Character Coding for*****Undorosaurus gorodischensis***

011??????? 0?????1?21 1?0???0001  
 0111001101 0100001001 0001

**Appendix 3. Character Coding for*****Paraophthalmosaurus saveljeviensis***

1?????1?10? 00?????1?0? ?1??????01  
 01110??1?1 0?0??????? ?011

**Appendix 4. Character Coding for*****Paraophthalmosaurus kabanovi***

101??????? ?????????? ???????0101  
 011101?1?1 0100?????1? ?111

**Appendix 5. Character Coding for*****Cryptopterygius kristiansenae***

011?111101 1?1?1?1??? ?1?????0101  
 01A100?101 0100001001 ?001