A prevalence of *Arthropterygius* (Ichthyosauria: Ophthalmosauridae) in the Late Jurassic – earliest Cretaceous of the Boreal Realm

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Abstract

The ichthyosaur genus *Arthropterygius* Maxwell, 2010 has heretofore been considered as rare and poorly known, although it is among the key taxa for understanding the evolution of derived Late Jurassic and Early Cretaceous ichthyosaurs. Recently excavated unique material from the Berriassian of Franz Josef Land (Russian Extreme North) and examination of historical collections in Russian museums provided numerous specimens referable to *Arthropterygius*. New data on *Arthropterygius* combined with personal examination of ichthyosaurs *Palvennia*, *Janusaurus* and *Keilhauia* from Svalbard give us reasons to refer all these taxa to *Arthropterygius*. Therefore we recognize four valid species within the genus: *Arthropterigius chrisorum* (Russell, 1994), *A. volgensis* (Kasansky, 1903) comb. nov., *A. hoybergeti* (Druckenmiller, Hurum, Knutsen & Narkem, 2012) comb. nov., and *A. lundi* (Roberts, Druckenmiller, Sætre & Hurum, 2014) comb. nov. Three of the species are present both in the Arctic and in the European Russia. This allows us to suggest that *Arthropterygius* was common and widespread in the Boreal Realm during the Late Jurassic and earliest Cretaceous. The results of our multivariate analysis of ophthalmosaurid humeral morphology indicate that at least some ophthalmosaurid genera and species, including *Arthropterygius*, could be easily recognized based solely on humeral morphology. Our phylogenetic analyses place the clade of *Arthropterygius* close to the base of Ophthalmosauria as a sister group either to ophthalmosaurines or to platypterygiines. Although its position is still uncertain, this is the most well-supported clade of ophthalmosaurids (Bremer support value of 5, Bootstrap and Jackknife values exceeding 80). This provides a further argument for the reliability of our taxonomic decision.

Introduction

Ichthyosaurs were common components of marine herpetofauna in the Late Jurassic. We know this thanks to several Late Jurassic formations that yielded significant ichthyosaur materials. These are primarily Kimmeridge Clay Formation of England and France (Hulke, 1871; Mansell-Pleydell,1890; Sauvage, 1911; Delair, 1960, 1986; McGowan, 1976, 1997; Grange *et al*., 1996; Etches & Clarke, 1999; Moon & Kirton, 2016), the Solnhofen Formation of Germany (Wagner, 1852, 1853; Meyer, 1864; Bauer, 1898; Bardet & Fernández, 2000), the Vaca Muerta Formation of Argentina (Fernández, 1997, 2000, 2007a,b; Gasparini et al., 1997, 2015), the Agardhfjellet Formation of Svalbard, Norway (Angst et al., 2010; Druckenmiller *et al*., 2012; Roberts *et al*., 2014; Delsett *et al*., 2016, 2017) and a number of formations of the Volgian (Tithonian) age in European Russia (Kabanov, 1958; Efimov, 1998-1999*b*; Arkhangelsky, 1997-2001; Zverkov, Arkhangelsky & Stenshin, 2015; Zverkov *et al*., 2015; Zverkov & Efimov, in press). Still our knowledge of the Late Jurassic ichthyosaurs is non-uniform: some taxa are well known thanks to complete and well-preserved specimens (*Grendelius* McGowan, 1976; *Caypullisaurus* Fernández, 1997; *Aegirosaurus* Bardet et Fernández, 2000; *Undorosaurus* Efimov, 1999*b*), whereas others are poorly known from only a small number of largely incomplete and/or poorly preserved specimens (e.g. *Nannopterygius* Huene, 1922, *Brachypterygius* Huene, 1922 and *Arthropterygius* Maxwell, 2010). Being in the list of these puzzling ichthyosaurs, *Arthropterygius* was heretofore supposed to be known by only fragmentary remains: its type and the only hitherto identified species is represented only by the holotype, an incomplete skeleton from Arctic Canada (Maxwell, 2010). Two more fragmentary specimens were subsequently referred to as *Arthropterygius*: one from Argentina (Fernández & Maxwell, 2012) and another from the Russian North (Zverkov *et al*., 2015), however, both of them were described in open nomenclature. Thereby the genus remained poorly known that hampered detailed comparisons with other Late Jurassic taxa and affected taxonomic decisions in a number of subsequent contributions.

In recent years, the Slottsmøya Member of the Agardhfjellet Formation of Svalbard has yielded numerous marine reptile specimens including four monotypic ichthyosaur genera, for most of which only one specimen is known (Druckenmiller *et al*., 2012; Roberts *et al*., 2014; Delsett *et al*., 2017). However, most of the characters used to distinguish the new taxa from Svalbard were based on skeletal regions poorly known for other ophthalmosaurids, which

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combined with misinterpretations resulted in an alleged diversity and endemism of Svalbard ichthyosaurs (Roberts *et al*., 2014; Delsett *et al*., 2016, 2017). It has already been demonstrated that one of the ichthyosaur genera from Svalbard, ‘*Cryopterygius*’, is a junior subjective synonym of *Undorosaurus* Efimov, 1999b (Zverkov & Efimov, in press). The other three genera are subjects of current revision and are all considered herein as junior subjective synonyms of *Arthropterygius.* Study of newly discovered materials from Franz-Josef Land (Russian Extreme North) combined with examination of ichthyosaurs in historical collections of several museums in Russia and in the Natural History Museum at the University of Oslo allow us substantially expand the knowledge of *Arthropterygius*.

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This research continues an ongoing project of taxonomic and phylogenetic revision of the Late Jurassic ichthyosaurs of the Boreal Realm. Here we focus on ichthyosaurs of *Arthropterygius* clade (Zverkov & Efimov, in press), their taxonomy, ontogenetic, intra- and interspecific variation along with their phylogenetic relations to other ophthalmosaurids.

Materials

During the fieldwork of A.P. Karpinsky Russian Geological Research Institute (VSEGEI) in Franz Josef Land, several ichthyosaur specimens were collected from the black shales of the Hofer Formation (Upper Jurassic to lowermost Cretaceous; Kosteva, 2005; Rogov *et al*., 2016). The first specimen represented by a medial fragment of the left scapula and proximal fragment of the right humerus of a big ichthyosaur was found by S. Yudin and P. Rekant in a scree of a slope formed by Kimmeridgian and Volgian sediments at Wilczek Land (Fig. 1A). NGZ had excavated two more relatively complete specimens at Berghaus Island (Fig. 1A): one skeleton of a juvenile, near 2.5 m long, and one skeleton of a young adult *c*. 3.5 m at estimated length. Both of them are referable to *Arthropterygius chrisorum* (see descripti~~v~~one ~~part~~). When found, skulls and some portions of postcranial skeleton of both CMGE 3-16/13328 and CMGE 17-44/13328 were already exposed and weathered, thereby a number of cranial elements are too fragmented~~al~~ for description and even more parts are missing, nevertheless, these specimens provide new data on the cranial morphology of *A. chrisorum*. The specimens were collected and prepared by NGZ, and scanned by NEP using Artec Spider 3D scanner.

Furthermore, studying the collections in museums of Russia, we found out several specimens referable to *Arthropterygius*. Four of them are from the Middle Volgian of the Volga Region (Ulyanovsk and Samara regions), the fifth, originating from the Russian North, was described ~~earlier~~ in previous work (Zverkov, *et al*. 2015). Two of the specimens, deposited in Vernadsky State Geological Museum (SGM, Moscow), were excavated at the beginning of the last century. One (SGM 1573) was discovered by outstanding Russian geologist and palaeontologist A.P. Pavlov and subsequently described by N.N. Bogolubov (1910) as *Ophthalmosaurus* cf. *thyreospondylus*, another specimen (SGM 1731-01–15), found in 1937 by an unknown collector, remained hitherto undescribed. A partial skeleton of a juvenile (KSU 982/P-213), described by P.A. Kasansky in 1903 as a new species, *Ichthyosaurus volgensis*, is deposited in the Museum of Geology and Mineralogy of Kazan State University (KSU). During its further studying history this specimen was referred to as *Ophthalmosaurus* Seeley, 1874, *Undorosaurus* and *Otschevia* Efimov, 1998 (Bogolubov, 1910; Arkhangelsky, 2000; Storrs *et al*., 2000; Arkhangelsky, 2008), and ~~even~~ was considered ~~as~~ undiagnostic (McGowan & Motani, 2003: 134). A series of dramatic events in Russian history happened since the original descriptions of SGM 1573 and KSU 982/P-213 left a partial missing of the bones as a legacy. The vertebral column (except for several small ~~tailfin~~ distal caudal centra) is now lost in KSU 982/P-213. Initially, the specimen excavated by A.P. Pavlov (SGM 1573) included 13 vertebrae, several neural arches, rib fragments, left coracoid, complete right scapula, interclavicle, left humerus, anterior accessory epipodial and several autopodial elements (Bogolubov, 1910). Currently, ten vertebrae, interclavicle, broken distal portion of the scapula and left humerus are deposited in SGM, the ~~rest of originally described~~remaining elements ~~were~~ either~~possibly~~ decayed or ~~missed~~lost (I.A. Starodubtseva pers. comm.). However, the available remains are sufficient for attributing SGM 1573 to *Arthropterygius chrisorum* and give an additional information on the morphology of the interclavicle, which is unknown for the holotype (CMN 40608) and most of the other specimens.

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Thee more specimens referable to *Arthropterygius* were found in Ulyanovsk Region in recent decades. Incomplete postcranial skeleton YKM 63548 was found by V. M. Efimov at the bank of the Volga River near Gorodischi Village and donated to YKM; an isolated humerus UPM 2442 was found by I.M. Stenshin (UPM); an isolated basisphenoid referable to as *Arthropterygius* cf. *chrisorum* from the Middle Volgian of Gorodischi locality was obtained by NGZ from an anonymous fossil dealer and donated to SGM, where it deposited now under the number SGM 1743-2.

Geological Setting

Stratigraphic position of specimens from European Russia. All *Arthropterygius* specimens from European Russia originate from black shales of the Upper Jurassic (Middle Volgian) formations: Paromes Formation of the Timan-Pechora Basin (Kravets, Mesezhnikov, Slonimsky, 1976) and Promza Formation of the Volga Region (Yakovleva, 1993; Mitta *et al*., 2012). These formations are corresponding to *Dorsoplanites panderi* Ammonite Biozone.

Stratigraphic position of specimens from Franz-Josef Land. Two ichthyosaur skeletons were found very close to each other, on the northeast slope of Berghaus Island, 150 m above sea level, in the uppermost part of a sequence of black shale and siltstone of the Hofer Formation (Kosteva, 2005). CCMGE 3-16/13328 was collected 5 m higher stratigraphically than CCMGE 17-44/13328. The layers with ichthyosaurs were filled with bivalves *Buchia unschensis*, *Buchia fischeriana* and *B.* cf. *volgensis* (identifications are made by V. A. Zakharov, GIN) characteristic of the Jurassic/Cretaceous transitional interval of the Boreal Realm (Zakharov, 1987). On the adjacent slope, at a slightly higher level, ammonites *Surites* cf. *praeanalogus* were collected, indicating *Hecteroceras kochi* Ammonite Biozone of the Ryazanian age (this and all subsequent ammonite identifications are made by M. A. Rogov, GIN); 20 m below, ammonites *Chetaites chetae,* index of the uppermost Ammonite Biozone of the Volgian of Arctic were collected; and finally, 50 m below the level of CCMGE 17-44/13328 on the same slope *Laugeites lambecki* and *Praechetaites* cf. *exoticus* were collected, indicating *Laugeites groenlandicus* Ammonite Biozone of the upper Middle Volgian (Rogov & Zakharov, 2009; Rogov *et al*., 2016). Absence of ammonite finds in the layers with ichthyosaurs do not allow to conclude with confidence whether they are from the uppermost Volgian or whether Ryazanian part of the section; however, it is almost unambiguous that the ichthyosaurs are of early Berriassian age (for comments on Jurassic–Cretaceous Boreal–Tethyan correlation see e.g. geological setting section of our previous paper, Zverkov & Efimov, in press).

Comment on stratigraphic position of CMN 40608. In the locality, Cape Grassy, Melville Island, shale and siltstone of the Ringnes Formation are conformably overlain by soft, clay shales of the Deer Bay Formation (Embry, 1994). Elsewhere these lithologically similar formations are separated by sandstones of the Awingak Formation (Embry, 1994; Poulton,

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1994). According to Embry (1994) the thickness of the Ringnes Formation in Cape Grassy is *c.* 20 m (Embry, 1994: fig. 6). Taking this into consideration, the fact that CMN 40608 was found 51 m above the base of the Ringnes Formation, withal weathered out on the surface of the outcrop and slightly scattered (Russell, 1994), indicates that CMN 40608 was actually found within the Deer Bay Formation, but not Ringnes Formation as indicated by Russell (1994). Considering that not much data is published on Late Jurassic invertebrates and biostratigraphy of Cape Grassy, it could not be said with certainty what is the stratigraphic volume of the Ringnes and Deer Bay formations in this locality. In general, the age of the Ringnes Formation is considered as Oxfordian to Kimmeridgian and the age of the Deer Bay Formation is considered as Volgian to Valanginian (Jeletzky, 1965, 1973; Embry, 1994; Poulton, 1994), thereby CMN 40608 is most likely Volgian or Ryazanian (Tithonian or Berriassian) in age.

Institutional abbreviations. CCMGE, Chernyshev's Central Museum of Geological Exploration, Saint Petersburg, Russia; CMN, Canadian Museum of Nature, Ottawa, Canada; GIN, Geological Institute of the Russian Academy of Sciences, Moscow, Russia; KSU, A.A. Shtukenberg Museum of Geology and Mineralogy of Kazan State University, Kazan, Russia; MOZ, Museo Prof. J. Olsacher, Dirección Provincial de Minería, Zapala, Argentina; PMO, Natural History Museum, University of Oslo (Palaeontological collection), Oslo, Norway; SGM, V.I. Vernadsky State Geological Museum of the Russian Academy of Sciences, Moscow, Russia; SVB, Svalbard Museum, Longyearbyen, Norway; UPM, Undory Palaeontological museum, Undory, Ulyanovsk Region, Russia; VSEGEI, A.P. Karpinsky Russian Geological Research Institute, St. Petersburg, Russia; YKM, I.A. Goncharov Ulyanovsk Regional Museum, Ulyanovsk, Russia.

Systematic Palaeontology

Ichthyosauria de Blainville, 1835

Ophthalmosauridae Baur, 1887

Arthropterygius Maxwell, 2010

2010 *Arthropterygius* Maxwell: 403

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2012 *Palvennia* Druckenmiller, Hurum, Knutsen, Narkem: 326

2014 *Janusaurus* Roberts, Druckenmiller, Sætre & Hurum: 4

2017 *Keilhauia* Delsett, Roberts, Druckenmiller & Hurum: 7

2018 *Palvennia* Druckenmiller, Hurum, Knutsen, Narkem 2012; Delsett, Druckenmiller, Roberts, Hurum: 8

Type species: *Ophthalmosaurus chrisorum* Russell, 1994

Other valid species: *Arthropterygius volgensis* (Kasansky, 1903) comb. nov., *A. hoybergeti* (Druckenmiller, Hurum, Knutsen & Narkem, 2012) comb. nov., *A. lundi* (Roberts, Druckenmiller, Sætre & Hurum, 2014) comb. nov.

Emended diagnosis: Moderate to large (3-5 m) ichthyosaurs with following unique combination of features (synapomorphies are marked with '*'): relatively short and anteriorly pointed snout, strongly ventrally bowed jugal; wide supratemporal anteromedial tongue covering the postfrontal (shared with *Athabascasaurus* Druckenmiller & Maxwell, 2010); extremely anteroposteriorly shortened medial symphysis of parietals posteriorly restricted by a pronounced excavation and notch*; large parietal foramen; gracile quadrate with poorly developed 'weak' condyle*; basioccipital with extracondylar area wide in lateral view and practically unseen in posterior view; stapedial and opisthotic facets of the basioccipital shifted anteriorly and poorly visible in lateral view* (laterally exposed in other known ophthalmosaurids); basisphenoid with foramen for the internal carotid arteries opening posteriorly*; basioccipital facet of the basisphenoid facing posterodorsally, occupying in dorsal view area equal or even larger than that of dorsal plateau*; stapes with extremely gracile shaft (shared with *Acamptonectes* Fischer *et al.*, 2012); short and robust paraoccipital process of the opisthotic; wide and extremely robust clavicles; bulge in the middle of the interclavicle posterior median stem*; large coracoids (proximodistal length of the scapula reduced in comparison to coracoid length); pronounced angle close to 90-100 degrees between the articulated coracoids*; ventral skew between the radial and ulnar facets of the humerus (ulnar facet:radial facet dorsoventral width ratio less than 0.8; as in *Sisteronia* Fischer *et al.*, 2014); three concave distal articular facets on humerus for a preaxial accessory element, radius and ulna; ulna larger than the radius in dorsal view and lacking posterior

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Commented [A10]: I see you have compared with some traits, please do this with all non-synapomorphic traits

Commented [A11]: Include which taxa it does not share this with perichondral ossification (uncommon for ophthalmosaurines *sensu* Fischer *et al*., 2012); ‘latipinnate’ forefin architecture with two distal carpals (4 and 3) contacting the intermedium, and distal ulnare/metacarpal 5 contact (among ophthalmosaurids shared with *Ophthalmosaurus* Seeley, 1874, *Brachypterygius* Huene, 1922 and *Aegirosaurus* Bardet & Fernández, 2000); autopodial elements circular in outline and loosely arranged (shared with *Ophthalmosaurus* Seeley, 1874); plate-like ishiopubis, lacking the obturator foramen (shared with derived platypterygiines); ?ilium anteroposteriorly expanded at the dorsal end.

Occurrence: Arctic Canada, Russian Extreme North (Franz Josef Land) and the European part of Russia, Norway (Svalbard) and Argentina (Neuquen Basin). Middle to Upper Volgian–Ryazanian (Tithonian–Berriassian) (see Maxwell, 2010; Fernández & Maxwell, 2012; Druckenmiller *et al*., 2012; Roberts *et al*., 2014; Zverkov *et al*., 2015; Delsett *et al*., 2016, 2017).

Remarks: Based on the type specimen solely, the characteristic features of *Arthropterygius* are: basisphenoid with foramen for the internal carotid arteries opening posteriorly; basioccipital facet of the basisphenoid facing posterodorsally and occupying a half of the element in dorsal view; basioccipital with extracondylar area wide in lateral view and practically unseen in posterior view; shifted anteriorly stapedial and opisthotic facets of the basioccipital; presence of ‘ulnar torsion’, with ulnar facet not as dorsoventrally wide as the radial facet, forming a distal skew of the humeral ventral surface (Maxwell, 2010; Zverkov *et al*., 2015). All these features could be observed in the type specimens of genera that are here synonymized with *Arthropterygius*, except for cases where an element is unknown or obscured from observation: basisphenoid is mostly hidden in the holotype of *Janusaurus lundi*; humerus is incomplete in the holotype of *Palvennia hoybergeti* and both basioccipital and humerus are absent in the holotype of *Ichthyosaurus volgensis*. Additional specimens of *Arthropterygius chrisorum* provided a number of other overlapping elements that bear diagnostic traits; these are postfrontal, jugal, quadrate, opisthotic, stapes, interclavicle, clavicle and scapula. We believe that this all makes our taxonomic decisions clear and convincing.

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Recently erected from the Berriassian of Svalbard *Keilhauia nui* is also referable to *Arthropterygius*, however, only in open nomenclature. The holotype and only known specimen of this taxon is poorly preserved skeleton of a small individual that was considered to be of ‘late juvenile to adult ontogenetic stage’ (Delsett *et al*., 2017: 14). Our personal observations of the holotype (PMO 222.655) allow to conclude that in fact, all the evidences proposed by Delsett *et al.* (2017) as supporting maturity of PMO 222.655 are misleading: the proximal portion of the humerus of PMO 222.655 is heavily weathered and its posterior portion is broken so that it is impossible to say something regarding its natural shape and its value for identification of maturity; the same concerns a texture of the humeral shaft, which along with other skeletal elements of PMO 222.655 is poorly preserved, weathered, and partially covered by matrix along with products of pyrite decay. It is unclear what Delsett *et al*. 2017 meant under the degree of ossification that '(when it is possible to observe) resembles mature finished bone', because all the available articular surfaces demonstrate markedly unfinished ossification: the facets of appendicular elements are poorly demarcated from each other, the ventral margin of the ischiopubis bears an excavation along its ventral margin which indicates a presence of extensive cartilaginous continuation of the element. Furthermore, a natural shape of the ischiopubis is unclear because its proximal portion is partially eroded and unnaturally compressed. PMO 222.655 is generally similar to CCMGE 3-16/13328, and it demonstrates a number of features that are diagnostic of *Arthropterygius*: the humerus of PMO 222.655 has ventral skew between the radial and ulnar facets, its ulnar facet:radial facet dorsoventral width ratio is less than 0.8; the facet for anterior accessory element is nearly as large as the radial facet (a diagnostic feature of *A, chrisorum*); the clavicle of PMO 222.655 is relatively large and robust; judging from the field photographs (J. Hurum pers. comm. Sept. 2017), the coracoid was originally longer anteroposteriorly than mediolaterally wide and extremely similar to that of CCMGE 3-16/13328, thus its current 'shape' is a result of unsuccessful conservation; the ischiopubis of PMO 222.655 is plate-like and lacks obturator foramen. What concerns the ilium of 222.655, its expanded dorsal portion is an important character that probably demonstrates a juvenile condition of what in *A. lundi* (PMO 222.654) developed in an 'anteromedial process' and posteriorly curved end. Thus, expanded dorsal portion of the ilium could also be a generic feature of *Arthropterygius*. Taking into account all the arguments above, we consider *'Keilhauia nui'* as a *nomen dubium* and identify its type specimen as *Arthropterygius* sp. juv. cf. *A. chrisorum*.

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What we do see is that when the jackets and specimens dry out before preparation during storage (in the case of this specimen 3-4 years), additional damage and cracking happens. So I would not blame this on the preparator, but on storage.

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***Arthropterygius chrisorum* (Russell, 1994)**

(Figs 2–10, 20A, B, D, S2)

v.1910 ?*Ophthalmosaurus thyreospondylus* Owen; Bogolubov: 474

*1994 *Ophthalmosaurus chrisorum* Russell: 198, fig. 3

2010 *Arthropterygius chrisorum* (Russell, 1993); Maxwell: 404, figs 2–5

v.2018 *Palvennia hoybergeti* Druckenmiller *et al.*, 2012; Delsett, Druckenmiller, Roberts, Hurum: 8, figs 5–13

Holotype: CMN 40608, fragmentary skeleton of a large mature individual (for details see Maxwell, 2010).

Referred specimens: SGM 1573, fragments of the skeleton of a large mature individual: ten vertebrae, interclavicle, broken distal part of the scapula, left humerus. CCMGE 3-16/13328, incomplete skeleton of a juvenile individual: left quadrate, partial basisphenoid, incomplete supratemporals, fragmentary parietal, and several other indeterminate cranial fragments, incomplete vertebral column (69 vertebrae from anterior dorsal to tailfin centra); rib fragments, right forefin, right scapula, coracoids. CCMGE 17-44/13328, incomplete skeleton of a young adult individual: right nasal, prefrontals, right postfrontal, fragmentary parietal, basisphenoid, left quadrate; fragments of palate bones and other indeterminate cranial remains; mandible, including articulated left surangular, angular, splenial and prearticular, isolated presacral and anterior caudal centra (31 fragment), multiple rib fragments, fragments of pectoral girdle (coracoids, scapulae, interclavicle and clavicle), incomplete right forefin, proximal part of the left humerus, left radius, partial ischiopubis, left femur. PMO 224.250, a partially articulated and almost complete anterior half of the skeleton of a moderately large ichthyosaur (for details see Delsett *et al.*, 2018).

Emended diagnosis: A moderately large (4–5 m) ichthyosaur, diagnosed relative to other species of *Arthropterygius* by the following unique characters: quadrate with strongly ventrally shifted articular boss, V-shaped in posteromedial view; absence of pronounced angular protrusion of the quadrate; basisphenoid trapezoidal in outline with maximum mediolateral width in its anterior part; posterior foramen for the internal carotid arteries not visible in ventral view in adults, separated from the ventral surface by a thin shelf; dorsoventrally high opisthotic with extremely reduced and robust paraoccipital process (hitherto found only in PMO 222.669); blunt termination of the lateral extremities of the interclavicle; strongly anteroposteriorly elongated proximal end of the humerus with reduced deltopectoral crest shifted to its anterior edge; extremely pronounced ventral skew between the ulnar and radial facets of the humerus; facet for the anterior accessory epipodial element of the humerus as wide as, and equal in size to the radial facet.

Occurrence: Upper Jurassic, Deer Bay Formation (Volgian) of Melville Island, Northwest Territories, Canada (type locality); Middle Volgian Promza Formation (*Dorsoplanites panderi* Ammonite Biozone) of Ulyanovsk Region, Russia; upper part of the Hofer Formation (uppermost Volgian to lowermost Ryazanian, Berriassian) of Franz-Josef Land, Russian Extreme North; Slottsmøya Member of the Agardhfjellet Formation (Middle Volgian part of the section) of Svalbard, Norway.

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Remarks: Recently referred to as *Palvennia hoybergeti*, PMO 222.669 shares all diagnostic features of *A. chrisorum*, but differs from *A. hoybergeti* in extremely shortened and robust paraoccipital process of the opisthotic (relatively elongated and dorsoventrally compressed in *A. hoybergeti*; see description of *A. hoybergeti* below); reduced deltopectoral crest of the humerus shifted to its anterior edge (well pronounced, plate-like, in *A. hoybergeti*); prominent ventral skew between the ulnar and radial facets of the humerus (cannot be observed in the holotype of *A. hoybergeti*, SVB 1451, but see description and discussion sections); facet for the anterior accessory epipodial element of the humerus semicircular in outline and comparable in size to the radial facet (comparatively small and anteriorly tapered in *A. hoybergeti*; Fig. S7 in Zverkov & Prilepskaya, documents); large and rounded in outline anterior accessory epipodial element (aae of *A. hoybergeti* SVB 1451 is relatively small, semicircular in outline, with nearly straight anterior margin).

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Delsett *et al.* (2018) provided a very restricted comparison of PMO 222.669 and *A. chrisorum* (holotype CMN 40608). According to that comparison, PMO 222.669 differs from *A. chrisorum* in the following features: anterior face of basioccipital lacks notochordal pit and basioccipital peg (not supported by our observations because of poor preservation of this region in PMO 222.669); dorsal margin of the articular is slightly concave in medial view (unclear degree of difference; this also could be ontogenetic and interspecific variation); the anterior notch of the coracoid is longer and narrower (the actual difference of the two is minute and easily explained by ontogenetic variation; see discussion); proximodistally shorter dorsal process of the humerus (ontogenetic variation, see discussion); not as convex articular faces of epipodial elements (ontogenetic and intercpecific variation; see discussion). In fact, none of these 'differences' is sufficient to distinguish the species. From our personal observations on

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PMO 222.669 (NGZ) we have not found any additional differences, thereby PMO 222.669 is referred herein to as *Arthropteryguis chrisorum*.

Description

Skull

The skull of *A. chrisorum* is now well-known thanks to a new find from Svalbard (PMO 222.669; Delsett *et al*., 2018). Thereby here we provide only some additional observations on the referred specimens, with special reference to new specimens from Franz Joseph Land. For more details on cranial morphology of *A. chrisorum* see the description of PMO 222.669 in Delsett *et al*. (2018).

Nasal. A supranarial portion of the right nasal is preserved in CCMGE 17-44/13328 (Fig. 2C, G, H). It is too fragmentary for substantial description, however, from this fragment it could be said that the nasal lamella is well developed and forms a lateral ‘wing’ overhanging the dorsal border of the external naris (Fig. 2G, H). In PMO 222.669 both nasals are preserved in articulation. To the description of these elements provided by Delsett *et al*. (2018), we could add that the nasal bears a pronounced lateral ‘wings’ over the external naris (Fig. 2L, M). The posterior portion of the nasal articulates with the postfrontal and frontal in a complex interdigitating suture, covering most of the frontal anteriorly (Fig. 2M). Posteriorly, the dorsal surface of the nasal is shallowly concave, forming an excavatio internasalis that is constricted laterally and medially by a raised areas.

Prefrontal. Although incomplete, both prefrontals are preserved in CCMGE 17-44/13328 (Fig. 2D–F). These elements are composed of a dorsal sheet and robust, anteroventrally directed strut, forming the anterodorsal margin of the orbit (Fig. 2C, K). A straight ridge along the medial edge of the dorsal sheet meets a deep groove in the lateral margin of the overlapping nasal (Fig. 2D, E). Anterior to it, there is a facet for articulation with the frontal. When articulated with other elements, prefrontal had little dorsal exposure, being covered by the anterior plate of the postfrontal posteriorly and by the nasal anteromedially. In PMO 222.669, prefrontals are practically unseen dorsally, being covered by postfrontals and nasals (Fig. 2L, M).

Parietal. Only posterolateral processes of the parietal are preserved in both CCMGE 3-16/13328 and 17-44/13328, thereby the only observation that could be made on their morphology is that the process was slender but not robust as in *Undorosaurus* and some other platypterygiines (for comments on this character see Zverkov & Efimov, in press). The parietals of PMO 222.669 are complete and articulated. In the original description (Delsett *et al.*, 2018), the skull was not completely prepared of embedded rock, so that the posteromedial excavation and notch of the parietals were not seen. In general, the parietal of PMO 222.669 demonstrates characteristic morphology with the relatively slender posterolateral process and short but robust medial symphysis restricted posteriorly by a pronounced notch (Fig. 2L, M).

Postfrontal. The partial right postfrontal is preserved in CCMGE 17-44/13328. An extensive facet of the supratemporal anteromedial tongue occupy nearly a half of the element mediolateral width dorsally and terminates right before the expansion of the anterior plate in an interdigitating suture (Fig. 2B, L, M). This condition is similar to that of *A. hoybergeti* (SVB 1451) and *A. lundi* (see descriptions below), and among other ophthalmosaurids, it occurs only in not closely related *Athabascasaurus* (Druckenmiller & Maxwell, 2010); thus it could likely be considered as a non-unique synapomorphy of *Arthropterygius*. Delsett *et al.* (2018) described more short and gracile ‘supratemporal finger’ = supratemporal anteromedial tongue, however, this is due to incorrect identification of sutures (see reinterpretation on Fig. 2L, M).

Commented [A23]: I am not entirely convinced that this is a new interpreatiation? We are talking about the anteromedial tougue, which you have also included in your reconstruction?

Supratemporal. Medial rami of both supratemporals are preserved in CCMGE 3-16/13328. These portions are massive and quite short mediolaterally bearing triangular and excavated medial facets for articulation with the parietal (Fig. 3S–U). Ventrolaterally to this facet, there is a small depression of the facet for the paroccipital process of the opisthotic (Fig. 3S–V).

Jugal. The jugal is a slender, strongly bowed J-shaped element (Fig. 2I, J). Its posterior part is mediolaterally compressed, ascending dorsally as a slender process and forming the posterior part of the orbit (Fig. 2K). On its medial surface, the process bears facets for the postorbital and quadratojugal (Fig. 2I). The suborbital portion of the jugal is strongly bowed, greater than that of *Ophthalmosaurus icenicus* (Moon & Kirton, 2016) but in similar degree to those of *Arthropterygius hoybergeti* and *A. lundi*.

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Quadrate. The quadrate is known for both CCMGE 3-16/13328 and 17-44/13328 (strongly compressed). It is a relatively gracile ear-shaped element. The posterodorsal part of the occipital lamella is broken in both CCMGE specimens so it is hard to say anything regarding its natural shape. Thanks to its complete preservation in PMO 222.669, we know that the occipital lamella is well developed. A shallow notch of the quadrate foramen restricts the posterolateral edge of the quadrate. The anterior edge of the pterygoid lamella is convex (Fig. 3J, K, O, Q). There is no marked angular protrusion (‘antero-internal angle’ of Andrews, 1910) on the quadrate. The articular condyle is weak and mediolaterally compressed. Its ventral surface is divided by the smooth groove into two bosses: large ventrally protruding medial boss for the articulation with the articular and reduced anteriorly shifted lateral boss for the articulation with the surangular (Fig. 3L–N). The ventral edge of the articular boss is somewhat V-shaped (Fig. 3J). Above the condyle, there is a pronounced circular depression – a facet for the quadratojugal (Fig. 3L, O, P). The stapedial facet, situated in the middle of the medial surface of the quadrate, is circular in outline (Fig. 3J, O).

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Basioccipital. The basioccipital is hitherto known for the holotype, CMN 40608, and for PMO 222.669. Although it was already described, we feel it necessary to add some remarks to the original description of Maxwell (2010). The extracondylar area is extremely reduced and completely unseen in posterior view, as in *A. hoybergeti* and *A. lundi* (Druckenmiller *et al*., 2012; Roberts *et al*., 2014). However, it is relatively anteroposteriorly wide in lateral view, unlike that of *Grendelius* spp. (McGowan, 1976; Zverkov, Arkhangelsky & Stenshin, 2015). Maxwell (2010) has misinterpreted a part of the extracondylar area as a stapedial facet, probably due to poor preservation of CMN 40608. The true stapedial facet faces anteriorly and is practically unseen in lateral view. An anterior protrusion of the basioccipital under the floor of the foramen magnum interpreted by Maxwell (2010) as an ‘incipient basioccipital peg’, is also present in *A. hoybergeti* and *A. lundi* (NGZ pers. obs.) and was reported for some other ophthalmosaurids (e.g. Moon & Kirton 2016). Although this structure is a vestige of a basioccipital peg, the condition observed in *Arthropterygius* could not be considered as a plesiomorphic state (i. e. the presence of a basioccipital peg), as was supposed and coded in some previous works (e.g. Fischer *et al*., 2011, 2012). In PMO 222.669 the anterior surface of the basioccipital is too badly preserved for any observations.

Commented [A26]: Long?

Commented [A27]: If you are talking here about the fragment that is protruding from the floor of the element, I would not use that as evidence. I considered that part myself when I described the specimen, the element is so fractured and weathered we decided to not describe it as a peg

Basisphenoid. The basisphenoid is the most peculiar element in basicranium of *Arthropterygius* due to an uncommon position of the posterior opening for the internal carotid arteries, which pierce the basisphenoid at its posterior edge (in most ophthalmosaurids this foramen situated close to the middle of the ventral surface). The ventral surface of the basisphenoid is trapezoid in outline (Fig. 3A, E). It is longer anteroposteriorly than mediolaterally wide, having the width to length ratio of 1.33 (see Tab. S5 in Zverkov &

Prilepskaya, documents). The mediolateral width of the anterior part is greater than the width of the posterior part. The basipterygoid processes are relatively reduced in comparison to *Undorosaurus*, *Grendelius* and most of platypterygiines (see Zverkov & Efimov, in press). The lateral facet of the basipterygoid processes is elongated-oval, lenticular in outline (Fig. 3D, G). The dorsal surface of the basisphenoid is divided into two surfaces – square posterodorsally faced basioccipital facet and pentagonal dorsally faced dorsal plateau (Fig. 3B, F). A median groove bisects the dorsal surface over the entire length. The high anterior wall is vertical, slightly curving posterodorsally on its lateral sides, lining the cranioquadrate passage. It raises the dorsum sellae in the middle, which is ventrally bounded by the funnel-like anterior foramen for the internal carotid arteries (Fig. 3C, H). Laterally the dorsum sellae is bounded by the ridges (crista trabeculares), which ventrally form the surfaces for their cartilaginous continuation; these surfaces are poorly pronounced in all specimens referred to *A. chrisorum* (Fig. 3C, H). Lateral to the crista trabeculares deep pits for attachment of the ocular musculature (likely retractor bulbi group) are situated. The posterior foramen for the internal carotid arteries opens posteroventrally in juvenile specimen CCMGE 3-16/13328, and posteriorly in mature individuals CCMGE 17-44/13328 and CMN 40608.

Opisthotic and stapes. The opisthotic and stapes are known only for PMO 222.669 (Fig. 4). Compared to other species of *Arthropterygius*, in *A. chrisorum* opisthotic is markedly higher dorsoventrally, and has more short and robust paraoccipital process (Fig. 4A, B). The medial head of the stapes is more massive than in *A. hoybergeti* and *A. lundi* and the lateral extremity of the stapedial process is more straight and somewhat dorsoventrally compressed (Fig. 4D, E, F): in other species, it is dorsoventrally expanded.

Mandible. In general, the mandible was well characterized for PMO 222.669 by Delsett *et al.* (2018). From other specimens, it is well enough preserved only in CCMGE 17-44/13328, however, lacking anterior and posterior portions, including the whole dentary and articular. Judging from its general proportions, it could be concluded that the whole jaw of CCMGE 17-44/13328 was relatively short anteroposteriorly (*c*. 65-70 cm at an estimated length).

Splenial. The splenial is an elongated and strongly mediolaterally compressed bone that covers most of the medial surface of the mandible (Fig. 5B, C). The dorsal ramus of the anterior forked part of the splenial is preserved, its medial surface is rugose forming a contribution to the mandibular symphysis. The ramus is thickened while the rest of the bone is a thin sheet that is

Commented [A28]: Which specimen..

slightly S-shape curved forming a medial wall of the Meckelian canal. The medial surface of the bone is pierced by a series of small foramina (Fig. 5B, C).

Surangular. The surangular of CCMGE 17-44/13328 is broken at its anterior and posterior ends. It is an elongate plate-like element, thickened along the dorsal margin; the medial and lateral surfaces of the surangular bear longitudinal grooves. The medial concavity comprises the lateral wall of the Meckelian canal. The lateral groove, fossa surangularis, runs along the lateral surface of the surangular. Posteriorly, before the paracoronoid eminence, it is pierced by an oval surangular foramen. The paracoronoid process is well pronounced and somewhat tapered, posterior to it, the lateral margin of the surangular forms a pronounced dorsally directed ridge, which probably functioned as attachment point of the *Musculus adductor mandibulae externus* (according to Moon & Kirton, 2016) (Fig. 5C). The surfaces of both these processes are rugose for attachment of jaw muscles.

Angular. The angular forms most of the ventral margin of the mandible. Its dorsal surface bears a floor of the Meckelian canal and several longitudinal grooves for articulation with other jaw elements. The more laterally situated groove is for the surangular. In lateral view, the angular forms a high sheet that covers the surangular and composes more than a half of the dorsoventral height at the posterior end of the mandible (Fig. 5A). The medial exposure of the angular is not as high. Medial to the ventral floor of the Meckelian canal a thin furrow for the articulation with the prearticular is placed.

Prearticular. The prearticular is an extremely thin sheet of a bone that form the medial wall of the Meckelian canal at its posterior part. Only a small portion of this element is preserved, so little can be said regarding its morphology.

Axial skeleton. A continuous series of 69 vertebral centra is preserved in CCMGE 3-16/13328, only a few fragmentary, severely deformed and weathered vertebrae are collected for CCMGE 3-16/13328, and ten vertebrae including atlas-axis complex are available for SGM 1573. This provides additional information to that published by Maxwell for the holotype (Maxwell, 2010).

The atlas-axis complex preserved in SGM 1573 is very similar to that of the holotype, however, diapophyses and parapophyses are relatively more protruding (Fig. 6A, C)**.** The vertebrae of *Arthropterygius chrisorum*, in general, are similar to those of *Ophthalmosaurus icenicus* (see Moon & Kirton, 2016). The middle and posterior dorsal vertebrae of the large mature specimen, SGM 1573, are characterized by strongly protruding diapophyses and parapophyses (Fig. 6F–I), whereas in juvenile CCMGE 3-16/13328 these apophyses are less well pronounced (Fig. 6L–S). A continuous vertebral series of CCMGE 3-16/13328 allows making some observations on vertebral count (Fig. S2 in Zverkov & Prilepskaya, documents). As anteriormost presacral centra are missing it is hard to say about the number of presacral vertebrae. Only thirteen anterior presacral vertebrae, in which diapophyses are fused with neural arch facets, are present in CCMGE 3-16/13328. A count of posterior presacral vertebrae is 17. Six anteriormost caudal vertebrae bear characteristic 8-shaped synapophyses that commonly mark a ‘sacral’ region (Fig. 6W). The rest preflexural caudal centra bear typical oval to circular rib facets (Fig. 6Y, A’). The shape of articular surfaces in caudal vertebrae is circular with the height slightly exceeding width in some anteriormost caudal vertebrae (Figs 6V, X; S2 in Zverkov & Prilepskaya, documents); in posterior caudal vertebrae, width markedly exceeds their height (Figs 6Z; S2 in Zverkov & Prilepskaya, documents). Several fluke centra preserved in CCMGE 3-16/13328 have circular articular surfaces with nearly equal width and length.

Both mature SGM 1573 and juvenile CCMGE 3-16/13328 individuals do not demonstrate such a high degree of regionalization in posterior dorsal to anterior caudal centra, which was observed by Maxwell (2010). It is possible that this condition is quite variable both in ontogeny and intraspecifically, thereby it is hard to assess its potential taxonomic value to the moment.

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Numerous rib fragments were collected for CCMGE 17-44/13328. The longest but incomplete rib is near 70 cm in preserved lengths. The ribs are from T-shaped to 8-shaped in cross-section in a proximal part of their length and becoming circular in cross-section distally.

Appendicular skeleton

Scapula. The left scapula is completely preserved in CCMGE 17-44/13328 (Fig. 7J–M). The element is robust: its proximodistal length is shorter than coracoid anteroposterior length. It is similar to that of *Ophthalmosaurus* icenicus in general morphology (Seeley, 1984; Andrews, 1910; Moon & Kirton, 2016). The scapular shaft is mediolaterally flattened and elongated-oval in cross-section. The glenoid contribution is well developed and equal in length to the coracoid facet. The acromial process is massive and well-prominent; it curves ventrolaterally, forming a nearly right angle with the lateral surface of the scapula (Fig. 7N).

Coracoid. The coracoid is slightly longer anteroposteriorly than wide mediolaterally (Fig. 7P). It is similar to that of *Ophthalmosaurus icenicus* and *Undorosaurus gorodischensis* (Andrews, 1910; Moon & Kirton, 2016; Zverkov & Efimov, in press), but differs in relative size, being anteroposteriorly longer than scapular proximodistal length. The medial symphysis is lenticular in outline; it occupies anterior two-thirds of the medial surface. The anteromedial process is prominent, laterally limited by an extensive anterior notch (anterior notch is relatively smaller in CCMGE 3-16/13328 than in the holotype, most likely as a reason of immaturity). The posterior portion of the coracoid is strongly compressed and convex posteriorly (Fig. 7P). The most interesting trait is that articulated coracoids form a pronounced angle of 100 degrees (Fig. 7O); this condition is unique for *Arthropterigius.* The scapular facet and glenoid contribution are offset by an angle of *c.* 140 degrees. Their surfaces are slightly convex and tuberous. The glenoid contribution surface is parallel to the medial symphysis of the coracoid, thus coracoid mediolateral length is constant, unlike caudally constricting coracoids of *Sveltonectes* (Fischer *et al.*, 2011), *Nannopterygius* (Hulke, 1871; Kirton, 1983) and ‘*Paraophthalmosaurus*’ (Arkhangelsky 1997; Efimov 1999a) and caudally expanding coracoids of *Undorosaurus* (Efimov 1999b).

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Commented [A31]: can you justify this with examples from other taxa?

Clavicle. The clavicle (Fig. 7X–Z) is a large and robust element. It is very similar to that of *A. lundi*, being dorsoventrally high and anteroposteriorly thick, compared to other known ophthalmosaurids. On its medial surface, there is a rugose circular facet for articulation with the acromial process of the scapula (Fig. 7Y). This facet is pronounced, but not as well developed as in *A. lundi* (see below).

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Interclavicle. The interclavicle of SGM 1573 is a large and slender T-shaped element. The anterior transverse bar of the interclavicle is straight, with a high dorsally rising wall; its lateral extremities extend far laterally, and their ends are rounded (Fig. 7C’, D’). There is no ventral knob observed in *Undorosaurus gorodischensis* and *Grendelius alekseevi* (Zverkov, Arkhangelsky & Stenshin, 2015; Zverkov & Efimov, in press). The posterior median stem is slender and bears a shallow trough along its dorsal surface. There is a prominent bulge in the middle of the ventral surface of the stem (Fig. 7C’, D’). In PMO 222.669 a displaced portion of the clavicle was erroneously interpreted as a wide interclavicle posterior median stem (Delsett *et al.* 2018). In fact, the interclavicle of PMO 222.669 is heavily distorted and broken into several disarticulated pieces due to a collapsing of pectoral girdle during the taphonomic process, but judging from the preserved fragments, its posterior median stem was quite slender.

Commented [A33]: Yes I can agree with this fully, I assisted the prep. Near impossible.

Humerus. The humerus is a large and robust bone with wide and dorsoventrally compressed midshaft. The humeral ‘torsion’ (angle between the long axes of the proximal and distal ends of the humerus) is *c*. 70 degrees. The dorsal process is prominent and plate-like, extending up to the half of the humeral midshaft (Fig. 7C, F, S). The deltopectoral crest is poorly developed and shifted to the anterior border of the humerus (Fig. 7A, E, G, I, T, W). The proximal end is semi-rectangular in outline, being anteroposteriorly longer than dorsoventrally thick (Fig. 7E, I, W). There are three distal concave facets for the preaxial accessory element, radius and ulna. The facet for the preaxial accessory element is large and semicircular in outline; it occupies nearly equal space as the radial facet. The radial facet is irregularly pentagonal in outline; its ventral edge is angular, forming in posterior half an abrupt skew to the ulnar facet (Fig. 7D, H, V). A ratio of the dorsoventral width of the radial facet to ulnar facet is 0.7–0.78 (see Tab. S1 in Zverkov & Prilepskaya, documents).

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Epipodial elements. The articular surfaces of the epipodial elements are convex for a peg-and-socket articulation with concave distal humeral facets; however, this condition varies even in mature specimens from extremely deep in CMN 40608 to more shallow in SGM 1573. The anterior accessory epipodial element is circular in dorsal view; its anterior edge lacks perichondral ossification as in *Ophthalmosaurus icenicus* (Andrews, 1910; Moon & Kirton, 2016). This element rapidly tapers anteriorly. The radius is pentagonal in dorsal and ventral views (Fig. 6A, F). The ulna is the largest element in the epipodial row, its dorsal and ventral cortical parts are roughly hexagonal in outline. The element gradually constricts in dorsoventral width posteriorly. A perichondral ossification of the posterior edge of the ulna is absent (Fig. 6A). The intermedium wedges between the radius and ulna, but not reach the humerus, however, a distance between the humerus and intermedium varies from relatively short in CCMGE 3-16/13328 and CMN 40608 to relatively long in CCMGE 17-44/13328. Distally intermedium bears two slightly demarcated facets for distal carpals three and four, indicating a ‘latipinnate’ forefin architecture. A statement of Maxwell that ‘the distal edge of the intermedium forms a surface for the articulation of a single distal carpal in the forefin of *Arthropterygius chrisorum*’ (Maxwell, 2010: 411) is likely a misinterpretation. Maxwell described the distal margin of the intermedium of CMN 40608 as ‘gently curved’(Maxwell, 2010: 410), so there are more likely two poorly demarcated facets for distal carpals three and four rather than a single convex ‘facet’. This becomes clear when other specimens with better-demarcated facets are considered (CCMGE 3-16/13328, CCMGE 17-44/13328, PMO 222.669).

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Distal limb elements. All the mesopodial and autopodial elements are strongly dorsoventrally thickened, circular in outline and loosely packed, indicating a large amount of cartilage in forefin, which is most similar to the condition observed in *Ophthalmosaurus icenicus* (Andrews, 1910; Moon & Kirton, 2016). One of the elements in CCMGE 17-44/13328 has a semicircular outline in dorsal view and bears a perichondral ossification along one of its edges, this probably represents a pisiform (Fig. 6A). The pisiform of exact same morphology is present in the left limb of PMO 222.669 (NGZ pers. obs.).

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Pelvic girdle. The only central portion of the ischiopubis has been collected for CCMGE 17-44/13328, which complicates the description of the element. The ischiopubis is plate-like, mediolaterally compressed (8 mm at its thickest part). The obturator foramen is likely absent (Fig. 8G).

Femur. The femur of CCMGE 17-44/13328 is slender with proximal and distal ends only slightly expanded (Fig. 8A). Its proximodistal length comprises 0.74 of the humeral proximodistal length (0.67 in the holotype CMN 40608). The femur of CCMGE 17-44/13328 is very similar to that of the holotype, possessing flattened ventral process terminating proximal to the mid-point, and thereby being more prominent than that of *A. lundi* (Roberts *et al*., 2014). The dorsal process is less pronounced than the ventral process and shifted to the anterior edge of the femur. There are two distal facets, which are concave and poorly demarcated, forming a common distal groove for the epipodial elements (Fig. 8D). The fibular facet is slightly inclined posterodistally, whereas the tibial facet faces nearly distally.

Measurements: See Tables S1 and S2 in Zverkov & Prilepskaya, documents.

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Ontogenetic changes and variation in Arthropterygius chrisorum

Thanks to new specimens of juveniles and young adults, we can now make some observations on the ontogenetic changes of *Arthropterygius chrisorum*.

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In general, changes in morphological proportions during growth of *A. chrisorum* are consistent with those observed in other ichthyosaurs (Huene, 1922; McGowan, 1973b; Deeming *et al*., 1993). Having largely incomplete specimens (Fig. 9) we are unable to assess the growth of the whole skull and the whole body, thereby we compared selected cranial and postcranial elements (Fig. 10). The growth of elements of the skull base and occiput of *A. chrisorum* is more or less isometric compared to each other. The same concerns the growth of elements of the

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appendicular skeleton (Fig. 10A). At the same time, the growth rates differ between the skeletal regions.

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Relative anteroposterior length of the basisphenoid and the humerus is among the few ratios that could be calculated for *A. chrisorum* in order to compare the growth of the cranial and postcranial skeleton. In juvenile CCMGE 3-16/13328 this ratio is 0.58, in young adult CCMG E 17-44/13328 – 0.42, and in mature individual CMN 40608 – 0.35; thus we observe typical negative allometry. It is not surprising that the growth of the cranial elements is negatively allometric relative to the growth of the appendicular elements. Interesting is that growth of the appendicular skeleton is positively allometric relative to that of the axial skeleton (Fig. 10A), whereas for *Ichthyosaurus* and *Stenopterygius* this reported as being isometric (McGowan, 1973b).

Judging from the available cranial elements, the general morphology and proportions of the occipital region have not undergone sufficient changes with age. Despite differences in size CCMGE 3-16/13328, CCMGE 17-44/13328 and PMO 222,669 have a characteristic shape of the quadrate condyle: it is dorsoventrally high with a V-shaped ventral margin of the articular boss. Furthermore, the quadrate do not develop the anterior protrusion with age. In all specimens of *Arthropterygius chrisorum*, the basisphenoid is trapezoidal in ventral outline, being mediolaterally wider anteriorly than posteriorly. The juvenile CCMGE 3-16/13328 has a narrower anterior profile when compared to those of adults CCMGE 17-44/13328, PMO 222,669 and CMN 40608 (Fig. 10B, C, D, E), supporting observations of Kear & Zammit (2014) on *Platypterygius australis*. The only marked difference of the basisphenoids is the relative position of the posterior foramen for the internal carotid arteries, which is still exposed ventrally in juvenile CCMGE 3-16/13328, but already separated by a grown shelf in young adults PMO 222,669 and CCMGE 17-44/13328 (Fig. 10B, C, D).

The coracoids of juvenile CCMGE3-16/13328 are more rounded in outline compared to those of adults (Fig. 10W, X, Y). This is primarily due to less developed anteromedial process and not yet developed posterior protrusion. It is interesting that there are no marked differences in humeral morphology between the juvenile and adults. The marked change is the angle between the radial facet and facet for the anterior accessory epipodial element that became less pronounced with age (Fig. 10M–Q). The absence of marked ontogenetic changes in relative size and shape of the humeral distal facets supports their diagnostic value; thereby the features related to humeral distal facets can be used to diagnose species of *Artropterygius* irrespective of osteological maturity.

All the specimens of *Arthropterygius chrisorum* have concave humeral distal facets and convex proximal articular facets of the epipodial element. A tendency for deepening of humeral distal facets with age could be observed, however, it is non-uniform. Although the old adult CMN 40608 has very deeply concave facets (Maxwell, 2010), comparable in size SGM 1502 has less concave facets and consequently should have had less convex proximal surfaces of the epipodial elements. Considering this variation and the fact that after the publication of Maxwell (2010) humerus-epipodial peg-and-socket articulation was reported for other ophthalmosaurids (Zverkov *et al.*, 2015), we have to assume that 'proximal surface of zeugopodial elements angular in outline for articulation with humerus' (Maxwell, 2010: 404) cannot be further considered as a diagnostic character of *Arthropterygius*.

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Arthropterygius hoybergeti (Druckenmiller, Hurum, Knutsen & Narkem, 2012) comb. nov.

(Figs 11–14)

v*2012 *Palvennia hoybergeti* Druckenmiller, Hurum, Knutsen & Narkem: 326, figs 12–21

Holotype: SVB 1451, a nearly complete skull, atlas/axis complex and fragmentary vertebra, right clavicle, fragments of left and right scapulae, proximal and distal portions of a humerus, limb elements and several disarticulated dorsal ribs.

Referred specimens: YKM 63548, a slab containing a series of 19 presacral vertebrae with articulated neural arches and ribs, right humerus, a cast of the left humerus with associated radius, ulna and intermedium (original forelimb was lost because of pyrite decay); UPM 2442, left humerus.

Emended diagnosis. A moderately large ophthalmosaurid (up to 4 meters) distinguished from other species of *Arthropterygius* by the following unique character combination: basisphenoid longer anteroposteriorly than mediolaterally wide, with the widest part in the region of basipterygoid processes; posterior foramen for internal carotid arteries opening on the posteroventral edge of the basisphenoid and forming a notch as in *A. lundi* and unlike *A. chrisorum*; small basioccipital facet of the opisthotic (large in other known species of *Arthropterygius*); relatively large teeth with circular in cross-section roots and robust ridged crowns as in *A. chrisorum* but unlike gracile subtly ridged crowns of *A. lundi*; slightly anteroposteriorly elongated proximal end of the humerus (as in *A. chrisorum* and *Undorosaurus gorodischensis*); well developed plate-like trochanter dorsalis and deltopectoral crest (unlike in other species of *Arthropterygius*); anterodistal facet for the anterior accessory epipodial element sufficiently smaller than the radial facet, being thus relatively smaller than that in *A. lundi* and *A. chrisorum*, ventral skew between the radial and ulnar facets is nearly absent, however, the ulnar facet is nonetheless markedly shorter dorsoventrally than the radial facet.

Occurrence: *Arthropterygius hoybergeti* is known from the Slottsmøya Member of the Agardhfjellet Formation of Svalbard (type locality), where it was found most likely within the *Dorsoplanites ilovaiskii* Ammonite Biozone (lower Middle Volgian). Two specimens from the Volga Region (both found on the right bank of the Volga River near Gorodischi Village, Ulyanovsk Region) referred here to as *A. hoybergeti* are corresponding to *Dorsoplanites panderi* Ammonite Biozone of Promza Formation.

Description

Here we provide some new observations on the holotype SVB 1451, which had been described in detail by Druckenmiller *et al*. (2012); thereby we discuss only some misinterpretations of Druckenmiller *et al*. (2012) and provide some additional information, not reported before.

Commented [A41]: Instead of saying misinterpretations, say new interpretations. It is more polite. Also some of the observations are subjective, so a new interpretation would be more accurate

Nasal. The nasal of SVB 1451 bears a well-pronounced lamella, a ‘wing’, overhanging the dorsal border of the naris.

Parietal. The parietal has a very short but robust medial symphysis and well-pronounced notch posterior to it (Fig. 11A). The element posseses a relatively elongated and slender supratemporal process (Fig. 11A).

Squamosal. Although reported as absent, the squamosal of SVB 1451 (Fig. 11B) was mentioned by Druckenmiller *et al*. (2012) as a “small rib-like element” of unclear identity, and even figured (Druckenmiller *et al*., 2012: 327, fig. 16E, F).

Quadrate. Both quadrates of SVB 1451 are preserved, but only partially exposed, so that dorsal portion of the right quadrate and ventral portion of the left quadrate are available for observations. The occipital lamella of the quadrate is extremely well developed (Fig. 12O).

The articular condyle is relatively weak; the articular boss is larger than the surangular boss and protrudes ventrally. There is a pronounced angular protrusion of the quadrate (absent in *A. chrisorum*).

Basisphenoid. The basisphenoid of SVB 1451 could be observed in ventral and dorsal views (Figs 11A; 12B). It is longer anteroposteriorly than mediolaterally wide. The widest part is the region of basipterygoid processes that are directed anterolaterally. A posterior foramen for the internal carotid arteries opens on the posteroventral edge of the basisphenoid and forms a notch as in *A. lundi* and unlike *A. chrisorum* (Fig. 12B).

Opisthotic. The opisthotic was not described for SVB 1451 by Druckenmiller *et al*. (2012), neither by Delsett *et al.* (2018), however, both opisthotics are well-preserved. The paraoccipital process of the opisthotic is short and robust, which is a common condition for ophthalmosaurids except for *Ophthalmosaurus* and *Acamptonectes* (Fischer *et al*., 2012). The facet for the supratemporal is oval in outline, being dorsoventrally compressed (Fig. 12I). The lateral muscular ridge is well developed (Fig. 12D, I). The stapedial facet is somewhat triangular in outline and bisected by a straight mediolateral canal for either VII or for IX nerve, as was interpreted by Kirton (1983) (see also Kear, 2005; Moon & Kirton, 2016). The facet for the basioccipital is relatively small and quadrant in outline with convex margin directed dorsolaterally, it is sufficiently smaller than the stapedial facet (Fig. 12C). The impression of semicircular canals of the otic capsule is V-shaped (Fig. 12G, H). Both impressions of the horizontal semicircular canal and posterior vertical semicircular canal are nearly equal in length, unlike in *Undorosaurus gorodischensis* and *Acamptonectes densus*, in which horizontal semicircular canal impression is markedly longer (Fischer *et al*., 2012; Zverkov & Efimov, in press). The impression housing the posterior ampulla, utriculus and the sacculus is expanded (Fig. 12G).

Exoccipital. Both exoccipitals are preserved in SVB 1451, however, right element was misidentified as left and figured upside down in the original description (Druckenmiller *et al*., 2012). The statement that ‘there is no evidence of any foramina for cranial nerves perforating the element’ (Druckenmiller *et al*., 2012: 331) is ~~not~~ incorrect and resulted from the state of preservation, as was also suggested by Delsett *et al.* (2018: 23). At least one hypoglossal foramen could be seen on the lateral side of the left exoccipital, although, indeed, columnar morphology with the reduced base of the occipital foot make the reduction of a number of hypoglossal foramina expected.

Stapes. Although the left stapes of SVB 1451 is still in situ, mostly covered by other elements (Fig. 11A), the isolated right stapes was misidentified as left and figured upside down in the original description (Druckenmiller *et al*., 2012; fig. 19). This misinterpretation has already been corrected by Delsett *et al.* (2018). The hyoid process of the stapes is relatively well developed and helps for correct spatial orientation of the element (Fig. 12L). The basisphenoid and basioccipital facets are clearly demarcated; dorsal to them there is an extensive facet for the opisthotic (Fig. 12J). Given that the stapedial facet of the basioccipital is directed anteriorly, and that there is some extent of stapedial curvature, the stapes, when articulated, was strongly rotated anteroventrally (Fig. 12A). This condition is very unusual for ophthalmosaurids but probably was typical for ichthyosaurs of *Arthropterygius* clade, as all of them have anteriorly directed stapedial facet of the basioccipital. The configuration of the articulated occipital region of *A. hoybergeti* was strongly protruding posteriorly, somewhat 'vaulted', which is probably a result of a strong reduction of the postorbital region.

Articular. The articular of SVB 1451 was recently described by Delsett *et al.* (2018: 8). It is roughly trapezoid in outline, only slightly longer anteroposteriorly than dorsoventrally high (Fig. S4 in Zverkov & Prilepskaya, documents). It is very similar to that of *A. chrisorum* (Maxwell 2010).

Dentition. The teeth of *A. hoybergeti* are relatively large. The crowns are robust, conical, ranging from straight to slightly recurved. The enamel ornamentation is composed of numerous tightly packed ridges, which are semicircular in cross-section (Fig. 13A). The ridges seem to extend to the apex of the crown and arranged around its entire circumference. The apicobasal length of the largest crown is *c*. 14 mm in apicobasal length and 9 mm in diameter at the base.

Vertebral column. There is no line of fusion of atlas and axis contra Druckenmiller *et al*. (2012: 334). An incomplete anterior presacral ('cervical') centrum is preserved and has characteristic oval outline slightly tapering ventrally (Fig. S05).

Clavicle. The right clavicle is nearly complete but badly preserved (11A), it is very robust and similar to those of *A. chrisorum* and *A. lundi*, thus typical of the genus.

Scapula. The preserved scapular dorsal rami are slightly curved and mediolaterally compressed having an oval cross-section of the shaft (Fig. 14B, C).

Humerus. A number of fragments of the right humerus are preserved (however, some of these fragments could belong to the left humerus). Most important are proximal and distal portions. The shape of the preserved proximal portion of the right humerus indicates that it was anteroposteriorly elongate and has a pronounced plate-like deltopectoral crest (Fig. 14D, E). The anterodistal fragment of the humerus demonstrates that it was dorsoventrally thick distally. A facet for the anterior accessory element is relatively small and triangular in outline (Fig. 14F; S7A in Zverkov & Prilepskaya, documents). Complete humeri of referred specimens allow to depict all the details of humeral morphology: in addition to plate-like deltopectoral crest, there was well-developed and plate-like dorsal process (Fig. 14H, I, K–M, Q). The radial facet is the thickest part of the distal humerus, which gradually flattens posteriorly to more elongated ulnar facet (Fig. 14J, N). There is no marked ventral skew between the radial and ulnar facets compared to that in *A. chrisorum* and *A. lundi*, however, the decrease in thickness between the radial and ulnar facets is apparent (Fig. 14J).

Epipodial and autopodial elements. Several epipodial and autopodial elements are preserved in SVB 1451, including the complete anterior accessory epipodial element, radius and intermedium as well as fragmental ulna (Fig. 14F). While not included in the original description (Druckenmiller *et al*., 2012), the elements were recently mentioned and figured by Delsett *et al*. (2018), however, with some misidentifications (anterior accessory epipodial element was misidentified as a pisiform; distal carpal 3 is identified with no grounds, whereas an element identified as the radiale herein was considered to be a metacarpal). YKM 63548 has articulated radius, ulna and intermedium (Fig. 14Q). The anterior accessory epipodial element present in SVB 1451 is semicircular in dorsal view, it strongly tapers along the anterior margin, which is nearly straight, but still not involved in perichondral ossification (Fig. 14F). The radius is typically pentagonal in dorsal view and has a strongly convex proximal articular surface. The ulna is somewhat hexagonal, it lacks perichondral ossification along the posterior edge; distally it bears three nearly equal facets for the intermedium, ulnare and the pisiform (Fig. 14Q). The intermedium is somewhat diamond-shaped in dorsal view, wedging between the radius and ulna and bearing two distal facets, evidently for distal carpals three and four (Fig. 14F, Q). The autopodial elements are circular in outline and were loosely arranged in the limb as in *Ophthalmosaurus icenicus* (see Moon & Kirton, 2016) and other species of *Arthropterygius*.

Remarks

We suppose that the fact that Delsett *et al*. (2018) referred *Arthropterygius chrisorum* PMO 222.669 to as *Palvennia hoybergeti* leaves no questions regarding why we identify '*Palvennia*' *hoybergeti* as a species within *Arthropterygius*. Indeed, both *A. chrisorum* and *A. hoybergeti* have very similar, although not identical, cranial anatomy and the main differences of the two species are related to the morphology and proportions of their appendicular skeleton. The following diagnostic features of the genus *Arthropterygius* present in the holotype of *Palvennia hoybergeti* (SVB 1451): (1) strongly ventrally bowed jugal; (2) wide supratemporal anteromedial tongue covering the postfrontal; (3) relatively gracile quadrate with a 'weak' condyle; (4) extracondylar area of the basioccipital wide in lateral view and practically unseen in posterior view; (5) stapedial and opisthotic facets of the basioccipital shifted anteriorly and poorly visible in lateral view; (6) basisphenoid with foramen for the internal carotid arteries opening posteriorly; (7) basioccipital facet of the basisphenoid facing posterodorsally, occupying in dorsal view area equal or even larger than that of dorsal plateau; (8) wide and extremely robust clavicles.

Commented [A42]: Couldn't this be intraspecific variation?

The specimens referred herein to as *A. hoybergeti* lack cranial remains, whereas the holotype lacks most of the postcranium resulting in poor overlap between these specimens. This could call into question our decision to refer UPM 2442 and YKM 63548 to *A. hoybergeti*, however, we suggest that this is a reasonable assumption. Despite the minute difference in size, the humeri of UPM 2442 and YKM 63548 are very similar one to another and bear diagnostic features of *Arthrthropterygius*: three concave distal articular facets for the preaxial accessory element, radius, and ulna; ulnar facet: radial facet dorsoventral width ratio *c.* 0.8; dorsoventrally compressed posterior edge of the humerus. Furthermore, YKM 63548 preserves epipodial elements and intermedium that are greatly consistent with those of other *Arthropterygius* species: ulna is larger than radius and lacks the posterior perichondral ossification; intermedium bears two nearly equal distal facets. At the same time, these humeri are distinct from humeri of *A. chrisorum* and *A. lundi* in absence of pronounced ventral skew between the radial and ulnar facet and in relatively small size of the facet for the anterior accessory epipodial element. Thus, UPM 2442 and YKM 63548 belong to *Arthropterygius*, but represent a species different from *A. chrisorum* and *A. lundi*. Although the humerus of *A. hoybergeti* is fragmented it also demonstrates relatively small facet for anterior accessory epipodial element and well developed plate-like deltopectoral crest, not characteristic for other species of *Arthropterygiu*s except for a 'species' represented by UPM 2442 and YKM

Commented [A43]: If this is the only point that justifies your referall, I would say that is not enough evidence and it should be referred to as *Arthropterygius sp. idet.*
Remember that the humerus in ichthyosaurs has a tendency to show a significant amount of intraspecific variation.

63548, hence our decision to consider UPM 2442 and YKM 63548 as belonging to *A. hoybergeti*.

Commented [A44]: Not enough evidence.

Measurements. See Druckenmiller *et al*. (2012).

Arthropterygius lundi (Roberts, Druckenmiller, Sætre, Hurum, 2014) comb. nov.

(Figs 13D, C, 15–17, 18F, S8)

v*2014 *Janusaurus lundi* Roberts *et al*.: 4, figs 3–14.

v.2015 *Arthropterygius sp.*, Zverkov, Arkhangelsky, Pardo Pérez, Beznosov: 84, figs. 3–7.

2016 Janusaurus lundi Roberts *et al*.; Delsett *et al*.: figs 6b, 9, 10b–d.

2017 Janusaurus lundi Roberts *et al*.; Delsett *et al*.: fig. 12J, K.

Holotype: PMO 222.654, an incomplete skeleton (for details see Roberts *et al*. 2014).

Referred specimens: SGM 1502 (for details see Zverkov *et al*. 2015); SGM 1731-01–15, 10 anterior presacral vertebrae with articulated neural arches; scapulae; left coracoid; left humerus with articulated epipodial and proximal autopodial elements.

Emended diagnosis: A medium sized ophthalmosaurid (3–4 meters long) diagnosed relative to other species of *Arthropterygius* by the following unique characters (including autapomorphies, marked with '*') and character combination: extremely gracile and constricted stapedial shaft*; basisphenoid trapezoid in ventral view with widest part in the region of basipterygid processes; posterior foramen for internal carotid arteries opening on the posteroventral edge of the basisphenoid and forming a notch as in *A. hoybergeti* and unlike *A. chrisorum*; large basioccipital facet on the opisthotic (reduced in *A. hoybergeti*); small teeth with gracile crowns and poorly pronounced ridges (relatively large teeth with ridged crowns in *A. hoybergeti*, although teeth are unknown for other species of *Arthropterygius*); interclavicle with pointed lateral extremities and deep trough on the dorsal surface of posterior median stem*; isometric proximal end of the humerus with nearly equal dorsoventral and anteroposterior length (as in *Ophthalmosaurus icenicus*, *Undorosaurus nessovi* and *U. trautscholdi*); reduced dorsal process and deltopectoral crest; strongly dorsoventally flattened posterior and distal parts of the humerus; anterodistal facet for the anterior accessory epipodial element nearly as long, but not as wide as the radial facet, being thus relatively smaller than that of *A. chrisorum* (this facet is sufficiently smaller in *A. hoybergeti*), ventral skew between the radial and ulnar facets is pronounced in a lesser degree than in the type species, but stronger than in *A. hoybergeti*; ?strongly expanded dorsal portion of the ilium with distinct anterodorsal process (could be a generic feature).

Occurrence: *Artropterygius lundi* is recognized in the European Russia and Svalbard. Everywhere it is found in the early Middle Volgian: Slottsmøya Member of the Agardhfjellet Formation in Svalbard (type locality), *Pavlovia rugosa* to *Dorsoplanites ilovaiskii* ammonite biozones; Paromes Formation in Timan-Pechora Basin and Promza Formation of the Volga Region, all these finds correspond to *Dorsoplanites panderi* Ammonite Biozone.

Description

Here we provide some new observations on the holotype (PMO 222.654) and description of SGM 1731-01–15. Description of SGM 1502 was given in Zverkov *et al*. (2015).

Skull. Several sutures in the holotype skull are reinterpreted herein (Fig. 15). The postfrontal medial contact with the supratemporal was imprecisely traced by Roberts *et al*. (2014) likely because of poor preservation. In fact, similarly to other species of *Arthropterygius* the supratemporal of PMO 222.654 forms an anteromedial tongue covering the postfrontal (Fig. 15A, B). The parietal of *A. lundi* has a typical morphology of *Arthropterygius* with a very short medial symphysis and well-pronounced notch posterior to it (Fig. 15A, B). The anterior portion of the parietal has likely contributed to a presumably large parietal foramen that was restricted by the frontals anterolaterally (Fig. 15). A ventral exposure of the parietal allows adding that the supratemporal process is relatively slender (Fig. 15C, D).

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Squamosal. A squamosal was ‘presumed to have been absent in PMO 222.654’ (Roberts *et al*., (2014: 7), on the basis that ‘the region in which this element is usually present is well preserved in the specimen’ (Roberts *et al*., (2014: 7), however, as in case of other specimens from Svalbard this assumption is likely misleading (Zverkov & Efimov, in press). In the postorbital region of PMO 222.654, there is an anteroposteriorly elongated depression along the ventral margin of the supratemporal and continuing anteriorly to postfrontal (Fig. 15A). Furthermore, the surface of the postorbital in this region is roughened. The depression has exact the same configuration as that of *A. hoybergeti* (SVB 1451) and presumably represents the facet of squamosal, thereby we conclude that there was a squamosal in *A. lundi* similar in morphology to that of *A. hoybergeti*. As this element is delicate and poorly attached to the rest of postorbital bar, it is not surprising that it was detached and in some cases missing in a number of specimens from Svalbard, including PMO 222.654.

Commented [A46]: Fair enough

Quadratojugal. Considering the slenderness and small size of the quadratojugal, as well as the configuration of its articulation with the quadrate, it is likely that in life this element was largely obscured in lateral view and exposed mostly posteriorly.

Quadrate. Judging from its exposed portions, the quadrate of PMO 222.654 has relatively 'weak' condyle and a shallow notch of the quadrate foramen; its occipital lamella presumed to be reduced (Fig. 15C, D). The dorsoventral height of the quadrate of PMO 222.654 is *c*. 105 mm. The facet for quadratojugal is located on the inner surface of the quadrate as in *A. chrisorum* (Fig. 15C, D; see Fig. 3J, L, O, P for comparison). Nearly the entire posteromedial surface of the quadrate is occupied by an extensive contact with the pterygoid, and only small region in its dorsal part has contact with the supratemporal (Fig. 15C, D). Evidently, there was no supratemporal-stapes contact.

Basisphenoid. The basisphenoid of PMO 222.654 is mostly hidden in the matrix and covered by other elements, thereby the only significant observation that could be made to the moment is that the facet for the basioccipital was strongly shifted dorsally, a condition typical of *Arthropterygius*. The basisphenoid was described in detail for SGM 1502 that is here referred to as *A. lundi* (see Zverkov *et al*., 2015).

Commented [A47]: I can't see how this is in anyway visible or to be trusted. I would not say any significant observation can be made.

Opisthotic. Although it was not reported by Roberts *et al*. (2014), the nearly complete right opisthotic is present in the holotype (PMO 222.654). The paraoccipital process of the opisthotic is relatively short and very robust. The facet for the supratemporal is triangular in outline (Fig. 16E). The lateral muscular ridge is well developed. The stapedial facet is roughly trapezoidal in outline (Fig. 16D). The facet for the basioccipital is quadrant in outline with convex margin directed dorsolaterally (Fig. 16B); it is as large as the stapedial facet. A V-shaped impression formed by two smooth-floored semicircular canals of the otic capsule is deep. Impressions of the horizontal semicircular canal and posterior vertical semicircular canal are nearly equal in length as in *A. hoybergeti*. The posterior vertical semicircular canal impression is only slightly wider. The impression housing the posterior ampulla, utriculus and the sacculus is expanded, especially in its anteroventral part, to where sacculus impression continues (Fig. 16F, G).

Commented [A48]: This I completely agree with! I did not recognize the element when I described the specimen. This element was collected from the weathered medial side of the specimen in the occipital region. You can add that as a pers. Coms. If it is useful.

Dentition. The dentition of *A. lundi* is weak compared to that of *A. chrisorum* (PMO 222.669) and *A. hoybergeti* (SVB 1451). The crowns are slender and their enamel is subtly ridged (Fig. 13B, C). An estimated crown height is less than 9 mm in PMO 222.654, as calculated by Roberts *et al.* (2014: 15). The largest crown of SGM 1502 is 10 mm high and has 5 mm in basal diameter.

Axial and appendicular skeleton. Not much could be added to the thorough description of the axial and appendicular skeleton of *Arthropterygius lundi* made by Roberts *et al*. (2014). Among the interesting traits not mentioned by the aforementioned authors are the extensive circular facet on the clavicle that formed a firm articulation with the acromial process of the scapula (Fig. 17D, E) and, typical of the genus, pronounced angle close to 90 degrees between the articulated coracoids (Fig. 17Q). A ‘foramen’ located on the ventral surface of the interclavicle of PMO 222.654, is likely an artefact of preservation, but not an autapomorphic trait as was supposed by Roberts *et al*. (2014). The interclavicular trough is very deep unlike in other species of *Arthropterygius* and in other ophthalmosaurids in general, thereby we support the statement of Roberts *et al*. (2014) that this could be considered as an autapomorphy. A bulge in the middle of the interclavicle posterior median stem is present in PMO 222.654 (Fig. 17F, G), supporting our assumption that this is a characteristic trait of *Arthropterygius*.

The well-preserved coracoid and scapula of SGM 1731-01–15 demonstrate a typical morphology of *Arthropterygius* (Fig. 17A–C). The coracoid is slightly longer anteroposteriorly than wide mediolaterally; it bears a prominent anteromedial process, laterally limited by an extensive anterior notch. The posterior portion of the coracoid is strongly compressed and forms a convex protrusion posteriorly (Fig. 17A). The scapula has a well-developed acromial process, nearly equal coracoid facet and glenoid contribution (the latter is slightly shorter) and typical mediolaterally compressed, oval in cross-section scapular shaft (Fig. 17B, C).

Humerus. Although coracoid and scapula do not bear any specific traits in *A. lundi*, the humerus does. Having humeri nearly identical to that of PMO 222.654, both SGM 1502 and SGM 1731-01–15 fit greatly to complement the hypodigm. The humerus of *Arthropterygius lundi* has a characteristic isometric proximal end as high dorsoventrally as long anteroposteriorly, and strongly flattened distal end and posterior portion of the shaft (Fig. 17H–L, N–P). The dorsal process and deltopectoral crest of the humerus are relatively poorly developed. The ventral skew between the radial and ulnar facets is pronounced in a lesser degree than in the type species, but stronger than in *A. hoybergeti*.

Epipodial and autopodial elements. The epipodial and autopodial elements in SGM 1731-01–15 and PMO 222.654 are virtually identical. The anterior accessory epipodial element is circular in dorsal view. The radius has a typical pentagonal shape in dorsal view. The ulna is markedly larger than the radius, it is somewhat hexagonal, lacking a perichondral ossification along its posterior edge. Distally ulna bears three nearly equal facets for the intermedium, ulnare and the pisiform (Fig. 17M, N). The intermedium is diamond-shaped in dorsal view, having equal contacts with the radius and ulna and bearing two distal facets, evidently for distal carpals three and four. The autopodial elements are mostly circular in outline and were loosely packed as in *Ophthalmosaurus icenicus* (see e.g. Moon & Kirton, 2016) and other species of *Arthropterygius*. Of certain interest are two small ossicles that are semicircular in outline, having perichondral ossification along one of the edges (Fig. 17N). These are probably the pisiform and an element of a postaxial accessory 6th digit.

Measurements. See Roberts *et al.* (2014), Zverkov *et al.* (2015) and Table S3 in Zverkov & Prilepskaya, documents.

***Arthropterygius volgensis* (Kasansky, 1903) comb. nov.**

(Figs 18, 19, 20E)

v*1903 *Ichthyosaurus volgensis* Kasansky: 29, Tabs I, II.

1910 Ophthalmosaurus sp.; Bogolubov: 472 [*pars*].

2000 Otschevia ?volgensis; Arkhangelsky: 550.

2000 ?*Ophthalmosaurus* sp.; Storrs *et al*.:197 [*pars*].

2008 Undorosaurinae gen. indet.; Arkhangelsky: 253 [*pars*].

Holotype: KSU 982/P-213, incomplete skeleton of a juvenile represented by cranial remains (including basisphenoid, opisthotics, quadrates, parietals, right supratemporal and articular), three posterior caudal and tailfin vertebrae; neural arches and rib fragments, coracoids; fragments of the interclavicle, scapula and clavicles, distal portion of the femur.

Diagnosis: *Arthropterygius volgensis* could be diagnosed relative to other species of *Arthropterygius* by the following characters: gracile articular condyle of the quadrate, less high dorsoventrally and less obtuse posteriorly, do not forming a pronounced ventral angle; and square ventral outline of the basisphenoid with posterior end of the element mediolaterally wider than the anterior end, due to a pronounced reduction of the basipterygoid processes.

Occurrence: *Arthropterygius volgensis* is known from only the type locality to the moment: the mouth of the Berezoviy Dol Ravine near Novaya Racheika Village, Syzran District, Samara Region. Upper Jurassic, Middle Volgian, *Dorsoplanites panderi* Ammonite Biozone.

Description

Skull

Supratemporal. A posterodorsal portion of the right supratemporal is preserved (for the figure see Kasansky 1903, Tab.1 fig. 10). The medial ramus is massive and mediolaterally short, it bears a concave facet for articulation with the parietal.

Parietal. The parietal is well preserved and similar to that of other *Arthropterygius* species. It possess a relatively elongated and slender supratemporal process (Fig. 18P). The posterodorsal surface of the supratemporal processes is rugose with the central ridge that contributed to a somewhat peg-and-socket articulation with the supratemporal (Fig. 18P). The medial articular facet is anteroposteriorly shortened; its surface is deeply ridged for a strong interdigitating articulation with the contralateral parietal. Posterior to the facet is a pronounced notch of finished ossification (Fig. 18P, S). Anteriorly, the parietal bears rugose facets for articulation with the frontal and postfrontal. Ventral surface of the element is divided into two areas: the deep and extensive impression of the cerebral hemisphere occupy more than a half of the anterior ventral surface (Fig. 18R, ich); posteriorly situated optic lobe impression, which is roughly circular in outline, occupies the rest of the element (Fig. 18R, iop). The dorsal surface of the parietal is convex and nearly horizontal along the midline in lateral view. There was no sagittal eminence.

Commented [A49]: Is there a pineal foramen?

Quadrate. The articular condyle of the quadrate is relatively reduced and dorsoventrally low compared to that of *A. chrisorum*. The articular and surangular bosses of the condyle are nearly equal in size (Fig. 18O, N). The articular boss is only slightly more pronounced ventrally, however its ventral margin is gradually curved, but not V-shaped as in *A. chrisorum*. The facet for the quadratojugal is a small depression on the dorsal surface of the condyle (Fig. 18N). The quadrate foramen is shallow due to a reduction of the articular condyle and the occipital lamella (Fig. 18L). The occipital and pterygoid lamellae are slightly demarcated one from another forming an angle of c. 145 degrees. A circular depression of the stapedial facet is located in the middle of the medial surface (Fig. 18L).

Basisphenoid. The basisphenoid is square in ventral view: its posterior and anterior ends are nearly equal in mediolateral length (Fig. 18A). The basipterygoid processes are reduced and faced anterolaterally. The basioccipital facet is a broad hexagonal irregularly pitted surface that faces posterodorsally. A pentagonal dorsal plateau is mediolaterally wide. The stapedial facet is oblique and relatively small (Fig. 18C). The anterior wall is high and vertical, even on the lateral sides. The dorsum sellae, located in the middle of the anterior surface, is smoothly bordered from the rest of the anterior wall (Fig. 18D). The impressions of a cartilaginous continuation of the crista trabecularis are well-pronounced (Fig. 18D). The posterior foramen for the internal carotid arteries opens posteroventrally, forming a medial notch of the posteroventral edge of the basisphenoid, as is CCMGE 3-16/13328, which may be due to the immaturity of these individuals.

Opisthotic. The paraoccipital process of the opisthotic is shortened and robust, however, this could be regarded as an immature condition as was discussed by Kear & Zammit (2014). The facet for the supratemporal is triangular in outline (Fig. 18H). The lateral muscular ridge is well pronounced. The trapezoid in outline stapedial facet is larger than the facet for the basioccipital, which is quadrant in outline with convex margin directed dorsolaterally (Fig. 18F, K). The stapedial facet bears a deep straight mediolateral groove either for VII or for IX nerve in its middle (Fig. 18K). The impressions for the semicircular canals of the otic capsule are deep and nearly equal in length as in other species of *Arthropterygius*. The impression of the posterior vertical semicircular canal is wider than that of the horizontal semicircular canal. The impression housing the posterior ampulla and the sacculus is expanded (Fig. 18J).

Articular. The articular is anteroposteriorly elongated and trapezoid in outline (Fig. 18T, U). It is highly similar to that of *Arthropterygius lundi* (Roberts *et al*., 2014), being more anteroposteriorly elongated than in *A. chrisorum* and *A. hoybergeti* (Fig. S4 in Zverkov & Prilepskaya, documents; Maxwell, 2010).

Commented [A50]: The articular in the referred PMO specimen is pretty elongated if I recall

Axial skeleton. The detailed description and measurements of the vertebral column (which is ~~nowadays missing~~lost) were provided by Kasansky (1903).

Pectoral girdle. The preserved middle fragments of clavicles (Fig. 19H) demonstrate morphology common of ophthalmosaurids: these are anteroposteriorly thin and dorsoventrally high elements, curving in dorsolateral direction. The clavicles are dorsoventrally high as in other species of *Arthropterygius*. The interclavicle (Fig. 19H, I) is a relatively large element, being approximately 2/3 of the coracoid length. Its posterior median stem is shaft-like, ventrally convex and dorsally bearing a shallow trough. The scapula is incompletely preserved in two fragments. The acromial process of the scapula is large and flattened, anteroventrally curving at the anterior edge (Fig. 19G). The scapular shaft is mediolaterally compressed, as in other species of *Arthropterygius* and ophthalmosaurines *Ophthalmosaurus icenicus* and *Acamptonectes densus* (Fischer *et al*., 2012; Moon & Kirton, 2016). Both coracoids are well preserved, they are rounded in general outlines; however, their anteroposterior length slightly exceeds mediolateral width. The ventral surface of the element is slightly saddle-shaped (Fig. 19B), whereas the dorsal surface is nearly flat (Fig. 19A). The scapular facet is demarcated by an obtuse angle (160 degrees) from the glenoid contribution. The medial symphysis is dorsoventrally thin, extending along anterior two-thirds of the coracoid, as in *A. chrisorum* and *A. lundi* (Roberts *et al*., 2014). The angle between articulated coracoids is close to 90 degrees (Fig. 19E).

Femur. The only distal portion of the right femur is preserved (Fig. 19J–M). Its distal facets are poorly ossified and slightly demarcated, thus it is even hard to say, whether two or three distal facets are present (Fig. 19J, K, M). The ventral process, located in the middle of the ventral surface is more prominent than the anteriorly shifted dorsal process (Fig. 19L).

Remarks. Kasansky originally incorrectly identified the femur as a humerus, at the same time two broken pedicles of the neural arches were misidentified as femora (Kasansky, 1903).

The holotype and only known specimen KSU 982/P-213 is a juvenile individual, thereby the value of features used as diagnostic could be questioned. Indeed, a number of observed traits could be interpreted as juvenile conditions: reduced occipital lamella of the quadrate, minimally developed basipterygoid processes and short paroccipital process of the opisthotic (see Kear &

Zammit, 2014). However, a series of specimens of different age classes available now for *Arthropterygius chrisorum* allows advocating some of our conclusions. Although the relative development of the basipterygoid processes of the basisphenoid during the ontogeny is supported by our observations, we state that the general ventral (or dorsal) outline of the basisphenoid is stable between all the age classes. Kear & Zammit stated that in the *in utero P. australis* 'the basipterygoid processes are minimally developed, giving the basisphenoid a much narrower anterior profile when compared with those of adults' (Kear & Zammit, 2014: 77). Based on this, they concluded that for characters dealing with a shape of basipterygoid processes, i.e. Maxwell (2010: char. 11) and Fischer *et al*. (2011: char. 17; 2012: char. 16), foetal individual scores differently than mature ones. However, this is not a fully justifiable observation, as in fact both foetal and mature *P. australis*, regardless the state of development of basipterygoid processes, preserve generally 'pentagonal' (or, it is better to say, trapezoidal) ventral outline of the basisphenoid with anterior region markedly wider than the posterior part. This is clearly seen from the fig. 5m of Kear & Zammit (2014). In contrast, taxa with 'square' ventral outline of the basisphenoid always have the same width of anterior and posterior basisphenoid (NGZ pers. obs.). All specimens of *Arthropterygius chrisorum* have basisphenoid that is mediolaterally wider anteriorly than posteriorly. Indeed, the juvenile CCMGE 3-16/13328 has narrower anterior profile when compared with those of adults CCMGE 17-44/13328 and CMN 40608 (Fig. 20), supporting the observation of Kear & Zammit (2014); still the anterior region of the basisphenoid of juvenile CCMGE 3-16/13328 is wider than the posterior region (Fig. 20A). In contrast, the posterior region of the basisphenoid of KSU 982/P-213 is wider than the anterior region (Fig. 20E); although CCMGE 3-16/13328 and KSU 982/P-213 represent close ontogenetic stages (basisphenoid and quadrate of KSU 982/P-213 are slightly smaller, whereas coracoid is bigger than those of CCMGE 3-16/13328). Another marked difference of CCMGE 3-16/13328 and KSU 982/P-213 is the shape of the condyle of their quadrates. Whereas CCMGE 3-16/13328, CCMGE 17-44/13328 and PMO 222.669, regardless differences in size, have similar shape of the condyle, KSU 982/P-213 differs in having less dorsoventrally high condyle with gradually curving (not V-shaped) ventral margin. This allows suggesting that the shape of the quadrate could also be regarded as interspecifically and ontogenetically stable feature. Thereby we conclude that at the current state of knowledge, *A. volgensis* should be regarded as a distinct valid species of *Arthropterygius* rather than a synonym of other known species of the genus or a nomen dubium.

Commented [A51]: I would not use this as an argument – again I have issues with your ontogenetic series proposition on fragmentary specimens. In addition, you are referring this specimen to a different species than your preposed ontogenetic series.

Commented [A52]: This I would argue is a subjective observation

Measurements. See Kasansky (1903) and Table S4 in Zverkov & Prilepskaya, documents.

Phylogenetic analysis

Method. For the phylogenetic analysis, we used recent matrix focused on ophthalmosaurids, presented by Zverkov & Efimov (in press). One unit, ‘*Keilhauia nui*’, was removed, and other two, *Arthropterygius volgensis* and *A. chrisorum* PMO 222.669 were added to the dataset. The scores for species of *Arthropterygius* were extended and partially changed based on new data (see supplemental materials for details). Six new characters related to the morphology of the supratemporal, parietal, quadrate, coracoid and humerus were added to the dataset (for details see Tab. S10 in Zverkov & Prilepskaya, documents). The new characters were coded from the literature for taxa that we have not personally examined (Tab. S11 in Zverkov & Prilepskaya, documents; Gilmore, 1905; Broili, 1907; Andrews, 1910; Fraas, 1913; Sollas, 1916; Romer, 1968; McGowan, 1972, 1973a; Johnson, 1979; Kirton, 1983; Wade, 1984, 1990; Godefroit, 1993; Fernández, 1994, 1997, 1999, 2007a; Bardet & Fernández, 2000; Maisch & Matzke, 2000; McGowan & Motani, 2003; Kear, 2005; Motani, 2005; Maxwell & Caldwell, 2006; Druckenmiller & Maxwell, 2010; Kolb & Sander, 2009; Zammit, Norris & Kear, 2010; Fischer *et al.*, 2011, 2012, 2014a,b; Maxwell, Fernandez & Schoch, 2012; Fernández & Talevi, 2014; Marek *et al*., 2015; Paparella *et al*., 2017). The analysis was performed using TNT 1.5 (Goloboff *et al*., 2016), applying traditional search with 10000 replicates and tree bisection and reconnection (TBR) with 100 trees saved per replication. The RAM allocation was extended to 1024 megabytes (`mxram 1024`) and the memory to 10 000 trees (`hold 10000`). Decay indices (Bremer support, ‘suboptimal’ = 5) and resampling methods to estimate the robustness of nodes (standard bootstrapping and jackknifing, 1000 iterations) were also computed in TNT 1.5.

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In order to eliminate problematic ‘wildcard’ taxa, we used an *a posteriori* approach of Pol & Escapa (2009) that is directly implemented in TNT 1.5 (`pcrprune`). The two taxa (*Athabascasaurus bitumineus* Druckenmiller & Maxwell, 2010 and *Platypterygius platydactulus* Broili, 1907) were identified as unstable and pruned from the second analysis. The pruned dataset was analysed using the exact same procedures as was used for the full dataset.

Results

Our analysis of the full dataset recovered ten most parsimonious trees of 310 steps with the consistency index (CI) = 0.416 and retention index (RI) = 0.662. The strict consensus (length of 321 steps; CI = 0.402; RI = 0.642) is relatively well resolved, however, supports for relationships within Ophthalmosauridae are still low (Fig. 19A). Despite the modifications of the original matrix, the recovered topology is nearly identical to that of Zverkov & Efimov (in press), except for minute changes in relations of derived-most platypterygiines that are even more badly resolved. A clade that includes species of *Arthropterygius* (‘A’ in Figure 18) is recovered as the sister group to Platypterygiinae (Fig. 19A). Sister relations of *Arthropterygius* and platypterygiines are supported by two synapomorphies: ‘T’-shaped prootic osseous labyrinth (49.0→49.1) and absence of the obturator foramen in the ischiopubis (98.1→98.2).

Only two most parsimonious trees (length of 300 steps, CI = 430, RI = 662) were recovered by the pruned analysis. In the strict consensus tree (length of 302 steps, CI = 425, RI = 656; Fig. 19B), Platypterygiinae is relatively better resolved. Surprisingly, *Caypullisaurus* is found as a sister, not to *Grendelius*, but to *Leninia* (based on two non-unique synapomorphies: presence of prefrontal dorsomedial expansion (16.0→16.1), and squared sqamosal (34.1→34.0). However, the relations of derived platypterygiines is not a focus of the current paper. Of our special interest is that *Arthropterygius* clade is recovered as a sister group to ophthalmosaurines, these two from a clade with low support, but sharing three synapomorphies (presence of the lateral ‘wing’ of the nasal (14.0→14.1); absence of supratemporal-postorbital contact (27.1→27.0); and circular shape of the basioccipital condyle (43.1→43.0).

Commented [A54]: As in previous analyses?

The *Arthropterygius* clade is supported by nine unambiguous synapomorphies: posterior position of the foramen for internal carotid arteries (unique, 40.1→40.2); dorsally facing basioccipital facet of the basisphenoid (non-unique, 41.0→41.1); raised opisthotic facet of the basioccipital (non-unique, 46.0→46.1); anteriorly shifted stapedial and opisthotic facets of the basioccipital (unique, 47.0→47.1); gracile stapedial shaft (non-unique, 52.0→52.1); robust clavicles (unique, 78.0→78.1), ulnar facet/radial facet ratio less than 0,83 (unique, 84.0→84.1); weak quadrate condyle (non-unique, 110.0→110.1); angle between the articulated coracoids less than 110 degrees (unique, 111.0/1→111.2).

In both the full and pruned analyses the *Arthropterygius* clade has very high Bremer support values (4 and 5), Bootstrap and Jackknife (more than 80), thus being the most well-supported clade in our analyses (Fig. 19). The result is of high importance for our taxonomic decision, as it leaves no substantial reasons to consider taxa within the *Arthropterygius* clade as representatives of separate genera.

Commented [A55]: I would not call this high – more moderate

Multivariate analysis of ophthalmosaurid humeral morphology

Commented [A56]: This needs to be mentioned more in the text and intro. Maybe include in a methods section?

One of the most peculiar skeletal elements of *Arthropterygius* is its humerus that bears a number of diagnostic features and could be easily recognized among humeri of other ophthalmosaurids. In order to highlight this, we provide the following principal component analysis (PCA) of ophthalmosaurid humeral morphology.

Commented [A57]: I think if you are going to include this analysis it needs to be made clear why you are doing it. What is your hypothesis you are testing?

Method. To compare humeri of ophthalmosaurids we gathered a series of metrics and ratios that collectively summarize morphology of the humerus (Tabs S6, S7 in Zverkov & Prilepskaya, documents). The metrics are: proximodistal length of the humerus, anteroposterior width of humeral proximal and distal ends, thickness of humeral proximal end; dorsoventral width of humeral distal end; anteroposterior width at midshaft, anteroposterior and dorsoventral width of the distal facets, and the angle between the ulnar and radial facets (for details see Fig. S1 in Zverkov & Prilepskaya, documents). Based on the metrics the following ratios were calculated (Tab. S7 in Zverkov & Prilepskaya, documents):

(1) Humeral proximal expansion: anteroposterior width of humeral proximal end divided by the humeral proximodistal length.
(2) Humeral distal expansion: anteroposterior width of humeral distal end divided by the humeral proximodistal length.
(3) Humeral stoutness: humeral minimal anteroposterior width at diaphysis divided by the humeral proximodistal length.
(4) Humeral proximodistal proportionality: anteroposterior width of humeral proximal end divided by the same measurement of its distal end. The character based on this ratio is used in current phylogenetic analyses and distinguish ophthalmosaurids, which commonly have

nearly equal proximal and distal humeral ends or proximal end slightly wider than the distal end see e.g. Fischer *et al*. (2011: Character 32).

(5) Isometry of the humeral proximal end (or ‘anteroposterior elongation’ of the humeral proximal end): anteroposterior width of humeral proximal end divided by the thickness of humeral proximal end (see Fig. S1 in Zverkov & Prilepskaya, documents). This ratio has extremely high value in ‘*Grendelius*’ *zhuravlevi* (2.587) for which strongly compressed humeral proximal end is considered as autapomorphic (Zverkov, Arkhangelsky & Stenshin, 2015); the standard values for ophthalmosaurids are 1.8–1.5; for taxa with ‘isometric’ humeral proximal end this value could be close to one (e. g. *Undorosaurus nessovi*, and *Platypterygius platydactylus* see Tab S7 in Zverkov & Prilepskaya, documents).

(6) Humeral distal compression: anteroposterior width of humeral distal end relative to the maximal dorsoventral width of humeral distal end.

(7) Relative anteroposterior width of facet for preaxial accessory epipodial element and radial facet.

(8) Relative anteroposterior width of ulnar and radial facets. As well as for ratio 4, there is a character based on similar ratios in current phylogenetic analyses, see e.g. Motani (1999: Character 52) and Moon (2017: Character 209). However, the referred character use ‘relative size’ of ulnar and radial facets, which is not always clear as ulnar facet could be longer than radial facet but the same time, less wide dorsoventrally (as in most specimens of *Arthropterygius*). In this regard, it is better to consider separately relative anteroposterior width of ulnar and radial facets and relative dorsoventral width of ulnar and radial facets.

(9) Relative dorsoventral width of ulnar and radial facets.

The dataset is resolved at the specimen level with left and right humeri considered separately in order to reveal the existing humeral asymmetry within an individual and to assess its possible effects on the results. Data (see Tabs S6, S7 in Zverkov & Prilepskaya, documents) were collected based on personal observations of NGZ and completed by measurements and in rare cases analysis of pictures of the following references: Broili, 1907; Nace, 1939; Wade, 1984; Delair, 1986; McGowan, 1972; Arkhangelsky, 1998; Kolb & Sander, 2009; Maxwell, 2010; Maxwell & Kear, 2010; Moon & Kirton, 2016. Only humeri with all documented ratios were considered, in rare cases, we completed our dataset by approximate ratios estimated based on oblique views (the case of *B. extremus* and *P. platydactylus*) or proportionally translated from other conspecific individuals (the case of *P. americanus*). The final dataset consisted of 39 humeri belonging to 29 individuals and ten variables (Tab. S8 in Zverkov &

Prilepskaya, documents). The ratios and angle between the ulnar and radial facets (in rad) were used as variables for the PCA. Data were scaled to equal variance by subtracting the mean value for each variable and then dividing each variable by the standard deviation. We then created a distance matrix with these data (Tab. S8 in Zverkov & Prilepskaya, documents). The dataset was analysed in PAST v. 3.20 (Hammer *et al.*, 2001).

Results

The first four axes describe over 81% of the total variance (33.8%, 20.7%, 16.8% and 10.5% respectively). All variables showed low loadings on PC1 (>-0.50; <0.50); among them better pronounced are humeral distal expansion (variable 2: 0.46), relative size of *faae* (variable 7: 0.41) and humeral stoutness (variable 3: 0.34), as well as relative dorsoventral width of ulnar and radial facets (variable 9: -0.39) and an angle between these facets (variable 10: -0.36). For the PC2 highest positive loadings are shown by variables 1 (0.59), 4 (0.50), 5 (0.47) and 3 (0.35) thereby PC2 characterise humeral proximal expansion, humeral proximodistal proportionality, humeral stoutness and isometry of the humeral proximal end. PC3 depicts humeral distal compression (variable 6: 0.53) and an angle between the ulnar and radial facets (10: 0.47) and in lesser degree proportions of the humeral proximal end (variable 5: 0.38) and proximodistal proportionality (variable 4: -0.31). PC4 is responsible for relative size and shape of humeral distal facets: relative anteroposterior width of ulnar and radial facets (8: 0.62); relative dorsoventral width of these facets (9: 0.35) and relative anteroposterior width of *faae* and the radial facet (7: -0.50). The distribution of variable loadings could be found in Tab. S9 (Zverkov & Prilepskaya, documents).

Considering low sampling for most of the taxa in our analysis, it is hard to say with confidence if the absence of marked morphospace overlap between ophthalmosaurid taxa is a true condition, or it is biased by the sampling. Whether or not, it is clear that some ophthalmosaurids are well separated, e.g. *Brachypterygius-Grendelius* cluster (low values on PC1 and high values on PC3) and *Arthropterygius* cluster (high values on PC1, low values on PC4) see Figure 22.

Our PCA (Fig. 22) demonstrate a relatively wide morphospace occupation for species of *Arthropterygius*, which is mostly due to *Arthropterygius hoybergeti*, having humeri that are morphologically closer to ‘standard’ ophthalmosaurid condition and thereby falling closer to other ophthalmosaurids, in particular, *Undorosaurus gorodischensis* and *Platypterygius* *hercynicus*. *A. lundi* is separated by positive values of the PC4 (Fig. 22C) and along with *A. chrisorum* demonstrate high values on PC1.

Species of *Undorosaurus* could also be potentially distinguished based on humeral morphology (Fig. 22A, D). *Undorosaurus gorodischensis* morphospace is separated from other species of *Undorosaurus* by the second principal component axis, as *U. nessovi* and *U. trautscholdi* demonstrate high negative values on PC2. In general morphology, *U. gorodischensis* have anteroposteriorly elongated humeral proximal end, that is of roughly oval outline, whereas *U. nessovi* and *U. trautscholdi* are characterized by a nearly circular outline of the humeral proximal end, which is depicted by PC2 partially responsible for humeral proximal expansion.

Several derived Cretaceous platypterygiines, added to our analysis, occupy different parts of the morphospace also demonstrating the potential of humeral morphology for distinguishing Cretaceous ichthyosaurs.

The interesting result of our analysis is that in some ophthtalmosaurid individuals left and right humeri can fall wider to each other than to humeri of other specimens of the species and even to other species and genera, indicating the presence of a pronounced humeral asymmetry in ophthalmosaurids. The most outstanding specimen with humeral asymmetry in our analysis is *Platypterygius hercynicus*. The asymmetry could only partially be explained by artefacts of preservation and/or pathologies, but, considering its presence in practically all the specimens with both humeri preserved, it is likely a natural condition.

Commented [A58]: This supports my point that humeral characters should be used with caution! Basing species of humeral characteristics alone is not sufficient.

Discussion

Variation in humeral morphology interspecific or infraspecific?

As in case of *Undorosaurus* (Zverkov & Efimov, in press) and *Grendelius* (Zverkov, Arkhangelsky & Stenshin, 2015), species of *Arthropterygius* could be potentially distinguished based exclusively on humeral morphology, which was already demonstrated above. Especially valuable is the outline of the humeral proximal end – each of these genera has species with anteroposteriorly elongated humeral proximal ends (*Grendelius zhuravlevi*, *Undorosaurus gorodischensis*, *Arthropterygius chrisorum*) and those with isometric proximal ends (*G. alexeevi*, *U. nessovi*, *U. trautscholdi*, *A. lundi*). We cannot exclude the possibility that some of these species may actually represent males and females, thus demonstrating sexual dimorphism, differing in limb morphology in a way, similar to that hypothesized for Triassic ichthyopterygians *Chaohusaurus* and *Shastasaurus* (Shang & Li, 2013; Motani *et al.*, 2018). However, given other existing differences (especially cranial) between the discussed species, and considering that in some genera more than one species with either elongated or isometric humeral proximal end could be present, it is impossible to say, which of the species are representing sexual morphs of the same species and which of them are morphs of other species. Thereby, in the current state of knowledge, we prefer to retain all the ‘morphs’ as separate species.

Commented [A59]: Again with the humeral morphology, it is great to use as a supporting character, but skull morphology is why more reliable.

Commented [A60]: Fair enough – but I would still refrain from referring volgaensis to a separate species.

Palaeobiogeographic implication of *Arthropterygus*

Commented [A61]: This has been talked about significantly in your previous work. Refer to it and then add what adds to our knowledge of the palaeobiogeography based on this work. This will also help cut down the length of the paper by a page or so.

After the discovery of *Arthropterygius* in Argentina (Fernández & Maxwell, 2012), this taxon, even being known from a couple of specimens, has already raised a question regarding the cosmopolitan distribution of ichthyosaurs (Fernández & Maxwell, 2012; Zverkov *et al.*, 2015). New discoveries further support the idea that most of ophthalmosaurids have had a widespread distribution.

For the analysis of dispersal routes of Late Jurassic ichthyosaurs the data on connections between the basins is of principal importance. According to palaeogeographic reconstructions, based primarily on invertebrates, the Middle Russian Sea and European basins were connected by the Brest (Pripyat) Strait until the beginning of the middle Volgian *Virgatites virgatus* Chron. This is determined by identical sequences of virgatitid ammonites in the Polish and Middle Russian seas (Fig. 23; Sasonova & Sasonov, 1967; Mesezhnikov & Zakharov, 1974; Rogov *et al.*, 2008; Rogov, 2012, 2013a). After the closure of the Brest Strait in the early *Virgatites virgatus* Chron, the Middle Russian Sea became isolated from the west and south until the beginning of the Cretaceous (Fig. 23; Sasonova & Sasonov, 1967; Baraboshkin, 1999, 2003). In the north, the Middle Russian Sea was connected with other Arctic basins via the Mezen-Pechora Strait (Sasonova & Sasonov, 1967). This connection was restricted during the middle part of the middle Volgian, but intense from the end of the middle Volgian, as ammonites of the *Virgatites virgatus* and contemporary *Dorsoplanites maximus* ammonite biozones are markedly different, whereas ammonite faunas of the *Epivirgatites nikitini* Ammonite Biozone and its correlatives are showing numerous common elements in

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the Arctic (Rogov, 2010; Kiselev & Rogov, 2018). Furthermore, during the Kimmeridgian and Volgian Arctic seas and seas of Northwestern Europe were connected by the Norwegian-Greenland Seaway (Mesezhnikov & Zakharov, 1974; Mutterlose *et al.,* 2003; Rogov, 2012). Judging from the data on the distribution of ammonites, immigration through the Norwegian-Greenland Seaway was limited in the Kimmeridgian (Rogov, 2012), but in the early Volgian the situation has changed significantly, and this time interval in the Panboreal Superrealm is characterized by nearly identical successions of Pectinatitinae ammonites from northern France to the Lena river basin in Siberia (Rogov & Zakharov, 2009). The similarity between ammonite faunas of the Anglo-Paris Basin with those of Arctic persisted in the early stages of the middle Volgian, but later a significant differentiation of ammonite communities began, and only for the late Volgian it is possible to identify the resumption of active faunal exchange between the NW Europe and the Middle Russian Sea, particularly noticeable at the end of the late Volgian (early Berriasian, *Volgidiscus lamplughi* Chron) (Rogov, 2013b, 2014; Kiselev *et al*., 2018).

For the Kimmeridgian – early middle Volgian (early Tithonian with its bipartite division) time interval we can observe a high similarity of ichthyosaurs of the Middle Russian Sea and seas of Northwestern Europe: both these basins are inhabited by small-sized ichthyosaurs of *Nannopterygius* clade and moderate to large representatives of the genus *Grendelius* (Fig. 23). Currently, these ichthyosaurs are not found elsewhere in contemporaneous deposits. Furthermore, for this time bin there are rare but widespread finds of *Ophthalmosaurus* in England, France, Russia, Mexico and ?Argentina (Bardet et al., 1997; Etches & Clarke, 1999; Buchy & López Oliva, 2009; Fernández & Maxwell, 2012; Moon & Kirton, 2016; Arkhangelsky *et al*., 2018).

Arthropterygius seem to be very common ichthyosaurs for this time bin: *Arthropterygius chrisorum* is found in Arctic Canada, Svalbard and Volga Region, thus indicating a wide distribution of this species across the Arctic basins and Middle Russian Sea. The same concerns *Arthropterygius hoybergeti* and *A. lundi*, which are both known from Svalbard and Volga Region. Additionally *A. lundi* is known from the Timan-Pechora, thus unambiguously demonstrating that the Mezen-Pechora Strait was used as a passage during this time interval. Discovery of *Arthropterygius* sp. in the Tithonian of Argentina indicate that representatives of the genus could distribute through the Arctic, and then to the South along the Paleopacific coast of the American continent to the Neuquen Basin (Fernández & Maxwell, 2012; Zverkov *et al*., 2015). Similar migration route was assumed for the Late Kimmeridgian ammonite

Zenostephanus (Rogov & Poulton, 2015). The Hispanic corridor connecting the Paleopacific and Tethys basins is less possible dispersal route for *Arthropterygius*, as among numerous ichthyosaur specimens from the Kimmeridgian and Tithonian of Western Europe (e.g. in Kimmeridge Clay and Solnhofen formations) there are still no diagnostic remains of *Arthropterygius*. In this regard, the Brest Strait and the Norwegian-Greenland Seaway are also unlikely were used as dispersal passages by *Arthropterygius* spp. However, a discovery of *Arthropterygius* in Western Europe could challenge this hypothesis.

After the closure of the Brest Strait *Grendelius* disappeared in the Middle Russian Sea, probably replaced by similar in size and apparently occupying the same ecological niche *Undorosaurus*. At the same time, representatives of *Nannopterygius* clade remained abundant in the Middle Russian Sea, and considering recent discoveries existed also at Svalbard (Fig. 23; Delsett *et al*., 2018: 35). It has recently been demonstrated that *Undorosaurus* first appeared in the Polish Sea in the early Middle Volgian and likely distributed to the Middle Russian Sea using the Brest Strait. After the closure of the Brest Strait in the *Virgatites virgatus* Chron *Undorosaurus* dispersed in the Middle Russian Sea and produced several species (see Zverkov & Efimov, in press). During the *Virgatites virgatus*–*Epivirgatites nikitini* chrons, *Undorosaurus gorodishensis* reached high latitudes of Svalbard, unambiguously demonstrating the exchange of herpetofauna between the Middle Russian Sea and Arctic basins.

Arthropterygius are currently unknown in the Middle Russian Sea from the *Virgatites virgatus* Chron, but they still existed at high latitudes during the late Volgian and Ryazanian (latest Tithonian and Berriassian), thus being among the few ichthyosaur taxa that are recognized in the Berriassian.

To conclude our palaeobiogeographic observations: for the Kimmeridgian – early Middle Volgian time bin we recognize three ichthyosaur taxa that unite the Middle Russian Sea and basins of Western Europe *(Ophthalmosaurus icenicus*, representatives of *Grendelius*, and *Nannopterygius* clade). At the same time, these ichthyosaurs are not yet found in the Arctic, except for possible *Nannopterygius* clade ichthyosaur PMO 222.658 recently reported from Svalbard by Delsett *et al.* (2018: 35). At the same time, three species of *Arthropterygius* demonstrate close relations of the Middle Russian Sea and Arctic basins. From the Middle Volgian *Virgatitus virgatus* Chron the unifying element of the Middle Russian Sea and Arctic basins is *Undorosaurus gorodischensis*, while *Arthropterygius chrisorum* occurs only at high latitudes. Interestingly, no ichthyosaur genera are yet to be found in all the three basins, giving reason to suggest the existence of concurrence between Late Jurassic ophthalmosaurids resulting in limitation of their aerials.

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Significance of the new finds and further perspectives in the study of ophthalmosaurids

The Beriassian fossil record of marine tetrapods is scarce and patterns of faunal turnover during the Jurassic–Cretaceous transitional interval are non-uniform (e.g. Benson *et al*., 2010; 2013; Benson & Druckenmiller, 2014; Tennant *et al.*, 2017; Zverkov *et al*., 2018). It has already been suggested that ichthyosaurs survived the Jurassic–Cretaceous transition relatively unscathed (Fischer *et al*., 2012, 2013). However, Berriassian ichthyosaur record is still poor (Fernández & Aguirre-Urreta, 2005; Fernández, 2007a; Ensom *et al*., 2009; Fischer *et al*., 2012; Green & Lomax, 2014; Delsett *et al.*, 2017). As was demonstrated above '*Keilhauia nui*' from the Berriassian of Svalbard is a *nomen dubium*, thus only one Berriassian ichthyosaur, *Caypullisaurus bonapartei* from the Neuquen Basin of Argentina, could hitherto have been recognized at the species level (Fernández, 2007a), demonstrating that this Tithonian species sucsessfully crossed the Jurassic–Cretaceous boundary. In this regard, discovery of *Arthropterygius chrisorum* in the Berriassian of Franz Joseph Land provides the second ophthalmosaurid species that unambiguously crossed the Jurassic–Cretaceous boundary, further argument that this transition had minimal (if some) effect on ichthyosaurs.

Commented [A63]: But you referred it to Arthropterygius?

A discrete character of the fossil record of ophthalmosaurids (see e.g. Cleary *et al*., 2015) has led to certain problems in the study of this group. The only more or less thoroughly investigated ophthalmosaurids to date are Callovian *Ophthalmosaurus icenicus* (Andrews, 1910; Appleby, 1956; Kirton, 1983; Moon & Kirton, 2016) and Albian *Platypterygius australus* (Wade, 1984, 1991; Kear, 2005; Zammit, Norris & Kear, 2010; Kear & Zammit, 2014). Other ophthalmosaurids are incomparably poorly known either due to a small sample size or because of fragmented and/or poor preservation. In such conditions, it is hardly possible to develop a strong phylogenetic hypothesis for ophthalmosaurids. The continuing replenishment of the ophthalmosaurid taxon list by new poorly known and difficult to compare (but having withal a number of autapomorphies) taxa do not make this task easier. The fair attempt to consider all the known ophthalmosaurid taxa and all the proposed phylogenetic characters results in the extremely poorly resolved Ophthalmosauridae (Moon 2017).

Recently Massare & Lomax (2018) demonstrated the effect of large sample sizes on the identification of taxonomically distinct morphological characters in *Ichthyosaurus*. This is what is actually needed for ophthalmosaurids: to have larger sample sizes for as many taxa as possible. In this regard, Late Jurassic to Early Cretaceous formations of Arctic, considering the abundance and exceptional preservation of marine reptiles (Delsett *et al*., 2016; NGZ pers. obs.), have great perspectives for collection of a large sample size, comparable to those of the Lias Group and Posidonia Shale lagerstaetten of Western Europe.

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Temporary links for review process:

Appendix 1 - https://figshare.com/s/86060e131038fe382ed6

Character-taxon matrix - https://figshare.com/s/3cccf2a076d5a68e9127

Appendix 3 Skeletal elements of juvenile *Arthropterygius chrisorum* CCMGE 3-16/13328 - https://figshare.com/s/9deb1ae8565441499385

Appendix 4 Skeletal elements of young adult *Arthropterygius chrisorum* CCMGE 17-44/13328 – https://figshare.com/s/18191adbeef7d2ffa2d7