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Simbirskiasaurus and *Pervushovisaurus* reassessed: implications for the taxonomy and cranial osteology of Cretaceous platypterygiine ichthyosaurs

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The ichthyosaur fossil record is interspersed by several hiatuses, notably during the Cretaceous. This hampers our understanding of the evolution and extinction of this group of marine reptiles during the last 50 million years of its history. Several Cretaceous ichthyosaur taxa named in the past have subsequently been dismissed and referred to the highly inclusive taxon *Platypterygius*, a trend that has created the impression of low Cretaceous ichthyosaur diversity. Here, we describe the cranial osteology, reassess the stratigraphic age, and evaluate the taxonomy and phylogenetic relationships of two Cretaceous ichthyosaurs from western Russia: *Simbirskiasaurus birjukovi* from the early Barremian and *Pervushovisaurus bannovkensis* from the middle Cenomanian, both formerly regarded as nomina dubia, and allocated to *Platypterygius* sp. and *Platypterygius campylodon*, respectively. We show that *Simbirskiasaurus birjukovi* and *Pervushovisaurus bannovkensis* are valid platypterygiine ophthalmosaurids, notably characterized by a peculiar narial aperture. The cranial anatomy and phylogenetic relationships of these taxa illuminate the evolution of narial aperture anatomy in Cretaceous ichthyosaurs, clarify the phylogenetic relationships among platypterygiines, and provide further arguments for a thorough revision of *Platypterygius*.

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ADDITIONAL KEYWORDS: Barremian – Cenomanian – external naris – platypterygiinae – *Platypterygius*.

INTRODUCTION

The extensive stratigraphic range of ichthyosaurs, extending from the Lower Triassic to the beginning of the Upper Cretaceous (Bardet, 1992; Motani, 2005), is interrupted by numerous hiatuses, most notably during the Middle Jurassic (e.g. Fernández & Talevi, 2014) and the Cretaceous (e.g. Bardet, 1994; Fischer *et al*., 2011a); however, the taxonomic diversity of Cretaceous ichthyosaurs has recently increased, with the recognition of several new taxa in the Albian of North America (Maxwell & Caldwell, 2006b, 2006a; Druckenmiller & Maxwell, 2010; Maxwell & Druckenmiller, 2011) and the Early Cretaceous of Eurasia and the Middle East (Fischer *et al*., 2011b, 2012, 2013, 2014a). Our knowledge of Cretaceous

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ichthyosaur diversity is still poor (Zammit, 2012), however, especially outside the better-known intervals of the latest Jurassic–earliest Cretaceous ('Volgian'; e.g. Fernández, 1997; Arkhangelsky, 1998a; Efimov, 1999; Fernández, 2007b; Druckenmiller *et al*., 2012) and the late Early Cretaceous (Albian; e.g. Maxwell & Caldwell, 2006a; Maxwell & Caldwell, 2006b; Fischer *et al*., 2014b). As a result, their final extinction, which occurred at the end of the Cenomanian (Bardet, 1992), is poorly understood (Fischer *et al*., 2014b).

Several taxa have been named from the Hauterivian–Barremian and Cenomanian strata of Europe, Russia, and South America; most were, however, regarded as nomina dubia or subjective junior synonyms referable to the cosmopolitan genus *Platypterygius* Huene, 1922 in the reviews of McGowan (1972), Maisch & Matzke (2000), and McGowan & Motani (2003; but for an account on *Platypterygius hauthali* Huene, 1927, see Fernández & Aguirre-Urreta 2005). Similarly, most of the Cenomanian material from Eurasia has been referred to *Platypterygius campylodon* Carter, 1846, by default (e.g. McGowan, 1972; Buffetaut, 1977). This taxonomic decision implies low ichthyosaur diversity during this part of the Cretaceous (but see Bardet, 1989). Note that the status of *Platypterygius* is subject to debate: Fischer (2012) demonstrated that this genus, which – as presently conceived – spans more than 35 million years, and is known from nearly all continents (McGowan & Motani, 2003), is a wastebasket taxon. Kear & Zammit (2014), however, proposed 'classic' diagnostic features for this entity (all of which are present in other ophthalmosaurid taxa; Fischer *et al*., 2011b; Fischer, 2012). A solid taxonomic background is therefore needed to better understand how ichthyosaurs diversified and became extinct during the Cretaceous. Notably, the status and morphology of the taxa that have been referred to *Platypterygius* in the past must be thoroughly reassessed under a modern taxonomic framework. Material from North America (Maxwell & Caldwell, 2006a; Maxwell & Kear, 2010; Adams & Fiorillo, 2011), South America (Fernández & Aguirre-Urreta, 2005), and Australia (Kear, 2005; Zammit, Norris & Kear, 2010; Zammit, 2011) attributed to *Platypterygius* has recently been re-assessed, but the Eurasian material, which constitutes the most diverse and taxonomically complex assemblage (e.g. McGowan, 1972), needs to be thoroughly revised (Fischer, 2012).

In this article, we describe the cranial osteology, reassess the taxonomy and stratigraphic age, and test the phylogenetic relationships of two Cretaceous ichthyosaurs from two poorly sampled intervals: the early Barremian *Simbirskiasaurus birjukovi* Ochev & Efimov, 1985 and the middle Cenomanian *Pervushovisaurus bannovkensis* Arkhangelsky, 1998b. These taxa are frequently used for comparative purposes when Cretaceous taxa are discussed (e.g. Sirotti & Papazzoni, 2002; Druckenmiller & Maxwell, 2010; Fischer, 2012), despite their poorly known and controversial osteology (Maisch & Matzke, 2000) and taxonomy (McGowan & Motani, 2003). As explained here, these taxa clarify the evolution of the narial aperture and the phylogenetic relationships of derived platypterygiine ichthyosaurs, provide valuable data points in inadequately known periods of ichthyosaur evolution, and add further support for the view that *Platypterygius* hides a mostly unappreciated diversity of Cretaceous ophthalmosaurids.

MATERIAL AND METHODS

Institutional abbreviations

CAMSM, Sedgwick Museum of Earth Sciences, Cambridge University, Cambridge, UK; IRSNB, Royal Belgian Institute of Natural Sciences, Brussels, Belgium; NHMUK, Natural History Museum, London, UK; RGHP, Réserve naturelle géologique de Haute-Provence, Digne-les-bains, France; SSU, Geological Museum, Saratov State University, Saratov, Russia; YKM, Ulyanovskia Oblastnoi Kraevedcheskia Museim I.A. Goncharova (Ulyanovsk Regional Museum of Local Lore named after I.A. Goncharov), Ulyanovsk, Ulyanovsk Region, Russia.

Geography, stratigraphy, and research history

Ulyanovsk area

The Ulyanovsk area has yielded two important Barremian ichthyosaur remains: YKM 65119, the holotype of *Simbirskiasaurus birjukovi*, and IRSNB R269, the holotype of *Sveltonectes insolitus* Fischer *et al*., 2011b. Few papers on the stratigraphy of this region are available; therefore, both specimens have been re-dated using *in situ* fossils. The holotype specimen of *Sveltonectes insolitus* has been dated using palynomorphs and is late Barremian in age (Fischer *et al*., 2011b). Ochev & Efimov (1985) considered that the preservation style of the bones and presence of the bivalve *Astarte porrecta* (most likely to be *Astarte* sp.) with YKM 65119 (the holotype of *Simbirskiasaurus birjukovi*) were indicative of a Hauterivian age. Although this evidence is scant, it was the only stratigraphic data available at the time; however, microconchs of the ammonite *Aconeceras* sp. were found within the skull during further preparation (I.A. Shumilkin, pers. comm., 2012). Blagoveschensky & Shumilkin (2004) described the Barremian section in the northern part of Ulyanovsk and determined that *Aconeceras* sp. occurs in the *Praeoxyteuthis pugio* Stolley, 1925 belemnite zone, which is early Barremian in age (Baraboshkin & Mutterlose, 2004). Accordingly, *Simbirskiasaurus birjukovi* should be regarded as originating from lower Barremian strata.

Although their age is now constrained, the precise place where both holotypes were discovered is unclear because the Hauterivian and Barremian strata of this area are tabular, and crop out along a stretch of the Volga River bank that extends over several kilometres. Ochev & Efimov (1985: 87) stated that the holotype of *Simbirskiasaurus birjukovi*: 'was discovered several years ago on the right bank of the Volga River, 25 km above the town of Ulyanovsk, between the Zakhar'yevskoye mine and the children's sanatorium', but this is unlikely as no Barremian strata are found in this area (I.V. Blagoveschensky, pers. comm., May 2013). Blagoveschensky & Shumilkin (2004) described a nearby Barremian section, between Ulyanovsk and Polivno, with abundant *Aconeceras* specimens, hence providing a possible source locality for YKM 65119. This corroborates the account of an eyewitness of the discovery (S.E. Biryukov, pers. comm., May 2013).

The taxonomic status of *Simbirskiasaurus birjukovi* has been debated. It was erected by Ochev & Efimov (1985); however, these authors described the skull before adequate preparation had been completed, and comparison of their drawings with the fossil in its current state indicates that both the narial and orbital regions were still covered by matrix when they described it. As a consequence, they interpreted artefacts as diagnostic features. They also noted the presence of basicranial bones without describing them. Maisch & Matzke (2000) considered *Simbirskiasaurus* a junior subjective synonym of *Platypterygius*, but regarded the species *Simbirskiasaurus birjukovi* as a valid taxon. McGowan & Motani (2003) went further and proposed that the holotype was not diagnostic, and hence referred YKM 65119 to *Platypterygius* sp.

Saratov area

The holotype of *Pervushovisaurus bannovkensis* (SSU 104a/24) was found near Nizhnaya Bannovka village, Krasnoarmeisk District, Saratov Region, along the right bank of the Volga River (Arkhangelsky, 1998b). The specimen was discovered in shales of the local *Lingulogavelenella globosa* Brotzen, 1945 zone, which constitutes the upper part of the middle Cenomanian of the Melovatskaya Formation, according to Zozyrev (2006). The specimen was studied by Arkhangelsky (1998b), who made it the type specimen of both a new subgenus and species within the genus *Platypterygius*: *Platypterygius* (*Pervushovisaurus*) *bannovkensis*. McGowan & Motani (2003) considered these taxa invalid: they regarded *Pervushovisaurus* as a subjective junior synonym of *Platypterygius*, and treated *Platypterygius bannovkensis* as a nomen dubium, with its material referrable to *Platypterygius campylodon*. As for *Simbirskiasaurus birjukovi*, these taxonomic opinions were not substantiated by direct observations of the material.

Phylogenetic analysis

We coded *Simbirskiasaurus birjukovi* and *Pervushovisaurus bannovkensis* in the largest data set devoted to ophthalmosaurids yet compiled (the data set from Fischer *et al*., 2014a, which is a slightly updated version of that of Fischer *et al*., 2012), using the morphological data from our reassessment alone, not the initial descriptions (except for character 23: posterior dorsal/anterior caudal centra of *Simbirskiasaurus birjukovi*, coded using Ochev & Efimov, 1985; see Appendix S1). The resulting matrix contains 52 characters and 20 taxa. Only 23.07% (12/52) and 13.46% (7/52) of the characters can be coded for *Simbirskiasaurus birjukovi* and *Pervushovisaurus bannovkensis*, respectively, because of missing material in their postcranial skeletons. We modified one character (character 6: descending process of the nasal on the dorsal border of the nares) to reflect our new observations on the external nares of some derived platypterygiine ophthalmosaurids; we added a new state (6.2) for ichthyosaurs having a complete division of the external naris, regardless of the reduction of its anterior part (see Appendix S1). As in Fischer *et al*.'s (2012; 2014a) original analyses, some characters were treated as ordered (characters 17, 39, and 45). Running the analyses with all characters unordered did not modify the topology or length of the consensus trees; it slightly improved the statistical support of the topology arising from the analysis of the full data set, but slightly decreased the statistical support of the topology arising from the analysis of the pruned data set (see below). We used the exact parsimony searches of TNT 1.1 (Goloboff, Farris & Nixon, 2010) to analyse the character matrix (exact algorithm, 10 000 trees in memory) and calculate the Bremer support, Jacknife (removal probability of 36, with 1000 replications), and bootstrap (standard, 1000 replications) values.

As this data set incorporates numerous taxa known from fragmentary remains (eight taxa out of 20 have more than 50% missing data), the statistical support for the topology is moderate to low (see Results, below). We therefore ran a second analysis where all taxa with more than 50% of data missing were excluded, with the exception of *Simbirskiasaurus birjukovi* and *Pervushovisaurus bannovkensis*. The following taxa were therefore excluded in the second analysis: *Stenopterygius cayi* (Fernández, 1994), *Arthropterygius chrisorum* (Russell, 1993), *Mollesaurus periallus* Fernández, 1999, *Maiaspondylus lindoei* Maxwell & Caldwell, 2006b, *Athabascasaurus bitumineus* Druckenmiller & Maxwell, 2010, and *Leninia stellans* Fischer *et al*., 2014a. The resulting matrix contains 52 characters and 14 taxa. The data set and the analytical procedure are otherwise identical to the first analysis. We optimized the phylogenetic trees using WINCLADA 0.9 (Nixon, 1999;

detailed character state distribution in all optimizations are available in Figs S1–S6).

SYSTEMATIC PALAEONTOLOGY

ICHTHYOSAURIA BLAINVILLE, 1835

OPHTHALMOSAURIDAE BAUR, 1887

PLATYPTERYGIINAE ARKHANGELSKY, 2001 (*SENSU* FISCHER *ET AL.*, 2012)

SIMBIRSKIASAURUS OCHEV & EFIMOV, 1985

Diagnosis and occurrence

As for the type and only species, *S. birjukovi*.

SIMBIRSKIASAURUS BIRJUKOVI OCHEV & EFIMOV, 1985

Simbirskiasaurus birjukovi Ochev & Efimov, 1985: 88–91, figs 1, 2 (original description).

Platypterygius birjukovi Maisch & Matzke, 2000: 82 (new combination).

Platypterygius sp. McGowan & Motani, 2003: 119.

Holotype

YKM 65119, a partial skull preserved in three dimensions. Storrs, Arkhangelsky & Efimov (2000: table 11.2) incorrectly cited 'SGU 104a/22' as the holotype specimen.

Emended diagnosis

Platypterygiine ophthalmosaurid characterized by the following autapomorphies: external naris divided by a nasomaxillary pillar; posterior opening of the narial complex with anteroposteriorly constricted dorsal extension; deeply interdigitating prefrontal–lacrimal suture [reminiscent of the basal neoichthyosaurian *Temnodontosaurus platyodon* (Conybeare, 1822); see Godefroit, 1993].

Simbirskiasaurus birjukovi is also characterized by the following unique combination of features: subnarial process of the premaxilla reaches the posterior margin of the external naris (shared with *Cryopterygius kristiansenae* Druckenmiller *et al.*, 2012); elongated anterior process of the maxilla, reaching anteriorly the level of the nasal [unlike in *Aegirosaurus leptospondylus* Bardet & Fernández, 2000 and *Sveltonectes insolitus* (Fischer *et al.*, 2011b)]; presence of a supranarial process of the premaxilla [shared with *Platypterygius australis* (McCoy, 1867), see Kear, 2005, and possibly *Pervushovisaurus bannovkensis* (Arkhangelsky, 1998b)].

Occurrence

Praeoxyteuthis pugio zone, Lower Barremian, Lower Cretaceous of the Ulyanovsk area, probably on the right bank of the Volga River, in between the north of Ulyanovsk and Polivno (see Material and methods, above), Ulyanovsk Region, Russia.

DESCRIPTION

Premaxilla

The fossa praemaxillaris is deep and narrow anteriorly (Fig. 1), becoming wider and shallower at the level of the emergence of the nasals. The premaxilla has a slight overhang dorsal to the fossa praemaxillaris. The labial wall of the dental groove is markedly thickened. The premaxilla decreases in height continuously after the emergence of the nasals, but a processus supranarialis is present, as it also is in *Platypterygius americanus* (Nace, 1939), *Ophthalmosaurus icenicus* Seeley, 1874, *Brachypterygius extremus* (Boulenger, 1904), *Aegirosaurus leptospondylus*, *Platypterygius australis*, and *Caypullisaurus bonapartei* Fernández, 1997 (see Romer, 1968; Kirton, 1983; Bardet & Fernández, 2000; Kear, 2005; Fernández, 2007b, respectively). The premaxilla forms the anterior and ventral edges of the anterior opening of the narial complex. Posteroventrally, the premaxilla forms an elongated subnarial process covering the maxilla and lacrimal; the posterior end of this process is broken off, but a well-delineated facet textured by ridges and furrows is present on the lacrimal and the maxilla, indicating the subnarial process reached the posterior margin of the external naris, as it does in *Cryopterygius kristiansenae* (see Druckenmiller *et al.*, 2012).

Maxilla

The maxilla has an elongated anterior process, as in many platypterygiines [Fig. 1; e.g. *Platypterygius americanus*, *Brachypterygius extremus*, and *Platypterygius hercynicus* (Kuhn, 1946); see Kuhn, 1946; Romer, 1968; Kirton, 1983; Fischer, 2012], and is peculiar in having a developed narial lamella forming a broad nasomaxillary pillar that divides the external naris in anterior and posterior openings (Fig. 2). The posterior opening of the narial complex has a slightly undulated ventral margin. There is no evidence for a posterior ascending process, such as that seen in *Athabascasaurus bitumineus* (see Druckenmiller & Maxwell, 2010), although this may be overlapped by the lacrimal.

Nasal

The nasal forms the dorsal edge of the naris and participates in the nasomaxillary pillar, although the relative contributions of the nasal and the maxilla to this pillar are uncertain (Fig. 1). The dorsal edge of the anterior opening of the narial complex is gently concave, whereas the dorsal surface of the posterior opening of the narial complex forms a deep ventral notch on the

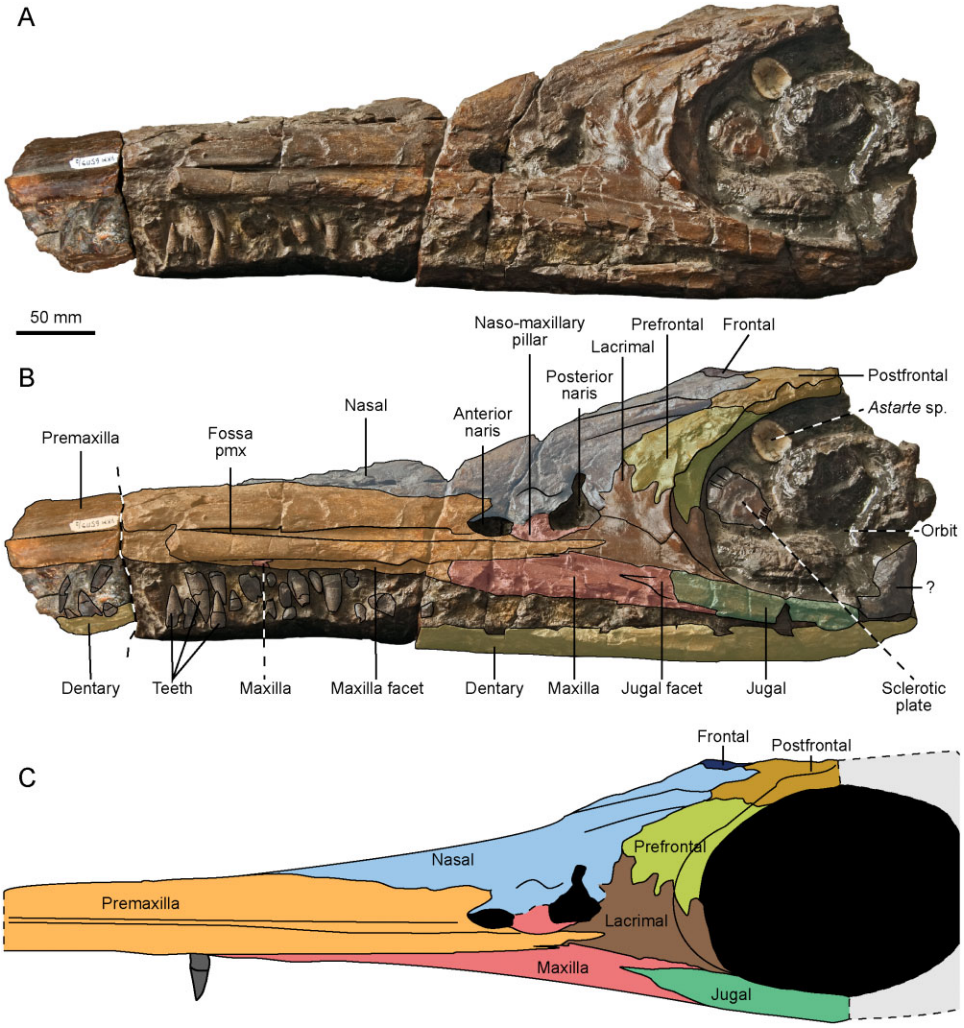

Figure 1. *Simbirskiasaurus birjukovi* Ochev and Efimov, 1985, holotype (YKM 65119) in lateral view: A, photograph; B, interpretation; C, reconstruction of the cranium.

lateral surface of the nasal, giving the posterior opening of the narial complex an 'hourglass' shape (Figs 1, 2). The posterodorsal margin of the external naris of *Cryopterygius kristiansenae* slightly resembles the condition seen in *Simbirskiasaurus*. Unlike in *Platypterygius australis*, *Acamptonectes densus* Fischer *et al*., 2012, and *Pervushovisaurus bannovkensis* (see Kear, 2005; Fischer *et al*., 2012; and this work, respectively), there is no trace of a lateral wing on the nasal. As in *Athabascasaurus bitumineus* and many other ophthalmosaurids (e.g. Druckenmiller & Maxwell, 2010), the nasal forms a bony ridge at the junction between its narial and medial lamellae; however, this ridge becomes narrower and wider posteriorly in YKM 65119, forming a crest over the posterior part of the prefrontal. The excavatio internasalis is present but shallow, as it is in *Platypterygius hercynicus* and *Pervushovisaurus bannovkensis* (see below; Fischer, 2012), but unlike the condition in *Platypterygius australis* (V.F. pers. observ. on un-numbered specimens housed in the NHMUK).

Lacrimal

The lacrimal participates in the posterior edge of the posterior opening of the narial complex, unlike in *Platypterygius australis* and *Athabascasaurus bitumineus* (see Kear, 2005; Druckenmiller & Maxwell, 2010, respectively), but over a short distance (Fig. 1). Posteriorly, the lacrimal forms a complex interdigitating suture with the prefrontal. The interdigitating bony processes are much larger than those reported in *Ophthalmosaurus icenicus*, *Athabascasaurus bitumineus*, and *Mollesaurus periallus* (see Kirton, 1983; Druckenmiller & Maxwell, 2010; Fernández & Talevi, 2014), and are set more ventrally, at a point relative to mid-height of the orbit. In many other ophthalmosaurids, the suture appears smooth and

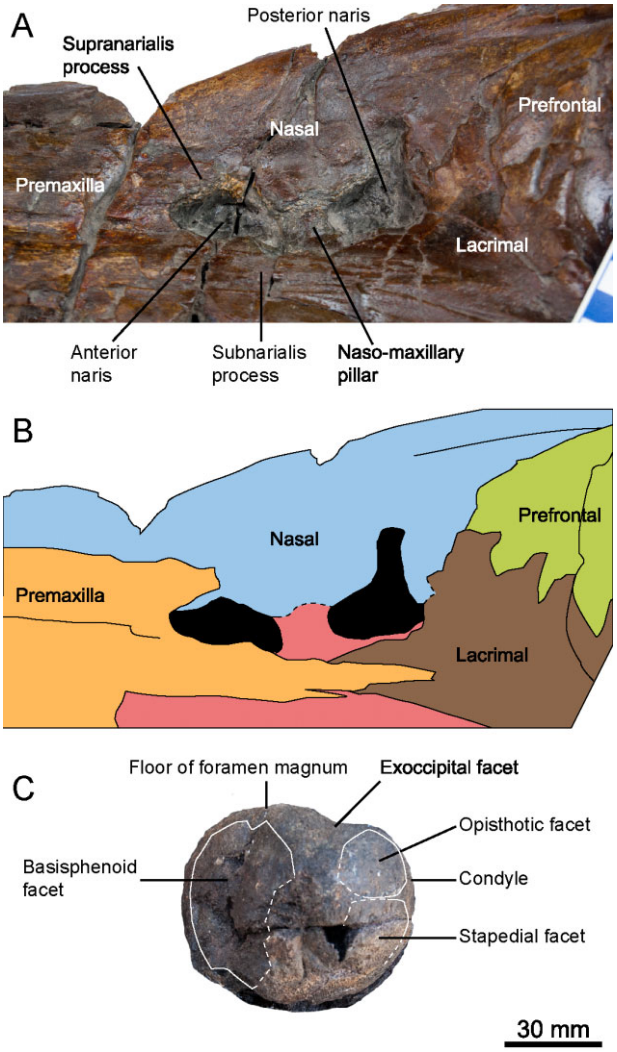

Figure 2. *Simbirskiasaurus birjukovi*, Ochev and Efimov, 1985, holotype (YKM 65119). Detail of the left narial region in lateral view: A, annotated photograph; B, interpretation (the colour scheme is the same as that used in Figure 1). C, basioccipital in anterolateral view. Note the ball-like basioccipital lacking an extracondylar area, which is typical of platypterygiine ophthalmosaurids.

straight (e.g. *Brachypterygius extremus*, *Platypterygius australis*, *Caypullisaurus bonapartei*, *Sveltonectes insolitus*, and *Cryopterygius kristiansenae*; see Kirton, 1983; Kear, 2005; Fernández, 2007b; Fischer *et al*., 2011b; and Druckenmiller *et al*., 2012, respectively).

Prefrontal

Unlike in *Aegirosaurus leptospondylus* and *Sveltonectes insolitus* (see Bardet & Fernández, 2000; Fischer *et al*., 2011b, respectively), the prefrontal does not participate in the narial aperture (Fig. 1). The position of the suture between the prefrontal and postfrontal is unclear because the surface of the bone is broken off in this area.

Postfrontal

The anterior part of the postfrontal is separated into wide medial and narrow lateral processes by the posterolateral process of the nasal. This condition is seen in many platypterygiines, including *Platypterygius hercynicus* and *Sveltonectes insolitus* (Fischer *et al*., 2011b; Fischer, 2012, respectively), but contrasts with the situation present in ophthalmosaurines (*Ophthalmosaurus* spp., see Gilmore, 1905; Kirton, 1983; and *Leninia stellans* Fischer *et al*., 2014a).

Frontal

The anterior part of the left frontal is preserved. Its dorsal surface appears extensively exposed, unlike in *Athabascasaurus bitumineus* (Druckenmiller & Maxwell, 2010). A long and concave area of smooth finished bone on the posterior edge of the frontal suggests that the frontal participates to the anterior margin of the supratemporal fenestra (Fig. 3), as it does in platypterygiine ophthalmosaurids (e.g. *Aegirosaurus leptospondylus*, *Platypterygius australis*, *Sveltonectes insolitus*, and *Platypterygius hercynicus*; see Bardet & Fernández, 2000; Kear, 2005; Fischer *et al*., 2011b; Fischer, 2012, respectively), with the exception of *Athabascasaurus bitumineus* (see Druckenmiller & Maxwell, 2010). The poor preservation of this region of the skull prevents unambiguous description on this feature, however. accordingly, we scored this character as unknown for *Simbirskiasaurus birjukovi*.

Jugal

The anterior part of the jugal forms a thin lamella that covers the posteroventral surface of the maxilla via an extensive well-delineated facet, textured by ridges and furrows (Fig. 1). This facet indicates that the anterior part of the jugal forms an acute process. Posteriorly, the jugal thickens and, together with the overlain maxilla, buttresses the posteroventral process of the lacrimal. There is no evidence for a premaxilla–jugal contact, unlike in *Brachypterygius extremus* (see Kirton, 1983).

Sclerotic ring

One large element of the sclerotic ring is preserved (Fig. 1). Both the internal (i.e. with respect to the pupil) and the external margins of the sclerotic ring are striated.

Basioccipital

The basioccipital (78 mm wide; Figs 2, 3) is partly freed from the matrix; only its posterior and right posterolateral surfaces are embedded. The basioccipital

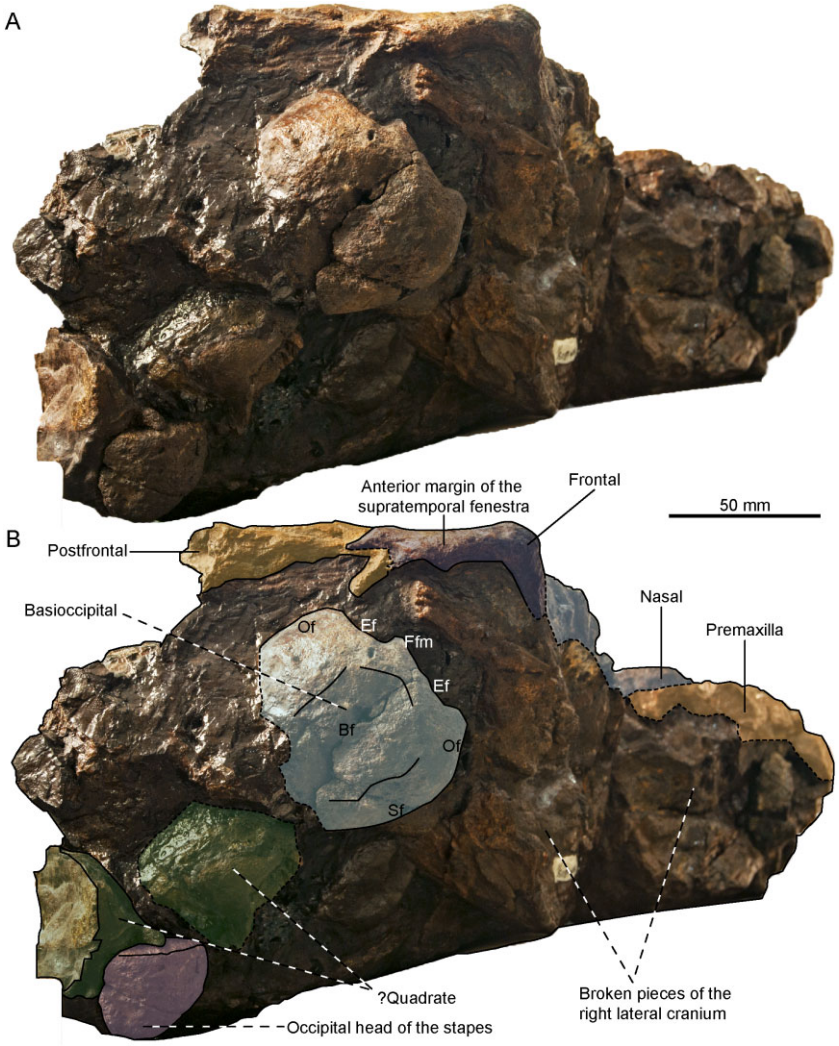

Figure 3. *Simbirskiasaurus birjukovi*, Ochev and Efimov, 1985, holotype (YKM 65119), in posterior view: A, photograph; B, interpretation. Note that the frontal likely forms the anterior margin of the supratemporal fenestra, a feature frequently found among platypterygiine ophthalmosaurids. Abbreviations: Bf, basisphenoid facet of the basioccipital; Ef, exoccipital facet of the basioccipital; Ffm, floor of the foramen magnum; Of, opisthotic facet of the basioccipital; Sf, stapedial facet of the basioccipital.

has no extracondylar area and lacks a peripheral groove, as is also the case in *Arthropterygius chrisorum* (see Maxwell, 2010; Fernández & Maxwell, 2012), platypterygiine ophthalmosaurids (Fischer *et al*., 2012), and possibly *Palvennia hoybergeti* Druckenmiller *et al*., 2012 (for which a single poorly preserved basioccipital is known). Among platypterygiines, the basioccipital of *Simbirskiasaurus birjukovi* is very similar to that of both some *Platypterygius* specimens (e.g. an unnumbered specimen in Bardet, 1989) and *Brachypterygius extremus* (CAMSM J68516; McGowan, 1976), lacking the raised opisthotic facets seen in *Sveltonectes insolitus* and Fischer *et al*., 2014 (Fischer *et al*., 2011b; Fischer *et al*., 2014b, respectively; Fig. 3). The anterior surface is flat and lacks dorsoventral grooves. There is a minute foramen on the left side, ventral to the exoccipital facet. The opisthotic facet is flat and its anterior edge is confluent with the condylar area, unlike in ophthalmosaurines, in which a groove separates the condyle from the body of the basioccipital (Fischer *et al*., 2012, 2014a). The condyle is markedly convex. The exoccipital facet is deep and elliptical. The floor of the foramen magnum is raised and narrow, and lacks the distinctive median structure present in *Acamptonectes densus*, where it is divided by a longitudinal ridge (Fischer *et al*., 2012).

Stapes
The medial surface of the occipital head of the left stapes is preserved (Fig. 3); this surface is quadratic in medial view. The opisthotic facet is relatively large and flat. A hyoid process is present, but this feature appears to be intraspecifically variable among ophthalmosaurids (Fischer *et al*., 2012).

Dentition
Numerous teeth are preserved (Fig. 1). The apex is pointed and the crown is elongated (the largest crown is 19 mm in length); it is also robust and textured with numerous apicobasal ridges. The acellular cementum ring is smooth. The root forms only half of the height of the tooth. Its peripheral surface bears apicobasal ridges and its cross section is squared, as is typical for platypterygiine ophthalmosaurids (Fischer *et al*., 2012), but it lacks the prominent and sharp angles seen in some *Platypterygius* specimens (Bardet, 1990; Fischer *et al*., 2014b).

Although relatively larger than in *Aegirosaurus leptospondylus* (see Bardet & Fernández, 2000), the shape and robustness of the teeth and the lack of specialized features suggest that *Simbirskiasaurus birjukovi* also occupied a 'generalist' feeding guild (see the scheme developed in Fischer *et al*., 2011a; Fischer *et al*., 2014b). Too few tooth apices are preserved to allow for the quantitative analysis of the wear pattern, but most crown apices are slightly polished and there is at least one broken-off tip with a polished broken surface; a very similar condition to that in the *Aegirosaurus* sp. specimen studied by Fischer *et al*. (RGHP LA 1; Fischer *et al*., 2011a).

Pervushovisaurus Arkhangelsky, 1998b

Diagnosis and occurrence
As for the type and only species, *Pervushovisaurus bannovkensis*.

Pervushovisaurus bannovkensis Arkhangelsky, 1998b

Platypterygius (Pervushovisaurus) bannovkensis Arkhangelsky, 1998b: 611–615, figs 1, 2 (original description).

Platypterygius campylodon McGowan &Motani, 2003: 121 (referral).

Holotype
SSU 104a/24, a complete rostrum.

Emended diagnosis
Platypterygiine ophthalmosaurid characterized by the following autapomorphies: presence of foramina along the ventral premaxillary–maxillary suture; presence of a semi-oval foramen on the lateral surface of the premaxilla, anteroventral to the external naris; presence of lateral ridges on the maxilla; presence of wide supranarial 'wing' of the nasal (a similar structure, although much smaller, is present in *Platypterygius australis* and *Acamptonectes densus*; see Kear, 2005; Fischer *et al*., 2012, respectively); robust splenial markedly protruding from the external surface of the mandible.

Pervushovisaurus bannovkensis is also characterized by the following unique combination of features: secondarily closed naris surrounded by foramina [as in *Platypterygius sachicarum* and *Platypterygius australis* (see Paramo, 1997 and Kear, 2005, respectively), and in *Simbirskiasaurus birjukovi*, although the 'anterior' naris is still present in this taxon (Maisch & Matzke 2000; this work)]; elongated anterior process of the maxilla, reaching anteriorly the level of the nasal [unlike in *Aegirosaurus leptospondylus* (see Bardet & Fernández, 2000) and *Sveltonectes insolitus* (see Fischer *et al*., 2011b)]; root cementum forming prominent 90° angles (as in *Platypterygius campylodon*; see Fischer *et al*., 2014b).

Occurrence
Middle Cenomanian, probably from the Melovatskaya Formation, Upper Cretaceous (Pervushov, Arkhangelsky & Ivanov, 1999) of the Nizhnaya Bannovka locality, Krasnoarmeisk District, Saratov Region, Russia.

Note
According to the principle of coordination (article 43.1 of the International Commission on Zoological Nomenclature, ICZN), Arkhangelsky (1998b) created *Pervushovisaurus* as a name of the 'genus group'; therefore, this name already exists at the generic rank and can readily be used as a genus-level taxon.

Description

Premaxilla
The premaxilla is elongated (Fig. 4) and appears slightly bent ventrally, as is also the case, though to a lesser degree, in *Platypterygius americanus* and *Platypterygius sachicarum* Paramo, 1997 (Romer, 1968; Paramo, 1997, respectively). The fossa praemaxillaris is deep, wide, and nearly continuous. In the anteriormost 100 mm of the rostrum, it forms a small series of aligned foramina. As in some other ichthyosaurs (e.g. *Aegirosaurus*; see Bardet & Fernández, 2000; Fischer *et al*., 2011a), there are multiple lateral foramina at the anterior extremity of the rostrum, which are not necessarily aligned with the fossa praemaxillaris. The dental groove is deep along the whole of its length (around 35 mm deep at the level of emergence of the nasal). As in *Athabascasaurus bitumineus* and

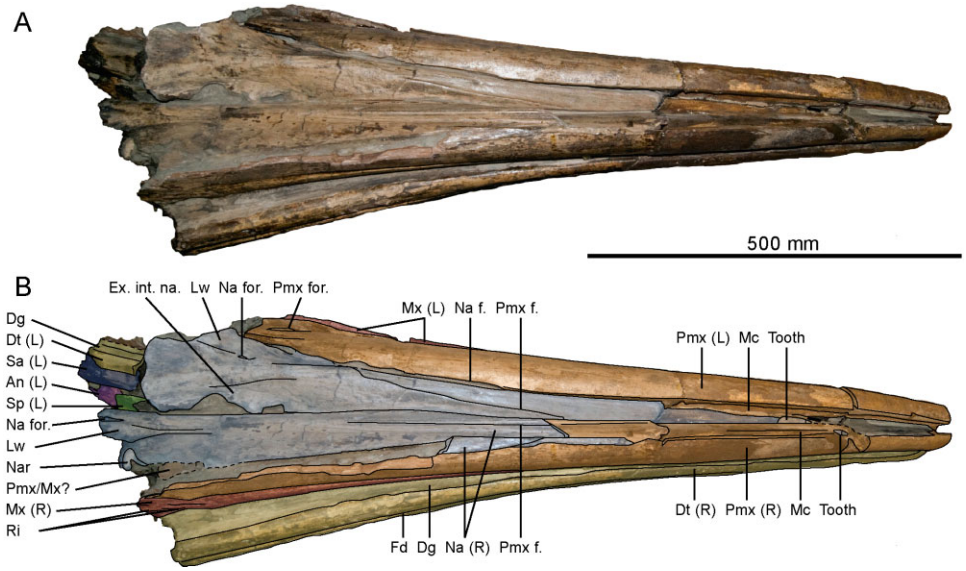

Figure 4. *Pervushovisaurus bannovkensis* Arkhangelsky, 1998b, holotype (SSU 104a/24), in dorsal view: A, photograph; B, interpretation. Note the elongated nasal, the premaxillary, and narial foramina, and the peculiar external naris. Abbreviations: An, angular; Dg, dental groove; Dt, dentary; Ex. int. na., excavatio internasalis; Fd, fossa dentalis; Lw, lateral 'wing' (lamella) of the nasal; Mc, Meckelian canal; Mx, maxilla; Na, nasal; Na f., nasal facet on the premaxilla; Na for., nasal foramen; Nar, naris; Pmx, premaxilla; Pmx for., premaxillary foramen; Ri, lateral ridges of the maxilla; Sa, surangular; Sp, splenial.

Sveltonectes insolitus, the dorsal edge of the premaxilla is strongly bent ventrally anterior to the narial aperture (Druckenmiller & Maxwell, 2010; Fischer *et al*., 2011b, respectively), but the premaxilla is incomplete and the presence of a supranarial process cannot be assessed unambiguously (Fig. 5). Unusually, there is a large semi-oval foramen ventral to the narial aperture (Fig. 5). Arkhangelsky (1998b) regarded this as a fenestra between the premaxilla and the maxilla; however, this foramen belongs to the premaxilla because no suture can be seen around it; furthermore, the premaxillary–maxillary suture is actually located ventral to it. Although the evolutionary origin and function of that foramen remains unclear, its presence is regarded as autapomorphic for *Pervushovisaurus bannovkensis*.

Nasal

The nasal is markedly elongated anteriorly, but unlike that of *Platypterygius hercynicus*, it is mostly hidden beneath the premaxilla (Fischer, 2012). This is clearly indicated by the presence of a well-defined contact zone, medial to which the nasal thickens abruptly, forming the dorsomedial portion of the rostrum (Fig. 4). The nasal emerges about 515 mm posterior to the tip of the premaxilla. Posteriorly, the nasal forms a subtle excavatio internasalis; there, the dorsal and lateral surfaces of the nasal meet perpendicularly via a thickened ridge. As in *Platypterygius australis* and *Acamptonectes densus* (see Kear, 2005; Fischer *et al*., 2012, respectively), the nasal lamella forms a lateral 'wing' overhanging the narial area, but this structure appears much more developed in *Pervushovisaurus bannovkensis* (Figs 4–6). A small foramen is present dorsal to that 'wing', 375 mm posterior to the emergence of the left nasal, and is present on both nasals (Figs 4–6). The right nasal is shifted medially by 90° and is dorsoventrally compressed; its narial lamella faces dorsally, whereas its medial lamella faces ventrally (Figs 4, 7). The nasal forms a small and semicircular notch with a thickened rim, which we interpret as the nasal contribution to the right narial aperture. The narial aperture is small, anteroposteriorly short, and deeply enclosed in the ventral edge of the nasal, as reconstructed on the left-hand side by Arkhangelsky (1998b), when the specimen was more complete. The external naris therefore appears similar to that of *Platypterygius australis*, as noted by Maisch & Matzke (2000: 92).

Maxilla

The anterior process of the maxilla is markedly elongated (Figs 4, 5, 8), emerging laterally at the same level as the nasals, in contrast to the condition in *Ophthalmosaurus icenicus*, *Aegirosaurus* sp., *Sveltonectes insolitus*, and *Acamptonectes densus* (see Andrews, 1910a; Bardet & Fernández, 2000; Fischer *et al*., 2011a; Fischer *et al*., 2011b; Fischer *et al*., 2012). Posteriorly, a series of ridges extend along its lateral surface

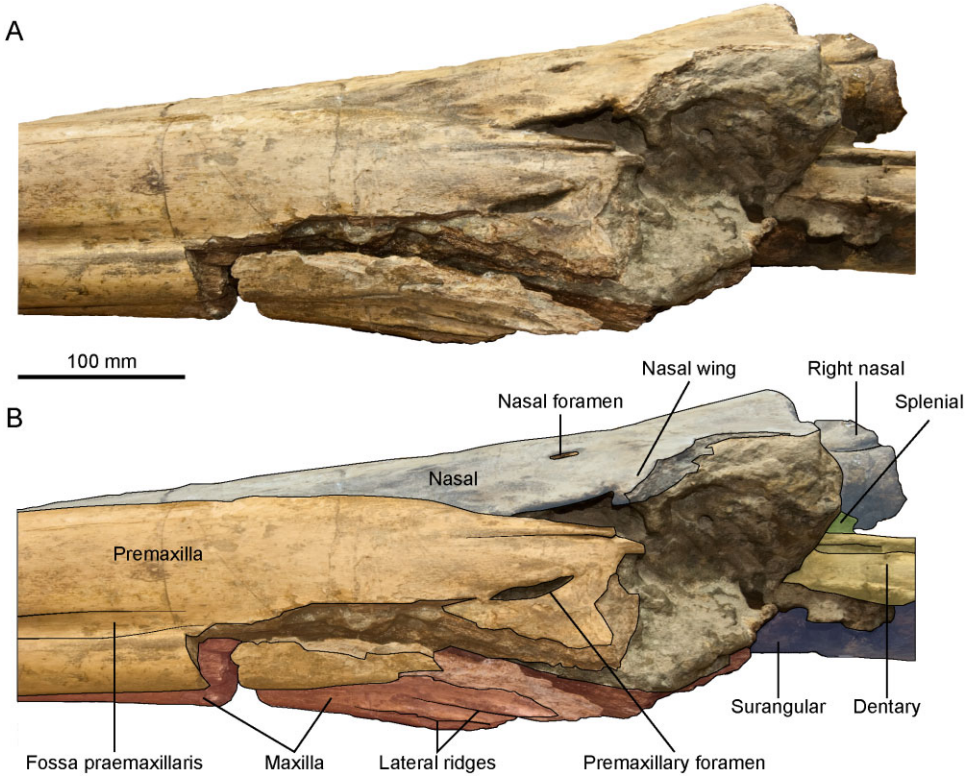

Figure 5. *Pervushovisaurus bannovkensis* Arkhangelsky, 1998b, holotype (SSU 104a/24), in left lateral view: A, photograph; B, interpretation. Note the premaxillary and nasal foramina, and the ridges on the lateral surface of the maxilla. The nasal is disarticulated from the premaxilla, as shown in Figure 4.

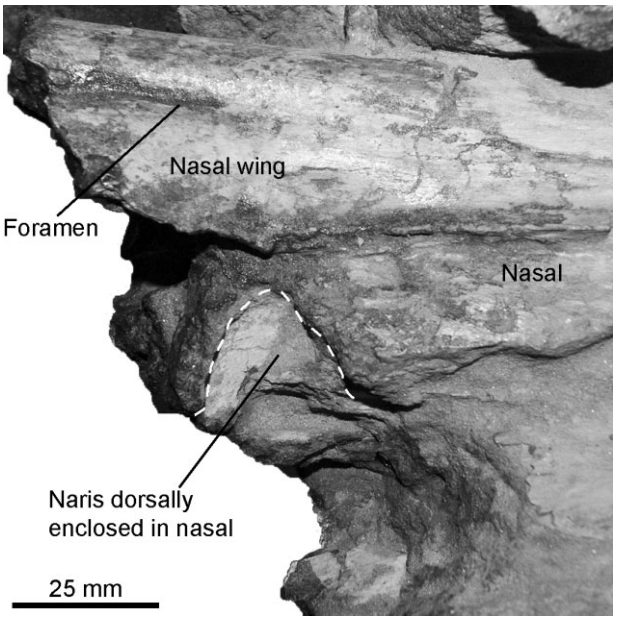

Figure 6. *Pervushovisaurus bannovkensis* Arkhangelsky, 1998b, holotype (SSU 104a/24), detail of the right narial region. Note the anteroposteriorly short external naris profoundly notching the nasal.

(Fig. 5). These may represent the articular facet for the jugal, but this is unlikely because this area is located anterior to the level of the narial aperture; this would imply an extremely elongated jugal, extending much farther anteriorly than the anterior edge of the external naris. The maxilla is dentigerous, but unlike in *Ophthalmosaurus icenicus* and *Platypterygius australis* (see Andrews, 1910b; Kirton, 1983; Kear, 2005), there are no individual pseudo-alveoli for maxillary teeth (Fig. 8). Anteriorly, the maxilla is a thin lamella lying on the medial surface of the labial wall of the premaxillary dental groove; the maxilla then progressively thickens and expands dorsally, then medially, as the dentigerous part of the premaxilla reduces. Approximately 710 mm posterior to the tip of the rostrum, the maxilla emerges medioventrally and forms the lingual wall of the dental groove. At that point, the medioventral part of the rostrum flattens and widens. There, the maxilla forms an oblique suture with the premaxilla, with two foramina that do not correspond to the internal naris.

Dentary

The dentary closely resembles the premaxilla. In lateral view, the tip of the rostrum is rounded, unlike the

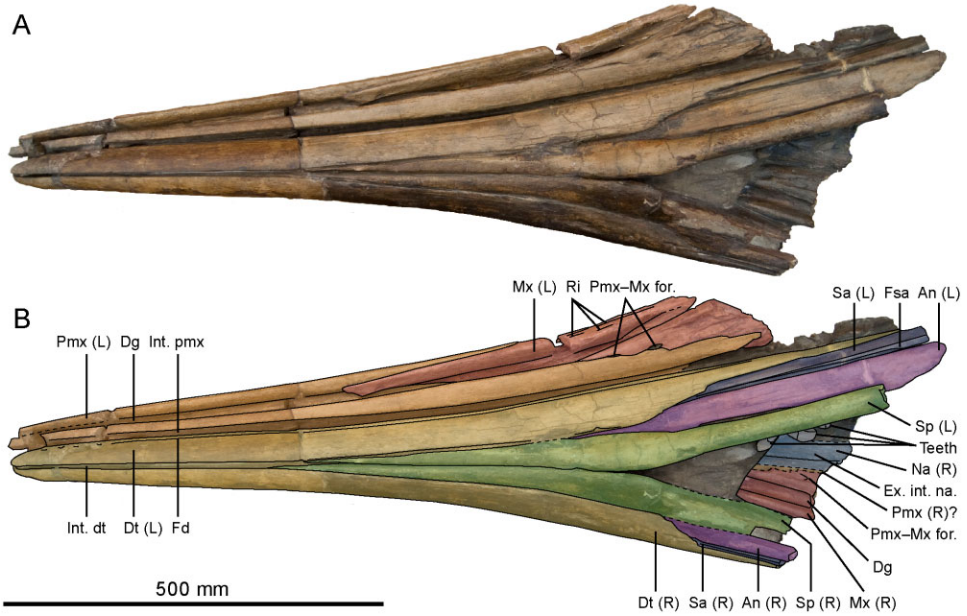

Figure 7. *Pervushovisaurus bannovkensis* Arkhangelsky, 1998b, holotype (SSU 104a/24), in ventral view: A, photograph; B, interpretation. Note the premaxillary–maxillary foramina and the thick splenials. Abbreviations: Fsa, fossa surangularis; Int. dt, interdentary suture; Int. pmx, interpremaxillary suture; Pmx–Mx for., premaxillary–maxillary foramina; for all other abbreviations, see Figure 5.

'beaked' tip of *Platypterygius australis* (see Kear, 2005). Posteriorly, the ventral and lateroventral components of the dentary are replaced by the splenial, the angular, and the surangular, successively; at this level, the dentary is reduced to a thin lamella covering the surangular (Fig. 7).

Surangular and angular

The surangular is thick and slightly T-shaped in cross section; the dorsal surface of the angular bears two deep grooves (Fig. 7). A fossa surangularis is present, unlike in *Sveltonectes insolitus* (see Fischer *et al*., 2011b) and embryonic *Platypterygius australis* (see Kear & Zammit, 2014).

Splenial

The splenial emerges ventrally 361 mm posterior to the tip of the mandible, and the symphysis is 695 mm in length. At the end of the symphysis, the splenial rapidly widens and thickens, forming a prominent ridge with a semicircular cross section, which is a unique feature of *Pervushovisaurus bannovkensis* (Figs 7, 8).

Dentition

The teeth are robust, although only a few are preserved. The largest one is 60 mm in total length, which is bigger than in most specimens of *Platypterygius* (55 mm, according to Bardet, 1990; Fig. 9). This appears small, however, relative to the skull size (anteorbital length ~1 m). The crown is conical, robust, and ridged along its entire height. The acellular cementum ring is smooth. As is the case in some specimens referred to *Platypterygius campylodon*, the roots of middle-snout teeth are thickened and form prominent 90° angles, although these are not as sharp and prominent as they are in *Platypterygius campylodon* (see Fischer *et al*., 2014b). This results in a markedly quadrangular cross section. The cross section is, however, rectangular rather than squared in the largest teeth, unlike in most specimens of *Platypterygius campylodon*, although this may partly result from diagenesis: one tooth (second from left in Fig. 9) is compressed labiolingually, the crown being flattened on one side, and another one of similar size (left-most tooth in Fig. 9) possesses a squared cross section. Subtle apicobasal ridges texture the labial and lingual surfaces of the root. Posterior teeth (the two on the right in Fig. 9) are smaller and have rounder, more bulbous roots.

RESULTS

Phylogenetic analysis

We recovered two most parsimonious trees in our unpruned analysis (of 103 steps, with a consensus tree of 104 steps; consistency index, CI = 54; retention index, RI = 67; Figs 10, S1–S6). The aim of this analysis is to provide a broad context to analyse the phylogenetic

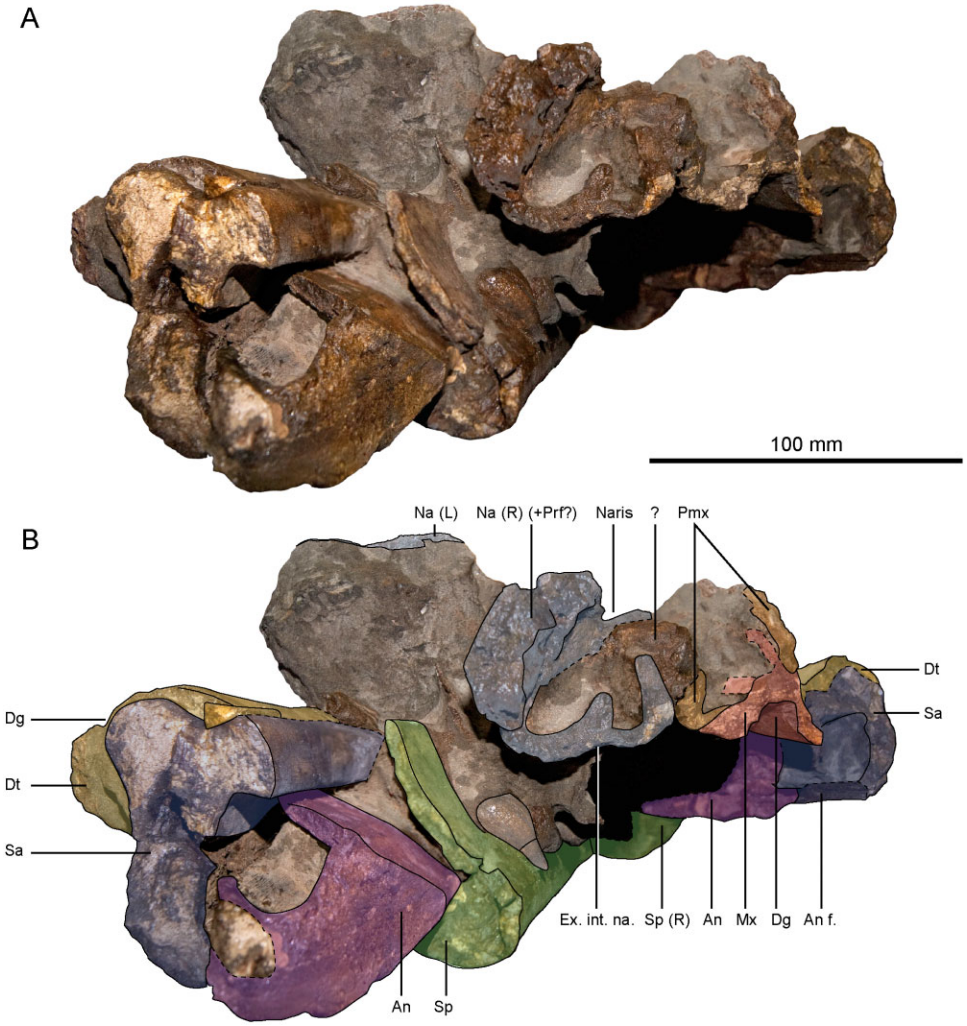

Figure 8. *Pervushovisaurus bannovkensis* Arkhangelsky, 1998b, holotype (SSU 104a/24), in posterior view: A, photograph; B, interpretation. Abbreviations: An f., angular facet of the surangular; Prf, prefrontal; for all other abbreviations, see Figure 5.

Figure 9. *Pervushovisaurus bannovkensis* Arkhangelsky, 1998b, holotype (SSU 104a/24), teeth in labial view.

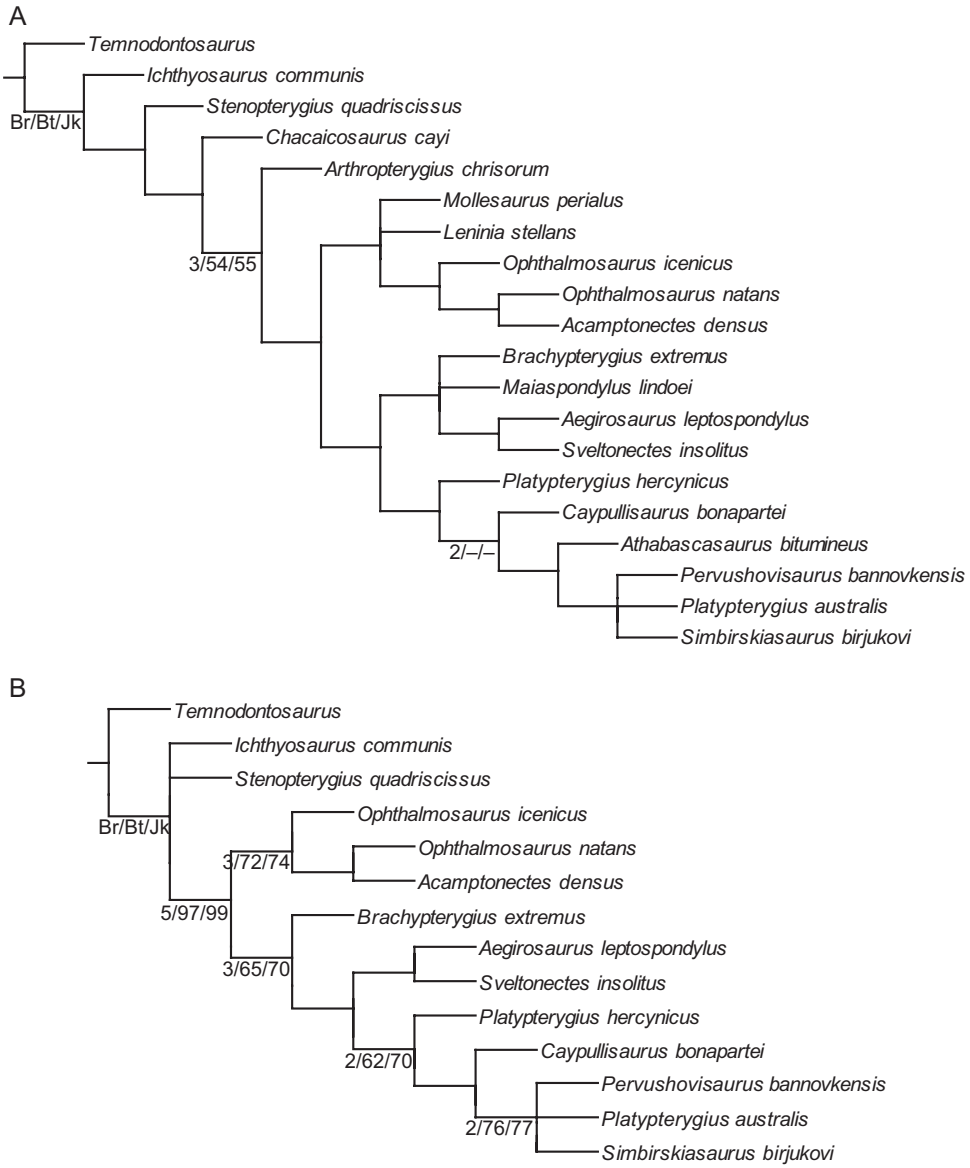

Figure 10. Phylogenetic relationships of *Simbirskisaurus birjukovi* and *Pervushovisaurus bannovkensis*. A, strict consensus of the two most parsimonious trees (each of 103 steps; consensus tree of 104 steps; consistency index, CI = 54; retention index, RI = 67) arising from the cladistic analysis of the 'full' data set, with significant support values (Bremer support > 1; bootstrap and jacknife values ≥ 50%). B, strict consensus of the two most parsimonious trees (each of 89 steps; consensus tree of 93 steps; CI = 61; RI = 68) arising from the cladistic analysis of the 'reduced' data set, with significant support values (Bremer support > 1; bootstrap and jacknife values ≥ 50%). Abbreviations: Br, Bremer support; Bt, bootstrap value; Jk, jacknife value.

positions of *Simbirskiasaurus birjukovi* and *Pervushovisaurus bannovkensis*; the data set therefore incorporates numerous highly incomplete taxa. As a result, the general support of the tree topology is moderate to low. The topology is similar to that of previous analyses, finding Ophthalmosauridae to form two distinct clades: Ophthalmosaurinae and Platypterygiinae (Fischer *et al.*, 2012, 2014a). The significant details of the topology for platypterygiines are discussed below.

The phylogenetic analysis of the pruned matrix yielded two most parsimonious trees (of 89 steps, with a consensus tree of 93 steps; CI = 61; RI = 68) with a topology similar to that of the unpruned analysis, except that the removal of *Stenopterygius*/*Chacaicosaurus cayi* from the data set created a polytomy at the base of Thunnosauria, and that *Brachypterygius* is recovered as a basal platypterygiine. The statistical support is, however, substantially increased (Fig. 10).

As in other morphological (Fischer, 2012) and phylogenetic (e.g. Druckenmiller & Maxwell, 2010; Fischer *et al*., 2012) analyses, the genus *Platypterygius*, as currently defined, is paraphyletic. We ran constrained analyses in TNT, forcing the monophyly of *Platypterygius* in both the full and pruned matrices; the shortest trees recovered were respectively one (104 steps) and three (92 steps) steps longer than the most parsimonious solutions; these topologies are therefore suboptimal. Whereas the precise interrelationships of platypterygiine ichthyosaurs are still poorly supported, our current analyses found support for a derived clade of platypterygiine ichthyosaurs comprising *Simbirskiasaurus birjukovi*, *Pervushovisaurus bannovkensis*, and *Platypterygius australis*, all of which share narial aperture division (Fig. 10).

DISCUSSION

Differences with the original description of *Simbirskiasaurus birjukovi*

Ochev & Efimov (1985) considered that YKM 65119 represents a new taxon belonging to the family Ichthyosauridae, and noted that this taxon is characterized by a very peculiar naris surrounded by four foramina. Subsequent preparation of the external naris indicates that these foramina are actually a large posterior opening of the narial complex, separated from the anterior one by a nasomaxillary pillar. This also revealed the presence of a large narial lamella of the maxilla beneath the lacrimal. These new observations permit a better understanding of the peculiar nares in some other derived platypterygiines, such as *Pervushovisaurus bannovkensis* and *Platypterygius australis* (see below). Besides minor differences in the interpretation of the dorsal surface of the skull roof and the extension of the maxilla, we found no evidence for a 'quadratic orbit', considered by Ochev & Efimov (1985) as a diagnostic feature. The postcranial material (sacral centra, ribs, and neural arches) mentioned in the original publication is apparently lost.

YKM 65119 represents a valid taxon; given the peculiarities of its cranial anatomy and its stratigraphic age, we argue that *Simbirskiasaurus birjukovi* should be reinstalled as a valid genus and species of Cretaceous ichthyosaur that requires removal from the wastebasket taxon *Platypterygius*. It represents an additional taxon in the Barremian of the Ulyanovsk area, probably with an ecological niche distinct from that of the smaller, more gracile *Sveltonectes insolitus* (see Fischer *et al*., 2011b). These taxa have not been found in close association, however: the holotype of *Simbirskiasaurus* is early Barremian, whereas the holotype of *Sveltonectes* is late Barremian.

The peculiar osteology and validity of *Pervushovisaurus bannovkensis*

Pervushovisaurus bannovkensis is based on a single skull described by Arkhangelsky (1998b). Despite numerous intriguing features initially described in this taxon (including a foramen at the premaxillary–lacrimal suture, an extremely long lacrimal, and a reduced naris), McGowan & Motani (2003) regarded it as a nomen dubium, referring the material to *Platypterygius campylodon*. Maisch & Matzke (2000) retained the species *Platypterygius bannovkensis* as provisionally valid, pending reassessment. Since the original description was published, the posterior part of the skull roof has been lost. Nevertheless, it is still possible to investigate the peculiar osteology of this specimen and evaluate the validity of the original description. The foramina on the premaxilla, maxilla, and nasal are genuine, although their functional significance is unclear; the peculiar narial shape is also genuine, and is actually present in other platypterygiine ophthalmosaurids, as discussed below.

Despite the incompleteness of the remains, *Pervushovisaurus bannovkensis* possesses numerous unique features, such as the numerous cranial foramina, the lateral ridges on the maxilla, the extensive supranarial wing, and the prominent splenial; moreover, the characters uniting this species to *Platypterygius*, such as the quadrangular cross section of the root, actually diagnose Platypterygiinae (see Fischer *et al*., 2012). Thus, *Pervushovisaurus bannovkensis* should be regarded as a valid taxon: its proposed inclusion within the genus *Platypterygius* was made by default, and has never been demonstrated. Our reasoning is as follows. (1) The type and only specimen of the type species of *Platypterygius*, *Platypterygius platydactylus* (Broili, 1907), is an immature ichthyosaur that was destroyed during World War II (McGowan & Motani, 2003; Kear & Zammit, 2014). Contrary to some published accounts (e.g. McGowan, 1972; McGowan & Motani, 2003), *Platypterygius platydactylus* is a lower Aptian taxon; indeed, Broili (1907) mentioned the associated presence of the ammonite *Hoplites deshayesi* (= *Deshayesites deshayesi* d'Orbigny, 1841), which is lower Aptian in age (Lehmann *et al*., 2009). (2) Additionally, phylogenetic analyses (e.g. Druckenmiller & Maxwell, 2010; Fischer *et al*., 2011b; Fischer, 2012; this work) repeatedly recover *Platypterygius* as paraphyletic; most of the previous features regarded as autapomorphic for *Platypterygius* are more widespread, and actually diagnose the diverse ophthalmosaurid clade Platypterygiinae (quadrangular root section, basioccipital with extremely reduced extracondylar area, large humeral trochanters; Fischer, 2012; Fischer *et al*., 2012). Therefore, we argue that Cretaceous ophthalmosaurid taxa should not be attributed to the genus *Platypterygius*

by default, as has been the case since the revision of McGowan (1972), especially for middle Cenomanian material, which is about 20 million years younger than *Platypterygius platydactylus* (using the numerical ages from Kuhnt & Moullade 2007 and Gradstein *et al*., 2012). As we propose in the Discussion, below, the name *Platypterygius* should be restricted to its type species for the time being. (3) *Platypterygius platydactylus* and *Pervushovisaurus bannovkensis* share no overlapping remains; with the current state of knowledge, there is thus no solid ground to refer the latter to the genus *Platypterygius*. For these reasons, we use the available genus rank name *Pervushovisaurus* for reception of the species *Pervushovisaurus bannovkensis*. Being middle Cenomanian in age, *Pervushovisaurus bannovkensis* represents one of the youngest valid ichthyosaur taxa known so far.

The complex taxonomy of *Platypterygius*

Our new data on *Simbirskiasaurus birjukovi* and *Pervushovisaurus bannovkensis* provide a further step towards the re-evaluation of *Platypterygius* and the true taxonomic diversity of Cretaceous ichthyosaurs. According to recent phylogenetic analyses (Druckenmiller & Maxwell, 2010; Fischer *et al*., 2012; Fischer *et al*., 2013; this work), there are three possible ways in which the name *Platypterygius* can be applied: (1) as the name for the most inclusive clade that contains all species referred to *Platypterygius* included here in our cladistic analyses; (2) as the name for the Cretaceous platypterygiine clade that contains *Pervushovisaurus bannovkensis*, *Platypterygius australis*, and *Simbirskiasaurus birjukovi* (all of which share a peculiar narial aperture); (3) or as restricted specifically to the type species of *Platypterygius* – *Platypterygius platydactylus* – or to another type species that should be selected via a formal ICZN proposal. It should be noted that V.F and D.N. have prepared such a proposal; however, informal contact made with various colleagues prior to the submission of this work revealed the lack of a consensus on this issue and, in fact, a significant diversity of opinion.

Option 1 would require that *Simbirskiasaurus* and *Pervushovisaurus* are recognized as valid species within *Platypterygius*, as argued by Maisch & Matzke (2000), but would invalidate the early Tithonian genus *Caypullisaurus* and the Albian genus *Athabascasaurus*. This particular taxonomic option would also result in a concept of *Platypterygius* that requires a near-global distribution as well as a stratigraphic range extending from the beginning of the Tithonian to the end of the Cenomanian, i.e. 58.2 Myr (using the timescale from Gradstein *et al*., 2012). This would make *Platypterygius* even more morphologically disparate and long-lived than as currently conceived. Although the concept of such a widespread, long-lived genus is not impossible, we consider it undesirable to interpret *Platypterygius* in this way in view of the alternatives.

Option 2 would include three species that are or have been referred to as *Platypterygius*, including the well-known *Platypterygius australis*, for which numerous descriptions and specimens are available (e.g. Wade, 1984; Wade, 1990; Kear, 2005; Zammit, 2010; Zammit *et al*., 2010; Maxwell, Zammit & Druckenmiller, 2012b); however, we conclude that this option is not advisable, predominantly because it would restrict the name *Platypterygius* to a clade that probably excludes the current type species, *Platypterygius platydactylus*, creating even more confusion. Furthermore, the application of the name *Platypterygius* to this clade would, like option 1, result in an unusual longevity for this taxon (early Barremian–middle Cenomanian, i.e. more than 30 Myr).

Given the paraphyly and absence of autapomorphic features of *Platypterygius* as currently defined (Fischer, 2012), we propose that the name *Platypterygius* should be restricted to its type species, *Platypterygius platydactylus* (or, perhaps less preferably, to a newly elected type species, left to be designated); this is option 3. Despite the numerous issues surrounding the holotype of *Platypterygius platydactylus*, many authors have pointed to unique or rare features present in this taxon, such as a fusion between the atlas, axis, and third cervical centrum, elongated posterior caudal centra, a peculiar quadrate, and more than two preaxial digits (e.g. Broili, 1907; Kolb & Sander, 2009; Maxwell & Kear, 2010). It cannot, therefore, be unambiguously considered a nomen dubium, and erection of a new type species is highly problematic, in part because it could require the renaming of *Platypterygius platydactylus*. For the purposes of taxonomic stability, this newly restrictive version of the name *Platypterygius* would require a detailed redefinition of the name *Platypterygius*; however, this alternative is (in our opinion) superior to the existing model in which the name is applied to a broad diversity of taxa: in the same way that the now abandoned name *Leptopterygius* was previously applied to diverse Early Jurassic taxa (see McGowan, 1996), the inclusive use of *Platypterygius* as currently conceived has persisted through social inertia. We feel that revision is needed, and that an adherence to the 'conventional' use of this name is confusing communication and stifling the appreciation of Cretaceous ophthalmosaurid diversity. This task is, however, beyond the scope of the present work, and will be dealt with in another article. Regardless of these taxonomic issues, it is clear from both recent morphological and cladistic analyses on Cretaceous ichthyosaurs that *Platypterygius* as conventionally conceived conceals a substantial diversity of Cretaceous ichthyosaurs.

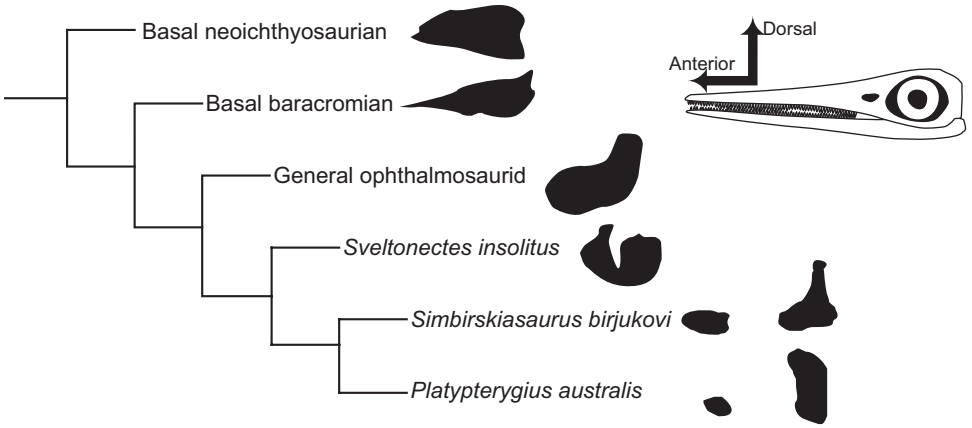

Figure 11. Schematic depiction of narial aperture evolution in parvipelvian ichthyosaurs. The narial aperture of many ophthalmosaurids is notched by a nasal process; the condition seen in the clade *Simbirskiasaurus birjukovi* + *Pervushovisaurus bannovkensis* + *Platypterygius australis* may therefore be derived from this common ophthalmosaurid configuration. External narial apertures not to scale. Basal neoichthyosaurian: *Temnodontosaurus eurycephalus* (NHMUK PV R1157, holotype; V.F., pers. observ.). Basal baracromian: *Stenopterygius* cf. *quadriscissus* (no specimen number, redrawn from Maisch & Ansorge, 2004). General ophthalmosaurid: based on photographs of *Ophthalmosaurus icenicus* (and Andrews, 1910a; Kirton, 1983), *Ophthalmosaurus natans* (see Gilmore, 1905; Gilmore, 1906), *Aegirosaurus leptospondylus* (see Bardet & Fernández, 2000), and *Cryopterygius kristiansenae* (see Druckenmiller *et al*., 2012); *Sveltonectes insolitus* (IRSNB R 269, holotype; redrawn from Fischer *et al*., 2011b); *Simbirskiasaurus birjukovi* (YKM 65119, holotype; this work); *Platypterygius australis* (AM F98273; redrawn from Kear, 2005).

Naris reduction in a derived platypterygiine clade

The phylogenetic analysis indicates the existence of a clade of derived platypterygiines containing *Simbirskiasaurus birjukovi*, *Pervushovisaurus bannovkensis*, and *Platypterygius australis*. *Simbirskiasaurus* extends the origin of this clade back to the early Barremian. In addition to being the youngest ichthyosaur clade to undergo radiation (the other parvipelvian clades arose prior to the Cretaceous; Fischer *et al*., 2012; Fischer *et al*., 2013), it also contains one of the youngest ichthyosaur species known: *Pervushovisaurus bannovkensis* from the middle Cenomanian. A complete division of the external naris into distinct anterior and posterior openings, as a result of the formation of a nasomaxillary process, characterizes this clade; it appears that the anterior section of the narial complex subsequently became reduced to one or a series of small foramina, except in *Simbirskiasaurus*. Maisch & Matzke (2000: 92) previously noted the substantial similarities of narial aperture present among these taxa.

Our new observations on *Simbirskiasaurus birjukovi* and *Pervushovisaurus bannovkensis* therefore corroborate Maisch & Matzke's (2000) hypothesis that the foramina anterior to the external naris in some Cretaceous ichthyosaurs represent relictual segments of the anterior part of the external naris. In fact, many ophthalmosaurids, including *Ophthalmosaurus* spp., *Platypterygius americanus*, *Aegirosaurus leptospondylus*, *Acamptonectes densus*, *Cryopterygius kristiansenae*, and possibly *Brachypterygius extremus* (see Gilmore, 1905; Romer, 1968; Kirton, 1983; Bardet & Fernández, 2000; Druckenmiller *et al*., 2012; Fischer *et al*., 2012), possess a ventral process of the nasal that protrudes inside the narial aperture to produce a kidney-like shape. This process is elongated and hook-like in *Sveltonectes insolitus*, although the maxilla of this taxon lacks a corresponding process; its naris is not, therefore, entirely divided. The situation seen in *Simbirskiasaurus birjukovi*, *Pervushovisaurus bannovkensis*, *Platypterygius australis*, and probably *Platypterygius sachicarum* (see Paramo, 1997) could therefore be regarded as an elaborate version of a feature otherwise widespread among ophthalmosaurids, thereby indicating a trend towards reduction of the narial aperture in these ichthyosaurs, especially notable when compared with the large, oval, and often elongated nares of more basal neoichthyosaurians [Fig. 11; e.g. *Leptonectes moorei* McGowan & Milner 1999; *Leptonectes* cf. *tenuirostris*; *Eurhinosaurus longirostris* (Mantell, 1851); *Temnodontosaurus platyodon* (Conybeare, 1822); *Hauffiopteryx typicus* (von Huene, 1931); *Stenopterygius quadriscissus* (Quenstedt, 1856); *Stenopterygius triscissus* (Quenstedt, 1856); see McGowan, 1979; McGowan, 1994; McGowan & Milner, 1999; Maisch & Matzke, 2003; Caine & Benton, 2011; Maxwell, 2012]. Interestingly,

the external naris of the Aalenian taxon *Stenopterygius aalensis* Maxwell, Fernández & Schoch, 2012a appears slightly kidney-shaped (Maxwell *et al.*, 2012a), possibly representing a prelude to the ophthalmosaurid condition. Such narial aperture reduction may appear counterintuitive given that ichthyosaurs apparently had a well-developed sense of smell, as suggested by the developed olfactory lobes of their brains (Maisch & Matzke, 2000). However, the derived platypterygiines *Caypullisaurus bonapartei* and *Platypterygius hercynicus* appear to have nares with convex dorsal margins (Fernández, 2007b; Fernández, 2007a; Fischer, 2012), indicating that this trend towards narial aperture reduction was not universal among ophthalmosaurids.

CONCLUSION

Simbirskiasaurus birjukovi and *Pervushovisaurus bannovkensis*, from the early Barremian and middle Cenomanian of Russia, respectively, are represented by diagnostic remains and are valid platypterygiine ophthalmosaurids. These taxa permit a re-evaluation of the peculiar narial aperture morphology encountered in other Cretaceous ophthalmosaurids, such as *Platypterygius australis* and possibly *Platypterygius sachicarum*, indicating the existence of a clade of platypterygiine ophthalmosaurids characterized by a reduction of the anterior part of the narial complex, following a complete division by a nasomaxillary process. Phylogenetic analysis indicates that *Simbirskiasaurus*, *Pervushovisaurus*, and *Platypterygius australis* form a clade, known to have persisted from the Barremian to the Cenomanian. Our phylogenetic analyses again indicate that the species currently referred to the widespread, long-lived genus *Platypterygius* are not close relatives: maintenance of this name as a catch-all for Cretaceous ophthalmosaurids is obscuring views on ophthalmosaurid diversity and disparity, and we therefore propose that the name should, for now, be restricted to the type species, *Platypterygius platydactylus*.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site:

Figure S1. Strict consensus of the two most parsimonious trees arising from the cladistic analysis of the 'full' data set, in unambiguous optimization.
Figure S2. Strict consensus of the two most parsimonious trees arising from the cladistic analysis of the 'full' data set, in fast optimization (ACCTRAN).
Figure S3. Strict consensus of the two most parsimonious trees arising from the cladistic analysis of the 'full' data set, in slow optimization (DELTRAN).
Figure S4. Strict consensus of the two most parsimonious trees arising from the cladistic analysis of the 'reduced' data set, in unambiguous optimization.
Figure S5. Strict consensus of the two most parsimonious trees arising from the cladistic analysis of the 'reduced' data set, in fast optimization (ACCTRAN).
Figure S6. Strict consensus of the two most parsimonious trees arising from the cladistic analysis of the 'reduced' data set, in slow optimization (DELTRAN).
Appendix S1. Codings and nexus of the two phylogenetic analyses.