

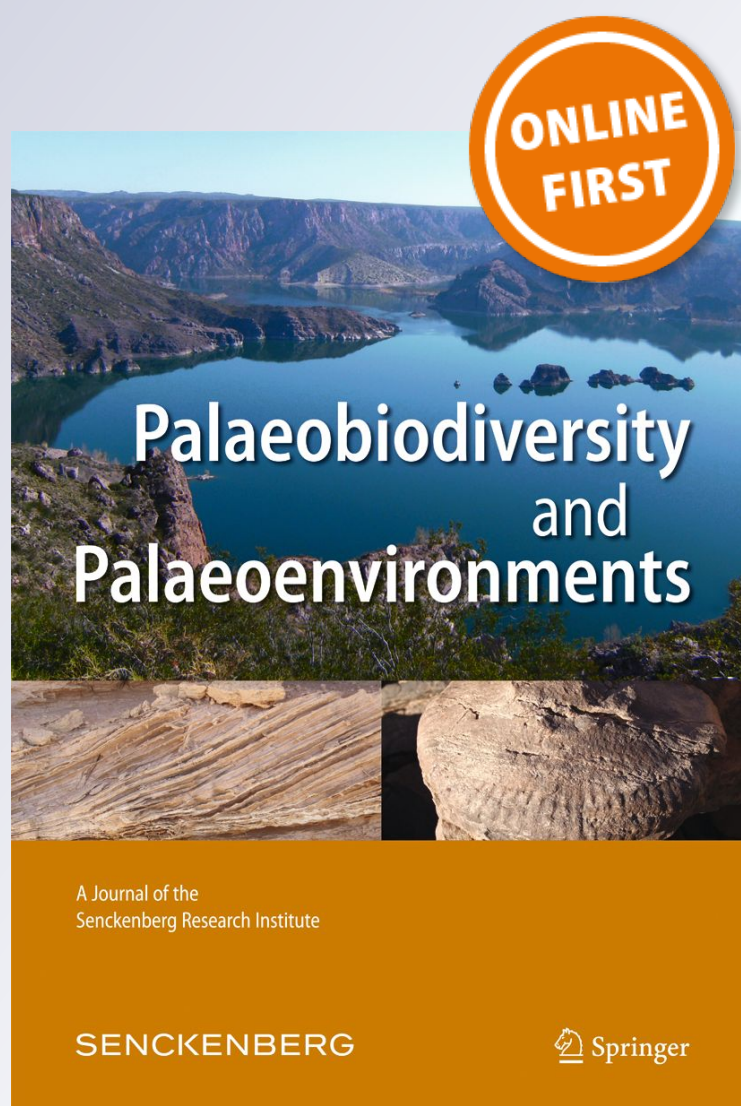
Colymbosaurines from the Upper Jurassic of European Russia and their implication for palaeobiogeography of marine reptiles

Maxim S. Arkhangelsky, Nikolay G. Zverkov, Mikhail A. Rogov, Ilya M. Stenshin & Evgeniya M. Baykina

**Palaeobiodiversity and
Palaeoenvironments**

ISSN 1867-1594

Palaeobio Palaeoenv
DOI 10.1007/s12549-019-00397-0



Your article is protected by copyright and all rights are held exclusively by Senckenberg Gesellschaft für Naturforschung and Springer-Verlag GmbH Germany, part of Springer Nature. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your article, please use the accepted manuscript version for posting on your own website. You may further deposit the accepted manuscript version in any repository, provided it is only made publicly available 12 months after official publication or later and provided acknowledgement is given to the original source of publication and a link is inserted to the published article on Springer's website. The link must be accompanied by the following text: "The final publication is available at link.springer.com".



Colymbosaurines from the Upper Jurassic of European Russia and their implication for palaeobiogeography of marine reptiles

Maxim S. Arkhangelsky^{1,2} · Nikolay G. Zverkov^{3,4,5} · Mikhail A. Rogov⁴ · Ilya M. Stenshin⁶ · Evgeniya M. Baykina⁷

Received: 20 September 2018 / Revised: 4 January 2019 / Accepted: 24 June 2019

© Senckenberg Gesellschaft für Naturforschung and Springer-Verlag GmbH Germany, part of Springer Nature 2019

Abstract

Plesiosaur specimens from the Upper Jurassic of European Russia are mainly referable to the genus *Colymbosaurus* Seeley, 1874, based on elongated propodials with extensive posterodistal expansion, and relatively short mid-cervical vertebrae. However, a historical specimen described by Bogolubov (1911) and subsequently revised as *Plesiosauria* indet. (Storrs et al. 2000) was hitherto the only and ambiguous evidence for the presence of *Colymbosaurus* in the Upper Jurassic of European Russia. Here, we provide descriptions of several specimens from the Volgian of European Russia referable to *Colymbosaurus* sp. and Colymbosaurinae indet. The presence of *Colymbosaurus* in the Late Jurassic (Volgian/Tithonian) of the Middle Russian Sea makes it possible to formulate hypotheses on herpetofauna exchange between NW Europe, Svalbard and European Russia. Found only in these basins, *Colymbosaurus* is a unifying element of marine herpetofauna in the Panboreal palaeobiogeographic superrealm.

Keywords Colymbosaurinae · *Colymbosaurus* · Palaeobiogeography · Jurassic · Volgian · Russia

Introduction

Plesiosaurian remains are common in the Upper Jurassic strata of European Russia (Bogolubov 1911; Novozhilov 1948; Pervushov et al. 1999; Zverkov et al. 2017). Most often they are represented by isolated vertebrae, phalanges and teeth; on rare occasions by articulated bones of limb girdles and flippers; and very rarely by incomplete skeletons (Storrs et al. 2000).

According to the revisions of the last decades, numerous plesiosaurian genera and species established by Russian researchers in the nineteenth–beginning of twentieth centuries

(Bogolubov 1909, 1911; Fischer von Waldheim 1846; Kiprijanow 1883; Trautschold 1860) from the Jurassic deposits of Moscow and the Volga region were considered as *Plesiosauria* indet. (Storrs et al. 2000; Arkhangelsky and Sennikov 2008), and only two plesiosaurian species from the Upper Jurassic of Central Russia considered to be valid. These are *Pliosaurus rossicus* Novozhilov, 1948 from the Chuvashia and Saratov Province and *P. irgisensis* Novozhilov, 1948 from the Saratov Province, and both are Volgian in age (Pervushov et al. 1999; Storrs et al. 2000; Knutsen et al. 2012b; Benson et al. 2013).

✉ Nikolay G. Zverkov
zverkovnik@mail.ru

Maxim S. Arkhangelsky
paleozoo@gmail.com

Mikhail A. Rogov
russianjurassic@gmail.com

Ilya M. Stenshin
cosmopolit4@yandex.ru

Evgeniya M. Baykina
baikina.eug@mail.ru

¹ Saratov State Technical University, Politeknicheskaya St. 77, Saratov 410054, Russia

² Saratov State University, Astrakhanskaya St. 83, Saratov 410012, Russia

³ Lomonosov Moscow State University, Leninskie Gory, 1, GSP-1, Moscow 119991, Russia

⁴ Geological Institute of RAS, Pyzhevski lane, 7, Moscow 119017, Russia

⁵ Borissiak Paleontological Institute of the Russian Academy of Sciences, Profsoyuznaya st., 123, Moscow 117997, Russia

⁶ Undory Paleontological Museum, village of Undory, Ulyanovsk 433312, Russia

⁷ State Darwin Museum, 57/1 Vavilova st., Moscow 117292, Russia

Here, we study the Upper Jurassic plesiosauroid specimens deposited in several Russian museums: Vernadsky State Geological Museum of Russian Academy of Sciences (Moscow), State Darwin Museum (Moscow) and Ulyanovsk Regional Museum of Local Lore named after I.A. Goncharov. A significant part of these collections comprises specimens referable to *Colymbosaurus* Seeley, 1874 or to Colymbosaurinae indet.

Colymbosaurus is currently recognised by a combination of features: propodials with extensive posterodistal expansion bearing a postaxial facet equal in size to the epipodial facets, a diamond-shaped fibula in dorsal view, a proximodistally short ulna that is anteroposteriorly wider than the radius, mid-cervical vertebrae marginally anteroposteriorly shorter than dorsoventrally tall and lacking a longitudinal ridge on the lateral surface and mid-caudal centra that are sub-rectangular in anterior view due to a flat ventral surface and possessing widely spaced chevron facets (Benson and Bowdler 2014; Roberts et al. 2017). Presently, it is considered that the genus *Colymbosaurus* includes two species *C. megadeirus* (Seeley, 1869) and *C. svalbardensis* (Persson, 1962). *C. svalbardensis* differs from *C. megadeirus* in proximodistally short hind limb epipodials, mid-dorsal vertebrae with a taller than wide neural canal and in a relatively gracile femoral shaft (Knutsen et al. 2012b; Benson and Bowdler 2014; Roberts et al. 2017).

To date, *Colymbosaurus* records are reliably known from the Kimmeridge Clay (Kimmeridgian to lowermost part of the middle Volgian) and Portland Stone (middle Volgian) Formations of England and the Slotsmøya Member of the Agardhfjellet Formation (middle to upper Volgian) of Svalbard, Norway (Owen 1869; Seeley 1869; Delair 1958; Casey 1973; Gallois 2011; Knutsen et al. 2012a; Benson and Bowdler 2014; Roberts et al. 2017) (Fig. 1). There are also possible finds from the Kimmeridgian and Volgian deposits of Northern France (Sauvage 1888, 1899, 1911; Brown 1981). Thus, the Russian material described below expands our knowledge of the geographical range of *Colymbosaurus*.

Institutional abbreviations

CAMSM, Sedgwick Museum of Geology, Cambridge, UK; CCMGE, Chernyshev's Central Museum of Geological Exploration, Saint Petersburg, Russia; NHMUK, Natural History Museum, London, UK; SDM, State Darwin Museum, Moscow, Russia; SGM, Vernadsky State Geological Museum of the Russian Academy of Sciences, Moscow, Russia; PIN, Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia; PMO, University of Oslo Natural History Museum, Oslo, Norway; YKM, Ulyanovsk Regional Museum of Local Lore named after I.A. Goncharov, Ulyanovsk, Russia.

Stratigraphic distribution of colymbosaurines

Significant faunal provincialism of the latest Jurassic–earliest Cretaceous has led to the long-term co-existence of independent stage nomenclature for Boreal (Portlandian, Bolonian, Volgian and Ryazanian Stages) and Tethyan (Tithonian and Berriasian Stages) successions (e.g. Cope 1993; Wimbledon 2008; Rogov and Zakharov 2009). During the last decade, significant progress has been achieved in direct Boreal–Tethyan correlation of the Jurassic–Cretaceous boundary beds by palaeomagnetic data (Houša et al. 2007; Bragin et al. 2013), but the position of all Tithonian zonal and substage boundaries within the Boreal succession remains unclear (Rogov 2014a).

On the other hand, in spite of differences even between Boreal fauna belonging to different faunal provinces, the single Volgian Stage can be used for all these areas (cf. Rogov, Zakharov 2009), and three substages of the Volgian are clearly recognised throughout the Panboreal superrealm.

Most *Colymbosaurus* remains have been collected from the Kimmeridge Clay Formation in England (Owen 1840, 1869; Lydekker 1888; Delair 1958; Brown 1981, 1984; Etches and Clarke 1999; Benson and Bowdler 2014), which corresponds to the whole Kimmeridgian Stage, lower Volgian Substage and lowermost part of the middle Volgian (=Bolonian Stage sensu Cope 1993) of the Boreal succession (Rogov and Zakharov 2009, see Fig. 2) as well as to the Kimmeridgian and lower Tithonian (with twofold subdivision of the Tithonian) of the International Geochronological Scale (Ogg and Hinnov 2012).

In European Russia, Colymbosaurinae remains have been found in all middle Volgian zones, corresponding to the Pallasioides—lowermost part of Preplicomphalus interval of the Portlandian succession (Fig. 2) (Rogov and Zakharov 2009). In England, this stratigraphic interval belongs to the upper part of the Kimmeridge Clay Fm. and overlying members which are characterised by variable thickness and lithologies (Cope et al. 1980, fig. 15). In general, the facial changes which occur at the base of the Virgatus Zone in the European Russia and at the base of the Albani Zone of England are very similar. In both cases, clayey succession with intercalations of black shale changes to marly and sandy rocks of relatively small thickness (Fig. 2).

The stratigraphic position of Norwegian specimens is indeterminate, primarily due to problematic control of reptile records by ammonite succession (see Knutsen et al. 2012a; Delsett et al. 2016). However, the stratigraphic interval from which the finds originate (Ilovaiskii–Maximus Zones) generally correlates with Panderi–Virgatus Zones of the European Russia (Rogov 2010b).

It is worthwhile to specify current understanding of a number of stratigraphic terms used for dating of historical colymbosaurine finds by V.A. Kiprijanow (Kiprijanow 1883) and N.N. Bogolubov (1911) (see Rosanow 1906). First of all, Bogolubov often uses the term “Portlandian” as the designation of the Upper Jurassic stratigraphic interval.

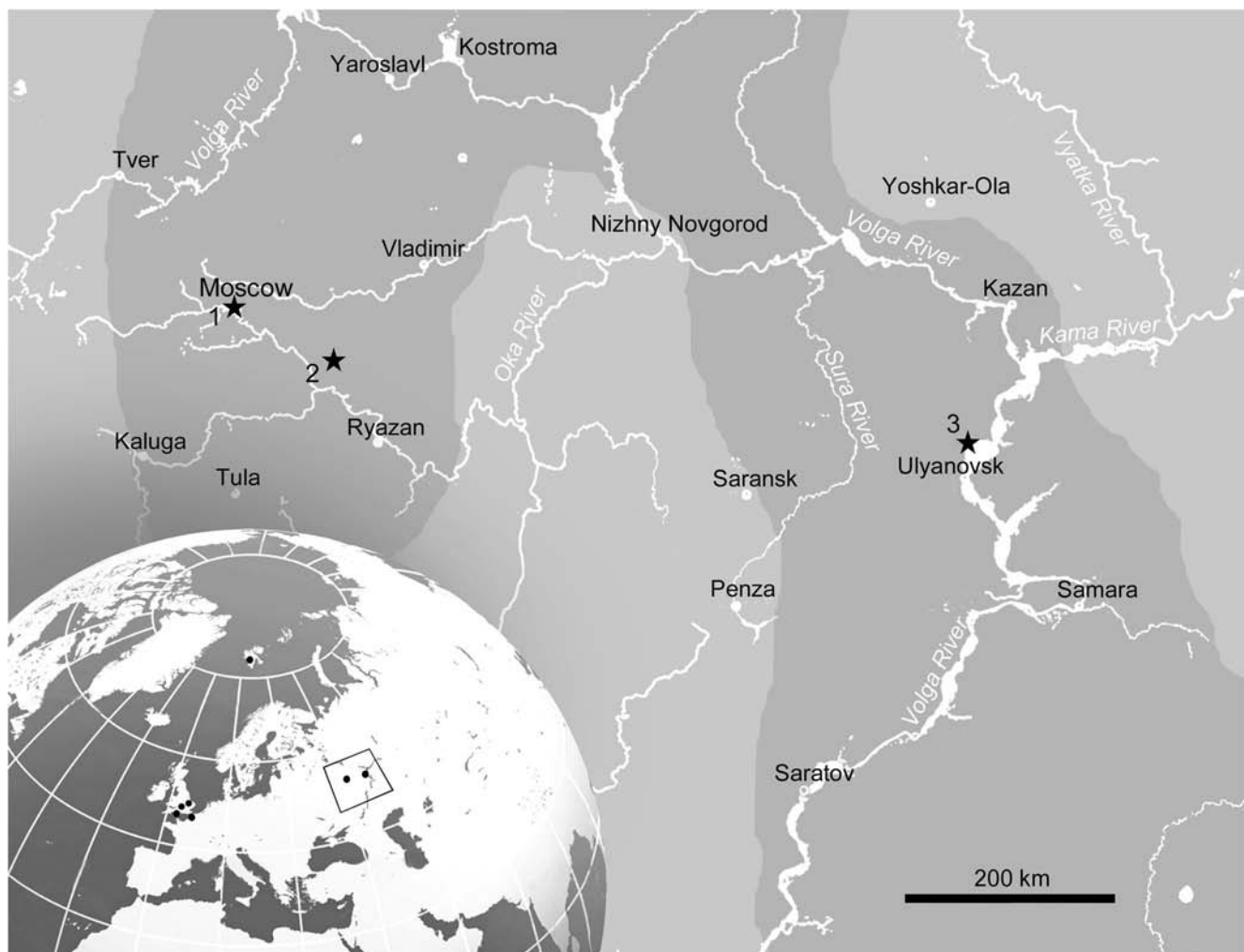


Fig. 1 Map showing the discovery sites of Colymbosaurinae specimens. Dark colour on the map of the European Russia shows an area occupied by the Middle Russian Sea during the Volgian according to Sasonova and Sasonov (1967). Localities are marked with an asterisk. 1 Moscow, 2

Lopatino phosphorite mine (Moscow Province), 3 bank of the Volga River near Gorodischi vill. (Ulyanovsk Province). Adapted from Zverkov and Efimov (2019)

This corresponds to the middle Volgian Substage. Kiprijanow (Kiprijanow 1883, p. 27) mentioned stratigraphic level with “*Ammonites virgatus*”, subsequently refined by Bogolubov as “the lower phosphorite horizon of Portlandian near Moscow” (Bogolubov 1911, pp. 271, 276). These strata are now referred to the middle Volgian Dorsoplanites panderi Ammonite Zone. “Phosphorites with *Perisph. dorsoplanus*” in Bogolubov (1911, p. 125) also correspond to the D. panderi Zone. Below we use modern terminology. It should be also noted that villages Mnevniki and Shchukino mentioned by Bogolubov are now Moscow districts.

Material and methods

Some of the specimens studied herein are part of the collection described by N.N. Bogolubov in 1911 (stored in SGM). Bogolubov was the first who identified the presence of the genus

Colymbosaurus in the middle Volgian Substage of European Russia (Bogolubov 1911). However, not all of his identifications can be supported by diagnostic characters (Table 1).

The records of *Colymbosaurus* and colymbosaurines closely related to *Colymbosaurus*, which originate from the Volgian deposits of the European Russia, are listed in Table 1.

Humerus and femur distinctions

Underwater locomotion with active use of both fore- and hind limbs causes the high similarity of their morphology in many plesiosaurs (e.g. O’Keefe and Carrano 2005; Carpenter et al. 2010; Muscett et al. 2017). However, there are some features by which forelimbs and hind limbs can be identified. These features vary in different clades of plesiosaurs.

In most of the derived thalassophonean plesiosaurids, humeri are markedly shorter than femora and possess broader diaphysis (e.g. Tarlo 1960; Andrews 1913). The morphology of

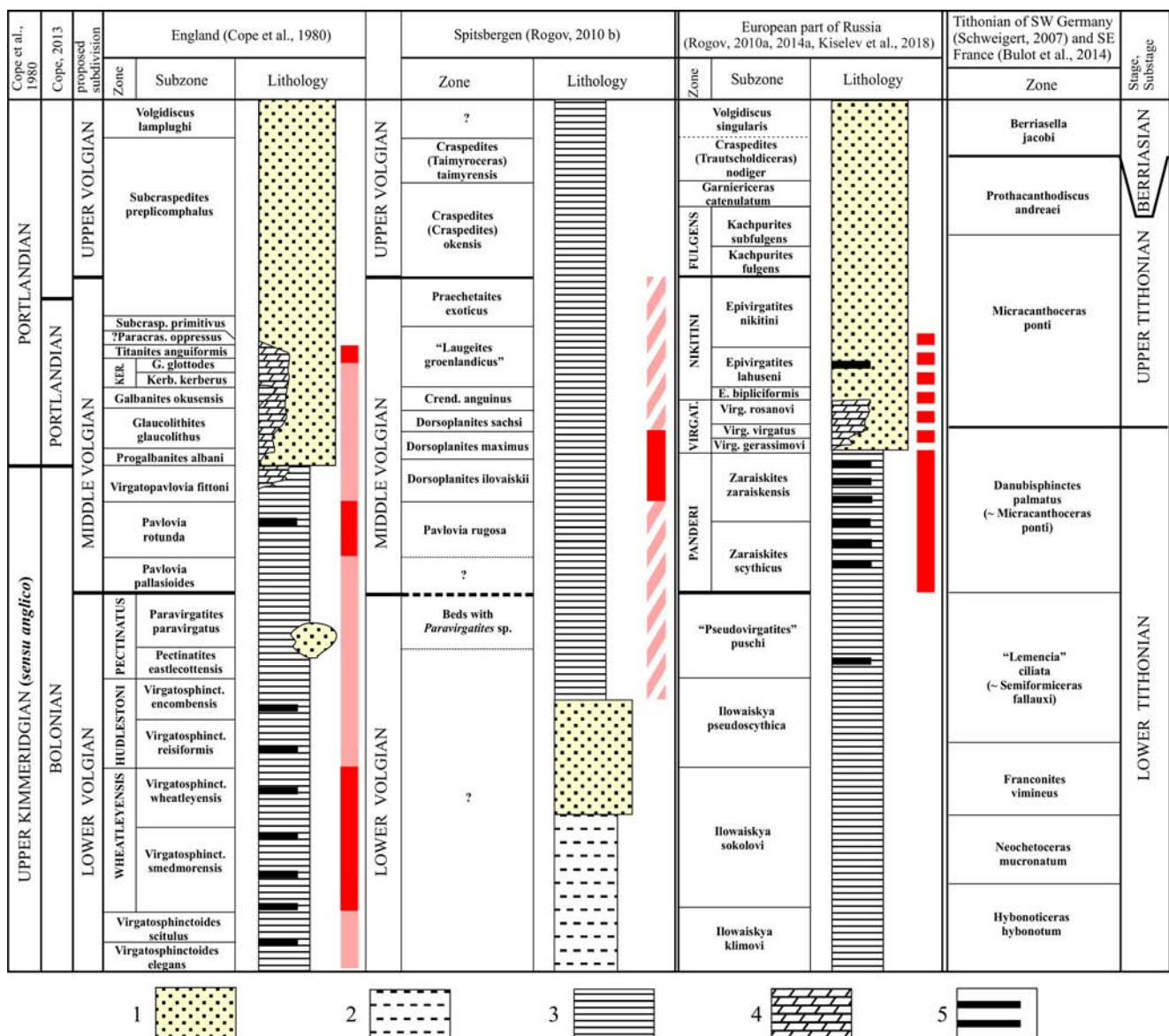


Fig. 2 Zonal correlation and lithology (simplified) of the Volgian Stage of the European part of Russia, Spitsbergen and England. Red columns show the distribution of *Colymbosaurus* spp. (diagonal hatching indicates uncertainty) and *Colymbosaurus*-like colymbosaurines (horizontal

hatching). 1 Sands and sandstones; 2 silts and siltstones, 3 mudstones, 4 marlstones and limestones, 5 shales. *KerKerberos*; Kerberos and Glottodes subzones are used here instead of “subzone a” and “subzone b” of the Kerberos Zone of Wimbledon (1984), respectively

distal and proximal ends does not allow unambiguous identification of these bones within thalassophoneans (NZ pers. obs.). In derived plesiosaurs, *Xenopsaria* Benson et Druckenmiller, 2014, the length of the humeri and femora are nearly equal (e.g. Welles 1962; Benson and Druckenmiller 2014; Schumacher and Martin 2015). The morphology of proximal ends of propodials in elasmosaurids shows that dorsal tuberosity of humerus is anteroposteriorly wide and postaxially offset to the capitulum, whereas the dorsal trochanter of the femur is less anteroposteriorly expanded and is not offset to the capitulum (or slightly offset preaxially) (see, e.g. Welles 1962, fig. 23).

In cryptoclidids, we observe a similar state to that in elasmosaurids: humeri are more massive than femora (with the exception of *Spitrasaurus* and *Djupedalina*, known from only immature specimens (Knutsen et al. 2012b, c)); the dorsal tuberosity of the humerus is wide anteroposteriorly and slightly postaxially offset to the capitulum; the dorsal trochanter of the femur is less anteroposteriorly expanded and is not offset to the capitulum (e.g. Andrews 1910; Brown 1981). One more peculiar feature we can observe is that dorsoventral flattening of the distal end of the humerus is more pronounced, than that of the femur (see, e.g. Brown 1981, fig. 17).

Table 1 Revised historical records of *Colymbosaurus* from European Russia and new materials referred to as *Colymbosaurus* sp. and Colymbosaurinae indet.

Catalogue numbers	Material	Identification (in current study/historical)	Locality	Age	Reference
SGM-1358-36	Pectoral centrum	Plesiosauria indet./ <i>Colymbosaurus</i> cf. <i>brachistopondylus</i> Hulke	Ivanovo region (in Bogolubov' time—Kostroma government), Privolzhsy district, Ples town	Middle Volgian	Bogolubov (1911, p. 266, pl. IV, fig. 4)
SGM-1358-15-25	Fragments of vertebra, fragments of ribs, phalanx	Cryptoclididae indet./ <i>Colymbosaurus</i> cf. <i>trochanterius</i> Owen	Moscow (Schukino vill.)	Middle Volgian Substage, <i>Dorsoplanites panderi</i> Zone	Bogolubov (1911, p. 277, pl. IV, fig. 8, 9, pl. V, fig. 6, 7)
SGM-1358-45	Fragments of 3 dorsal vertebra	Plesiosauria indet./ <i>Colymbosaurus</i> cf. <i>trochanterius</i> Owen	Moscow (Mnevniki vill.)	Middle Volgian Substage, <i>Dorsoplanites panderi</i> Zone	Bogolubov (1911, p. 276, pl. IV, fig. 10)
SGM-1358-14	Dorsal centrum	Plesiosauria indet./ <i>Colymbosaurus</i> cf. <i>trochanterius</i> Owen	Moscow district	Middle Volgian Substage, <i>Dorsoplanites panderi</i> Zone	Kiprijanoff (1883, taf. XV, fig. 3), Bogolubov (1911, p. 271)
SGM-1358-32	Articular surface of the dorsal centrum	Plesiosauria indet./ <i>Colymbosaurus</i> <i>sklerodirus</i> Bogolubov	Moscow district	Middle Volgian Substage, <i>Dorsoplanites panderi</i> Zone	Bogolubov (1911, p. 293, pl. V, fig. 3)
SGM-1358-34, 35	Mesopodial element and phalanx	Plesiosauria indet./ <i>Colymbosaurus</i> <i>sklerodirus</i> Bogolubov	Moscow, Vorobyovy Gory	Middle Volgian Substage, <i>Dorsoplanites panderi</i> Zone	Bogolubov (1911, p. 301, pl. VII, fig. 5–8)
SGM-1358-26–29, 33, 35, 36, 93 (disjunctive numbers are due to inadvertence of SGM worker)	Two cervical vertebrae, fragments of neural arches and ribs, left humerus, fragment of indeterminate bone	Colymbosaurus sp./ <i>Colymbosaurus</i> <i>sklerodirus</i> Bogolubov, 1911	Moscow, Vorobyovy Gory	Middle Volgian Substage, <i>Dorsoplanites panderi</i> Zone	Bogolubov (1911, p. 280, pl. IV, fig. 5; pl. V, fig. 1, 2, 4, 5, 8; pl. VI, fig. 1–7; pl. VII, fig. 5–8)
SGM-1358-46 SGM-1445-08	distal fragment of propodial bone Incomplete propodial bone	Colymbosaurinae indet. Colymbosaurinae indet.	Moscow (Mnevniki vill.) Moscow (detailed information on the specimen is missing)	Middle Volgian Substage Volgian Stage	Bogolubov (1911, p. 303, pl. VII, fig. 1, 2)
YKM 44028/1-24	Incomplete vertebral column and hind limb	<i>Colymbosaurus</i> sp.	Bank of the Volga River near Gorodischi vill., Ulyanovsk district, Ulyanovsk region	Middle Volgian Substage, <i>Dorsoplanites panderi</i> Zone	
YKM 55413	Incomplete limb in matrix	Colymbosaurinae indet.	Bank of the Volga River near tp. Detsky sanatory, Ulyanovsk region	Middle Volgian Substage, <i>Epivirgates nikitini</i> Zone	
KP OF-9476/1-30	Incomplete postcranial skeleton, including dorsal and sacral vertebrae and hind limb	Colymbosaurinae indet./ <i>Colymbosaurus</i> sp. 1	Lopatino phosphorite mine, Moscow region	Middle Volgian Substage, <i>Virgates virgatus</i> Zone	Mitta (1984, p. 131), Gerashimov et al. (1995)
CCMGE 782/925	Incomplete propodial bone ?femur	Colymbosaurinae indet.	Moscow (Mnevniki vill.)	Middle Volgian Substage, <i>Virgates virgatus</i> Zone	Nikitin (1890, p. 213)

Colymbosaurines possess a dorsal trochanter comparable in anteroposterior width to the capitulum and even inclined anteriorly in some specimens (Knutsen et al. 2012a); the tuberosity of the humerus is markedly offset postaxially (Brown 1981; Benson and Bowdler 2014). The distal end of the humerus is very thin dorsoventrally (Benson and Bowdler 2014), whereas the distal end of the femur is relatively thick dorsoventrally (Benson and Bowdler 2014), and this corresponds well to the state in more basal cryptoclidids.

The features discussed above are applied herein for the identification of humeri and femora among isolated propodials in studied material.

Systematic palaeontology

Sauropterygia Owen, 1860

Plesiosauria de Blainville, 1835

Cryptoclididae Williston, 1925

Colymbosaurinae Benson et Bowdler, 2014

Ontogenetic state and diversity of Russian colymbosaurines

Propodial bones of different sizes are present in the described material. Unfortunately, their fragmentary preservation does not make it possible to take measurements for morphometric analysis. However, the difference in sizes is considerable: there are small specimens with a distal end width of 92–100 mm (SDM KP RP-9476/15 and SGM-1358-46) and large (SGM 1358-26; YKM44028/2), similar in size to some British specimens (e.g. NHMUK PV OR31787; CAMSM J.59736), with a preserved width of the distal end of 250 mm (full width could be up to 280 mm) and a length of 545 mm (YKM44028/2). Both the large and small propodial bones belong to mature animals, having clearly demarcated distal facets and a prominent anteroposteriorly orientated distal ridge on the facets. Epipodial and mesopodial elements are well ossified and polygonal in outline. Delayed mesopodial ossification is characteristic for many tetrapods, including sauropterygians (Caldwell 1997). Rounded, poorly ossified and loosely arranged epipodial and mesopodial elements, as well as the lack of demarcated distal facets on propodials, have been described in juvenile individuals of *Cryptoclidus* (Brown 1981; Caldwell 1997), *Djupedalia* and *Spitrasaurus* (Knutsen et al. 2012b, c). In the adult plesiosaurs, epi- and mesopodial elements are polygonal and tightly packed (Caldwell 1997).

The fusion of neural arches and centra is completed without any visible suture in all studied specimens, both large (SGM-1358-26; YKM44028/1-24) and small (KP RP-9476/15), which indicates an adult state, and this is a leading criteria for maturity identification sensu Brown (1981).

From this, we conclude that all specimens we have studied are adult or young adult animals. This implies the existence of

two size classes of colymbosaurines (and probably representatives of two different taxa) in the Middle Russian Sea during the middle Volgian (see discussion). The large colymbosaurines, similar to *C. megadeirus*, have been recovered exclusively from the Dorsoplanites panderi Ammonite Zone, whereas the smaller individuals originate from the Virgatites virgatus and Epivirgatites nikitini zones.

Anatomical description

Colymbosaurus sp. SGM-1358-26–29, 33, 35, 36, 93 (Fig. 3)

SGM-1358-26–29, 33, 35, 36, 93 (Fig. 3) was originally described by Bogolubov as a new species of *Colymbosaurus*—“*Colymbosaurus sklerodirus*” (Bogolubov 1911)

The specimen includes two posterior cervical vertebrae (SGM-1358-27, SGM-1358-93) (Fig. 3c–j). The vertebra possess a thin ridge, connecting the rib facet and neural arch (Fig. 3g, j). Articular faces are circular in outline; their lateral edges bear a rugose texture (Fig. 3c, d). Rib facets are dorsoventrally high and located in the lower part of the lateral surface of the centrum (Fig. 3g, j).

The element (SGM-1358-33) referred to by Bogolubov as a coracoid is strongly weathered bone fragment, without any distinctive facets and surfaces.

The left humerus (SGM-1358-26) has been repaired using plaster. This bone is massive and elongated, being 403 mm long as preserved. It is characterised by pronounced posterodistal expansion (Fig. 3a). The tuberosity is wide and markedly offset postaxially, but partially eroded in the posterior part (Fig. 3b). The proximal end of the bone has a massive capitulum (105 mm in diameter) partially destroyed by boring animals: traces of *Gastrochaenolites* isp. are common in bones and other fossils from the Dorsoplanites panderi Zone of Moscow and surroundings (Baraboshkin 2017; Zverkov et al. 2017). The capitulum flattened surface is set at an angle of 75° relative to the long axis of the bone. The diaphysis is rounded in cross-section (diameter—100 mm). The distal end is strongly weathered and damaged by bioerosion, and therefore, any distal ridge is not preserved (Fig. 3k).

Colymbosaurus sp. YKM 44028/1-24 (Figs. 4, 5 and 6)

The incomplete vertebral column YKM 44028/1-24 (Figs. 4 and 5) includes 6 cervical, 11 dorsal and 6 caudal vertebrae all of which are isolated.

The articular faces of the cervical vertebrae are circular in outline, and their dorsal surface is flattened and slightly concave at the floor of the neural canal (Fig. 4a, b, h, k). The vertebrae are anteroposteriorly shorter than dorsoventrally tall (length to height ratio = 0.8; length to width ratio = 0.68). The



Fig. 3 Left humerus and vertebrae of *Colymbosaurus* sp.: **a, b, k** humerus (SGM-1358-26) in dorsal (**a**), proximal (**b**) and distal (**k**) views; **c–j** posterior cervical vertebrae SGM-1358-27 (**c, e, g, h**) and

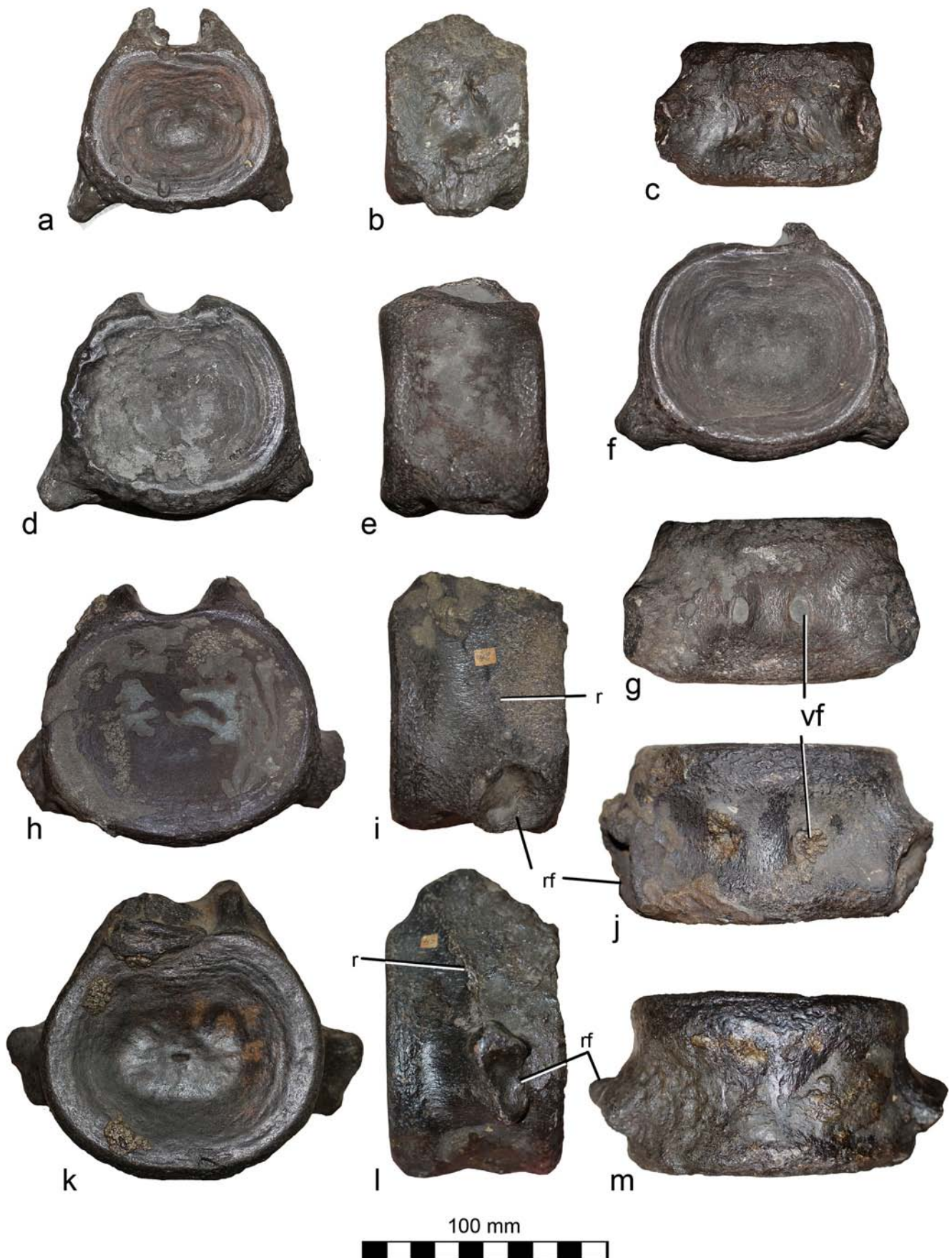
SGM-1358-93 (**d, f, i, j**) in anterior (**c**), posterior (**d**), dorsal (**e, f**), right lateral (**g, j**) and ventral (**h, i**) views. *Gastrochaenolites* traces are shown with arrows

ventral surfaces are weakly convex, lack a narrow ventral ridge and bear large oval vascular foramina (Fig. 4c, g, j, m). The rib facets of posterior cervical vertebrae are connected to the neural arches by a thin ridge (Fig. 4i, l). The rugose texture on peripheral edge of posterior cervical vertebrae is less pronounced than in SGM-1358-27 and SGM-1358-93.

Dorsal vertebrae are rounded and taper slightly dorsally in articular view, with a shallow indentation at the base of the neural canal (Fig. 5a, b). The height to width ratio is 0.9. They are relatively anteroposteriorly short (length to height ratio = 0.65; length to width ratio = 0.6). Preserved neural arches demonstrate medially confluent zygapophyses (anterior zygapophyses to centrum width ratio is 0.5; Fig. 5a, d).

The anterior caudal vertebrae possess circular articular faces, with a height to width ratio of 0.85 (Fig. 5e) and lack chevron facets (Fig. 5e, g). The articular faces of middle caudal vertebrae are hexagonal in shape (Fig. 5h). They are relatively short (length to height ratio = 0.6). Chevron facets are prominent on both anterior and posterior edges and somehow hastate in outlines (Fig. 5i, j). The flattened ventral surface bears paired vascular foramina (Fig. 5j).

The right femur YKM 44028/2 (Fig. 6) is damaged and lacks the posterodistal expansion—the supernumerary facet is broken. There are rugose muscular crests near the proximal end on the ventral surface of the bone. The entire ventral and dorsal surfaces of the bone are covered by well-defined



◀ **Fig. 4** Selected cervical vertebrae of *Colymbosaurus* sp. (YKM 44028/1-24): **a–g** anterior to middle cervical vertebrae, **h–m** posterior cervical vertebrae, in anterior (**a, d, h, k**), left lateral (**b, e, i, l**), posterior (**f**) and ventral (**c, g, j, m**) views. Abbreviations: r—ridge, connecting neural arch and rib facet; rf—rib facet; vf—vascular foramina

grooves running proximodistally. The proximal end is roughly circular in outline with a protruding dorsal trochanter which is not offset relative to the capitulum (Fig. 6b). The distal portion of the femur is slightly flattened dorsoventrally (Fig. 6h). The angle between the distal tibial and fibular facets is about 170°. Tibia, fibula, tibiale, the first and fourth distal carpals and nine autopodial elements (some of which may be metatarsals) are associated with the propodial bone. The tibia has a characteristic trapezoidal shape in dorsal view with a tapered anterior edge (Fig. 6f, l), and the fibula is diamond-shaped in dorsal view and considerably short proximodistally compared to its anteroposterior length. Both zeugopodial elements bear grooves on their proximal surfaces for the articulation with the distal ridge of the femur (Fig. 6l, m). However, it appears that the epipodial proximal grooves have been deepened by dorsolateral compression during preservation. There is a row of preaxial accessory ossifications, two of which articulate with the tibia and one with the tibiale (Fig. 6f, i).

Colymbosaurinae indet. SDM KP OF-9476/1-30 (Figs. 7 and 8a–n)

The specimen SDM KP OF-9476/1-30 represented by incomplete limb and a continuous series of 15 vertebrae, mounted on wooden plate, which makes difficult its study. Several vertebra were detached and photographed in all standard views (Fig. 7).

There are 13 dorsal and 2 sacral vertebrae. They are significantly elongated compared to YKM 44028/1-24 (length to height ratio is 1).

The articular surfaces of the dorsal vertebral centra are oval in outline, being mediolaterally wider than tall (height to width ratio is 0.8). They are concave just under the neural canal. The neural canal is taller than wide, as in *Colymbosaurus svalbardensis* (Roberts et al. 2017). Vascular foramina are widely spaced dorsolaterally (Fig. 7c, e, h, i). The anterior zeugopophyses of posterior dorsal vertebrae are relatively mediolaterally wide, constituting 65% of centrum width (Fig. 7f). The rib processes on the sacral vertebrae are protruding and directed posterolaterally, and the rib facets of sacral vertebrae are semi-oval in outline, tapered ventrally (Fig. 7l).

Although the only distal portion of the propodial bone is preserved in SDM KP OF-9476/1-30 (Fig. 8a), it is similar to those previously described and is characterised by a prominent distal ridge on the articular surface. The angles between the facets for the radius/tibia, ulna/fibula and postaxial supernumerary facet are respectively 150° and 140°. Epipodial and autopodial elements are associated with the propodial bone.

The radius/tibia has a trapezoidal shape in dorsal view, tapering anteriorly; ulna/fibula is semi-pentagonal in outline in dorsal view, posteriorly it contacts a postaxial supernumerary ossicle (pisiform). The other mesopodial elements are roughly rectangular in outline and isometric in dorsal and ventral views (their height and length are substantially equal) (Fig. 8d–f). There are isolated metatarsals/metacarpals and phalanges in the material (Fig. 8g–n).

Colymbosaurinae indet. SGM-1445-08, CCMGE 782/925, SGM-1358-46 (Fig. 8p–v)

Several partial propodials of small colymbosaurines from Moscow (several historical localities on Moscow River, which are now agglomerated by Moscow) are similar to SDM KP OF-9476/1-30 with strong posterodistal expansion and distal ridges on the epipodial facets.

The posterior part of the distal end of SGM-1358-46 (Fig. 8u, v) is broken. The distal end is strongly flattened dorsoventrally similar to the humerus NHMUK PV OR31787 (see Benson and Bowdler 2014, fig. 1). The surface of the bone is rugose, covered with furrows. The facets are oriented as in the propodials described above. The angle between the facets for the radius/tibia and ulna/fibula is 40°. There is a prominent ridge on the distal epipodial facets.

Colymbosaurinae indet. YKM 55413 (Fig. 8t)

Radius/tibia, ulna/fibula and two postaxial supernumerary elements are preserved in situ articulated with an incomplete propodial bone YKM 55413 (Fig. 8t). The posterior edge of the distal end expands posteriorly which greatly increases the width of the distal end of the bone. The maximum width of the distal end of the propodium is 114 mm. The anterior edge of the bone protrudes slightly forward near the distal end, forming a keel. The distal facet is oriented as in the specimens described above. The angle between the facets of the radius/tibia and ulna/fibula is in the range 140–150°. The facet for the postaxial ossifications is one third of the width of the distal edge. The postaxial accessory element is subtriangular in outline and resembles that of *C. svalbardensis* (Knutsen et al. 2012a) but is more elongated anteroposteriorly. Posterior to this is another small element, rounded in outline. The epipodial elements appear to be fused with each other and with the propodial bone, which could indicate that the animal is an old adult (Brown 1981; Caldwell 1997). The limb YKM 55413 looks similar to the forelimb of '*Plesiosaurus*' *manselii* in Hulke (1870 t. 1, fig. 3) in general proportions and by the presence of elements tightly adjacent to each other and to the propodial bone.



Fig. 5 Selected dorsal and caudal vertebrae of *Colymbosaurus* sp. (YKM 44028/1-24): **a–d** dorsal; **e–g** anterior caudal; **h–j** caudal; in anterior (**a**), posterior (**e**, **h**), lateral (**c**, **f**, **i**), dorsal (**d**) and ventral (**g**, **j**) views. Abbreviations: chf—chevron facets; pz—posterior zygapophysis; rf—rib facet; tp—transverse process; vf—vascular foramina

Discussion

Accessory limb ossifications

The limbs in colymbosaurs as in some other representatives of the family Cryptoclididae (Caldwell 1997; Knutsen et al. 2012b) contain additional pre- and postaxial ossifications variously expressed in different specimens.

Postaxial ossification in colymbosaurines is represented by two elements located along the posterodistal edge of the propodial bone. The position of the first large element and its contact with the posterior edge of ulna/fibula suggests that this element is homologous to pisiform bone, and is interpreted in this way by other authors (Andrews 1910;

Smellie 1917; Caldwell 1997). The location of the second postaxial element is not homologous with known elements, and it should therefore be considered as a neomorphic ossification.

Preaxial ossifications in the form of small rounded bones were described for some plesiosaur individuals (Andrews 1910; Smellie 1917; Brown 1981; Caldwell 1997; Knutsen et al. 2012b). In some plesiosaurs, preaxial accessory elements are well developed and form a preaxial accessory digit (Knutsen et al. 2012b). In case if preaxial ossifications are present, the leading edge of the epipodial and mesopodial elements lacks perichondral bone. The emergence of preaxial ossifications and loss of perichondral bone on the leading edge of the epi- and mesopodial elements could be linked to a partial loss of regionalisation in the limbs, as was hypothesised for ichthyosaurs (Maxwell et al. 2014). Preaxial elements were possibly not always ossified and could be cartilaginous, ossifying during ontogeny as in *Cryptoclidus* (Caldwell 1997); thereby, the possible presence of preaxial

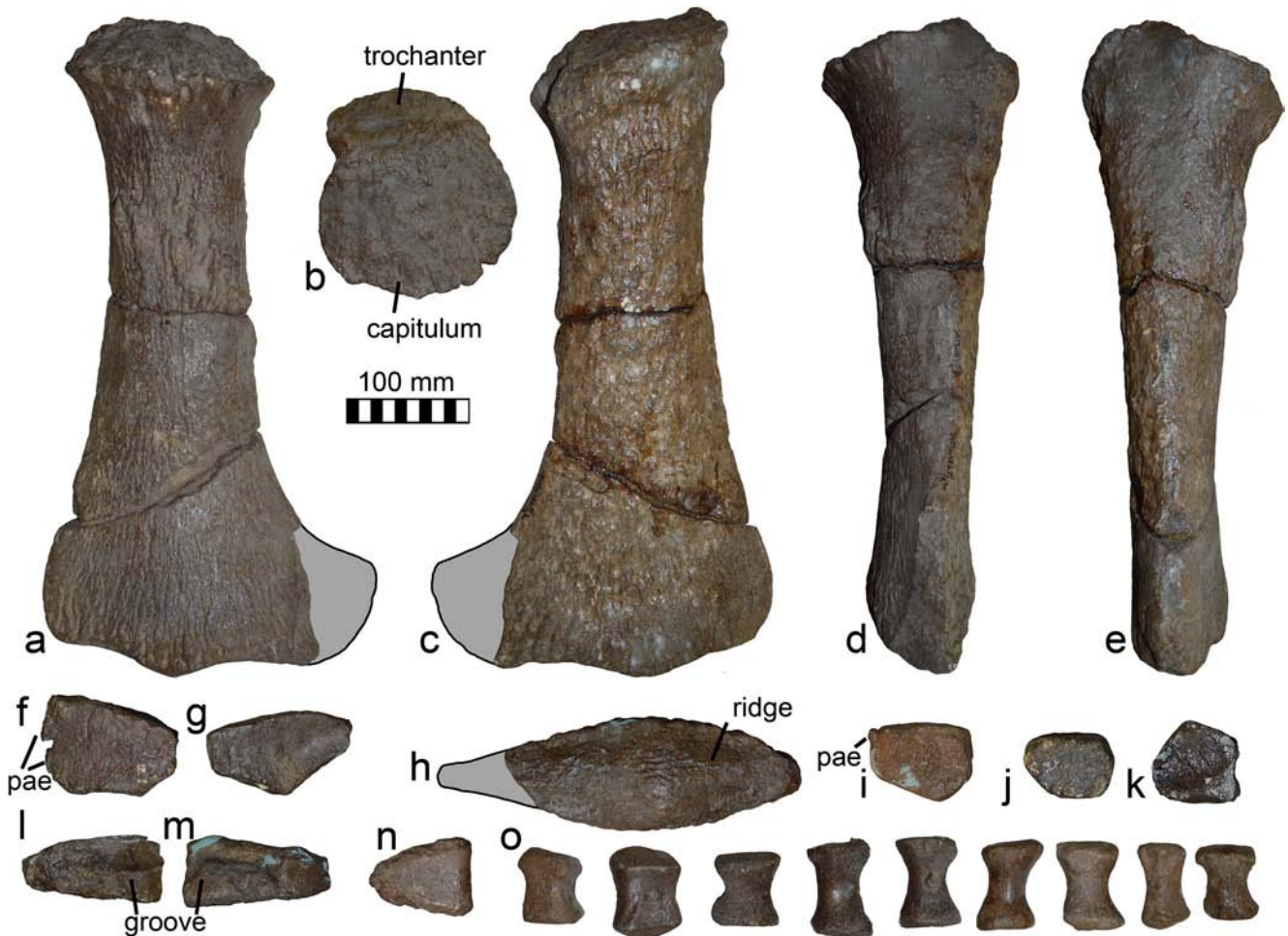


Fig. 6 Incomplete limb of *Colymbosaurus* sp. (YKM 44028/2): **a–e**, **h** right femur in ventral (**a**), proximal (**b**), dorsal (**c**); posterior (**d**), anterior (**e**) and distal (**h**) views; **f**, **l** tibia in ventral and proximal views; **g**, **m** fibula in ventral and proximal views; **i**, **n** tibiale in ventral and proximal

views; **j** distal tarsal one in ventral view; **k** distal tarsal fore in ventral view; **o** autopodial elements metatarsals and phalanges as mounted. Abbreviations: pae—preaxial accessory elements. Restored areas are coloured by grey



Fig. 7 Vertebrae of *Colymbosaurinae* indet. (SDM KP OF-9476/1-30): **a–e** dorsal vertebra in anterior (**a**), posterior (**b**), right lateral (**c**), dorsal (**d**) and ventral (**e**) views; **f–i** posterior dorsal vertebra in anterior (**f**), posterior

(**g**), left lateral (**h**) and ventral (**i**) views; **j–n** sacral vertebra in anterior (**j**), posterior (**k**), left lateral (**l**), dorsal (**m**) and ventral (**n**) views; **o–q** sacral vertebra in anterior (**o**), ventral (**p**) and right lateral (**q**) views

accessory elements could be expected in individuals with anterior edges of epipodial and mesopodial elements not involved in perichondral ossification and thus bearing “facets”. In YKM 44028/2, there are preaxial ossifications (Fig. 6f, i), indicating that these elements could emerge in *Colymbosaurus*.

The *Colymbosaurus* hind limb CAMSM J.29654-91, described by Benson and Bowdler (2014), demonstrates a peculiar configuration (J.29596 etc. in Benson and Bowdler 2014; because the individual has complex number—CAMSM J.29596–29691, J.59736–59743). If we assume that the limb is mounted correctly (which is highly unlikely; NGZ pers.

obs. Dec 2019), then there are two additional elements which form a preaxial digit anterodistally to the tibiale. These elements were interpreted by the aforementioned authors as the first digit; however, in this case, all the other digits are shifted one position preaxially, the second metatarsal bone almost loses contact with its distal tarsal bone and the fourth metatarsal develops wide contact with the distal tarsals 2 + 3 and has a weak contact with the distal tarsal 4. Such a configuration appears very unconvincing, differing from all other known sauroptrygians, and requiring a “frame-shift” (see, e.g. Wagner and Gauthier 1999; Wang et al. 2011). In view of the absence of the distal tarsal 5 in CAMSM J.29654-91, we assume that in the specimen the fifth digit could be absent in the material (lost during preservation), which led to a misinterpretation of the elements. If this assumption is correct, the preaxial accessory digit is present in CAMSM J.29654-91. This assumption is supported by the absence of perichondral ossification on the leading edge of the epipodial and mesopodial elements of CAMSM J.29654-91. The other way to resolve this problem is shifting of four most anterior digits postaxially one position in CAMSM J.29654-91. The discussed configuration and morphology distinguishes *Colymbosaurus megadeirus* from *C. svalbardensis*, in which the first metatarsal is more robust and lacks the diaphyseal ossification along the anterior edge; thereby, this is an additional character for distinguishing the species of *Colymbosaurus*.

Discussion on the possible routes of marine reptile distribution during the Late Jurassic

Currently, a number of taxa of the Late Jurassic marine reptiles are known only from certain localities and their representatives are not found elsewhere: e.g. plesiosaurs—*Kimmerosaurus* (Brown 1981), *Tatenectes* (O’Keefe and Street 2009), *Spitrasaurus* (Knutsen et al. 2012b), *Djupedalia* (Knutsen et al. 2012c) and *Vinialesaurus* (Gasparini et al. 2002); ichthyosaurs—*Caypullisaurus* (Fernandez 1997) and *Nannopterygius* (Huene 1922).

However, examples of reptiles with wide geographical distribution allow us to propose distribution routes and relationships of the Mesozoic marine herpetofauna (Bardet et al. 2014). Such investigations have been already made by different researchers, in particular to explain the similarities of the Mesozoic marine herpetofauna of Europe and South America (Gasparini 1992; Gasparini and Spalletti 1993; Gasparini and Fernández 1997, 2005; Gasparini and Iturralde-Vinent 2006; Fernández and Maxwell 2012; Pardo Pérez et al. 2012; Stinnesbeck et al. 2014; Zverkov et al. 2015a; Zverkov and Efimov 2019; Zverkov and Prilepskaya 2019).

According to palaeogeographical reconstructions (Fig. 9), the Brest (Pripyat) Strait connected the Middle Russian Boreal Basin with the Polish Basin until the end of the middle Volgian Panderi Chron or early beginning of the Virgatus

Chron (Sasonova and Sasonov 1967; Mesezhnikov and Zakharov 1974; Rogov et al. 2008; Rogov 2012, 2013a). It is determined by identical sequences of virgatitid ammonites developed exclusively in the Polish and Middle Russian seas. Since the *Virgatus* Chron (except its early beginning, as *Virgatites gerassimovi* Mita and *V. pusillus* (Michalsky) were identified from the Polish Lowland, cf. Matyja and Wierzbowski, 2016), the Brest (Pripyat) Strait disappeared and the Middle Russian Sea became almost isolated from the west and south, where the low-lying accumulative plains, lakes, lagoons and river systems were formed (Sasonova and Sasonov 1967; Baraboshkin 2002, 2003). This has led to a considerable isolation of the Middle Russian Boreal Sea from the Tethys, and still the connection with Arctic basins persisted (Sasonova and Sasonov 1967; Baraboshkin 2002, 2003). Only in the Early Cretaceous (Berriasian) was communication between the basins restored by re-opening of the Brest (Pripyat) Strait, as well as by appearance of direct connection from the south (Sasonova and Sasonov 1967; Baraboshkin 2002, 2003).

In addition, during the Kimmeridgian and Volgian, the Middle Russian Sea and NW European basins were connected by the Norwegian–Greenland Seaway (Fig. 9; Mesezhnikov and Zakharov 1974; Mutterlose et al. 2003; Rogov 2012). Judging from the data on the distribution of ammonites in the Kimmeridgian, immigration through the Norwegian–Greenland Strait was limited (Rogov 2012), but in the early Volgian, the situation has changed significantly. Initially evolved in northwestern Europe, Pectinatitinae ammonites widely spread from northern France to the Lena River basin, where the nearly identical successions of these ammonites are found (Rogov and Zakharov 2009). This degree of similarity between ammonite faunas of the Anglo-Paris Basin with those of Arctic persisted also in the beginning of the middle Volgian. Later, a significant differentiation of ammonite communities began, and only for the late Volgian, it is possible to identify the resumption of active exchange of fauna between the NW Europe and the Middle Russian Sea, particularly noticeable at the end of the late Volgian (Early Berriasian, Lamplugh Chron) (Rogov 2013b, 2014b). During the Kimmeridgian and Volgian, Boreal ammonites penetrated from the Russian Basin southwards to the present-day Northern Kazakhstan (Sokolova 1939; Mesezhnikov et al. 1987), while buchiid bivalves spread to Azerbaijan at the end of the Tithonian (Zakharov and Kasumzade 2005). Data from ammonites shows that at the same time a connection between the Middle Russian Sea and the Arctic Basin by the Mezen–Pechora strait system was open from the end of the middle Volgian (Rogov 2010b), but was restricted during the middle part of the middle Volgian. Ammonite faunas of the Nikitini Zone and its correlatives are showing numerous common elements elsewhere in the Arctic, while ammonites of the *Virgatus* and *Maximus* Zones are markedly different.

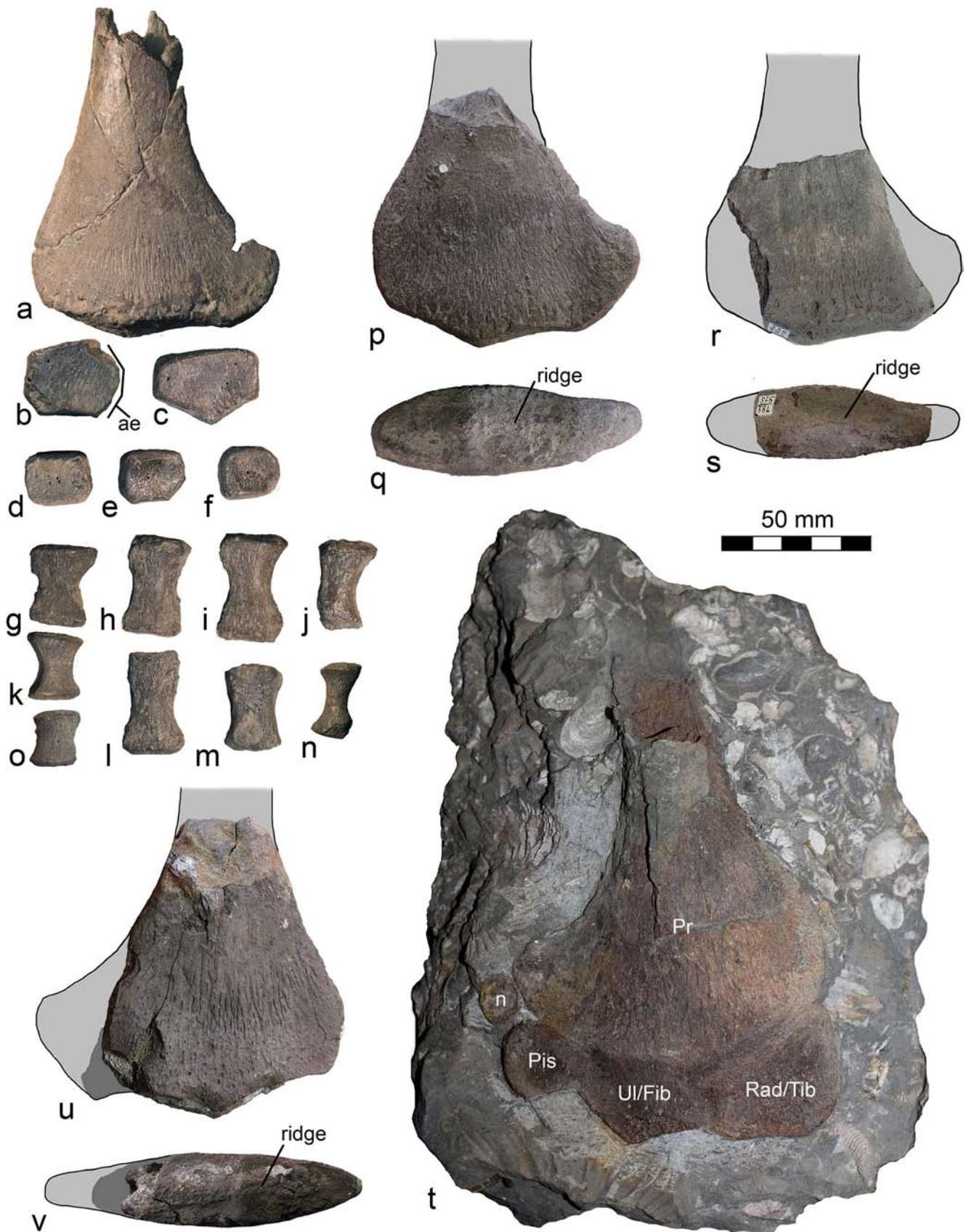


Fig. 8 Incomplete limbs and propodial bones of Colymbosaurinae indet. **a–o** Incomplete limb SDM KP OF-9476/1-30: **a** femur/humerus; **b** tibia/radius; **c** fibula/ulna; **d–f** mesopodial elements; **g–n** autopodial elements phalanges and metatarsals/metacarpals; **t** YKM 55413 in situ; **p, q** SGM 1445-08; **r, s** CCMGE 782/925; **u, v** SGM-1358-46; in dorsal/ventral (**a, p, r, u, t**) and distal (**q, s, v**) views. Restored areas are coloured by grey; dark area is state of preservation during Bogolubov's (1911) investigations. Abbreviations: *ae* anterior edge; *n* neomorphic ossification, *Pispisiform*, *Prpropodium*, *Rad/Tibradius/tibia*, *Ul/Fib* ulna/fibula

The presence of the Hispanic corridor (Fig. 9) during the Kimmeridgian is not obvious and data are insufficient (Stanley 1994; Hillebrandt et al. 1992), although the similarity of the Kimmeridgian ammonite faunas of Mexico and Southern Europe allows us to consider it as one of the migration routes of invertebrates (Villaseñor et al. 2012). In the early Tithonian, the Hispanic corridor apparently began to operate more intensively, which led to an exchange of fauna of the Eastern Paleopacific and the Western Tethys basins (Damborenea and Manceñido 1979; Hillebrandt et al. 1992; Gasparini 1992; Gasparini and Spalletti 1993; Gasparini and Iturralde-Vinent 2006).

The “Boreal route” (Fig. 10), according to the analysis of the distribution of invertebrates, functioned in the north–south

direction (Zakharov and Rogov 2003) and northern elements penetrated only to the territory of modern Mexico (bivalves and rarely belemnites, see Buitrón 1984; Zell et al. 2013) or to California (often bivalves and belemnites, rarely ammonites; Imlay 1961; Imlay and Jones 1970). Southward immigration of Boreal and Subboreal ammonites along the Pacific coast of North America is indicated by the distribution of aulacostephanids and cardioceratids (Rogov and Poulton 2015).

Ammonite distribution shows that the “Trans-Erythraean corridor” (through the strait between Africa and Antarctica and beyond) opened in the Tithonian (Cecca 1999).

To reconstruct possible migration routes of the Jurassic marine herpetofauna, we have applied data on the palaeobiogeographical distribution of some widespread ichthyosaurs and plesiosaurs. Only a few widespread genera and groups of closely related taxa are known: genus *Ophthalmosaurus* Seeley 1874; *Arthropterygius* Maxwell, 2010 (Zverkov and Prilepskaya 2019); *Undorosaurus* Efimov, 1999 (Arkhangelsky and Zverkov 2014; Zverkov and Efimov 2019); group of ichthyosaurs with intermedium–humeral contact *Brachypterygius* Huene, 1922, *Aegirosaurus* Bardet et al (1993) and *Grendelius* McGowan, 1976 (see Zverkov et al. 2015b). Among

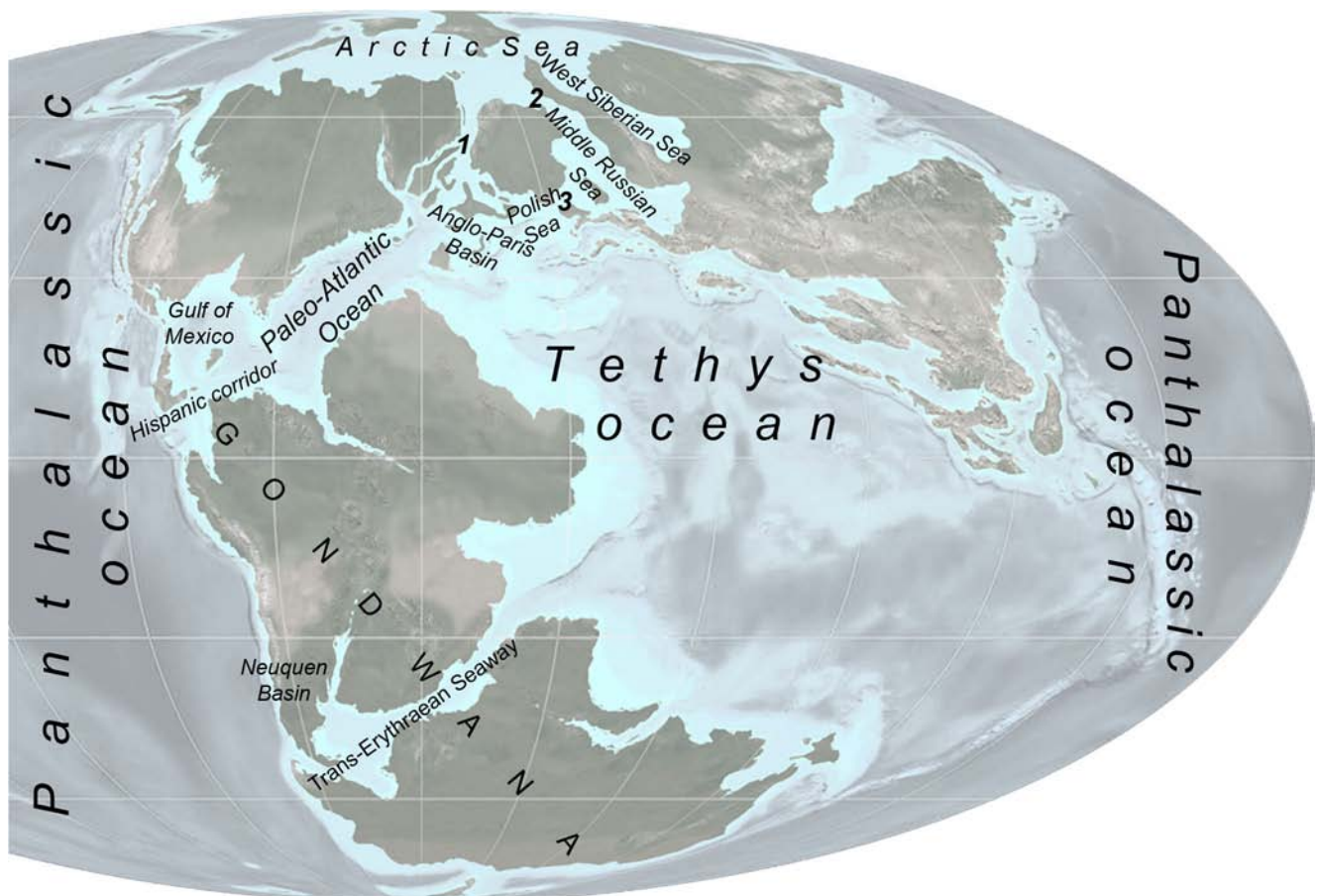


Fig. 9 Palaeogeographical map of the Upper Jurassic. 1 Norwegian–Greenland Seaway; 2 Mezen–Pechora strait system; 3 Brest (Pripyat) Strait. Palaeogeographical reconstruction used by courtesy of R. Blakey (Blakey and Colorado Plateau Geosystems, Inc. 2011)

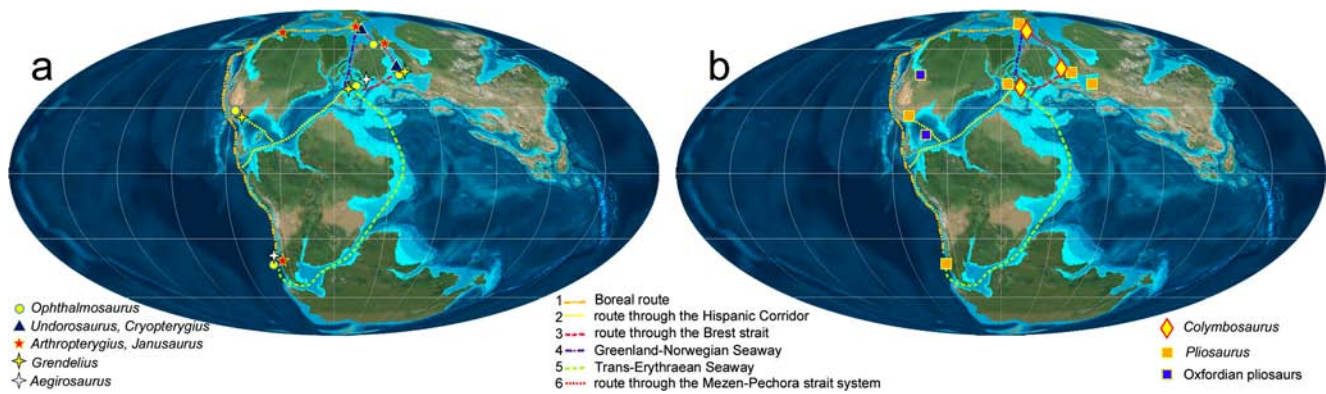


Fig. 10 Occurrence of some ichthyosaurs (a) and plesiosaurs (b) during the Late Jurassic (Kimmeridgian–Tithonian/Volgian) showing the possible dispersal routes. Palaeogeographical maps used by courtesy of R. Blakey (Blakey and Colorado Plateau Geosystems, Inc. 2011)

plesiosaurs, only two genera—*Pliosaurus* Owen, 1841 (Owen 1841a, b) and *Colymbosaurus*—have had a wide distribution. Analysing dispersion of the aforementioned taxa in the Upper Jurassic localities of the World, we assume the following distribution (Table 2).

Boreal ichthyosaurs such as *Arthropterygius* (Northern Canada, Svalbard, Franz Josef Land, European Russia and Argentina) demonstrate widespread dispersion in high latitudes (Zverkov et al. 2015a; Zverkov & Prilepskaya 2019). It was suggested that *Arthropterygius* originated in the Arctic, and then migrated to the South along the Paleopacific coast of the American continent to Antarctic latitudes (Fig. 10a; Fernandez and Maxwell 2012; Zverkov et al. 2015a). A similar migration route was assumed for the late Kimmeridgian ammonites *Zenostephanus* (Rogov and Poulton 2015). However, the Hispanic corridor connecting the Paleopacific and Tethys basins can be also used by *Arthropterygius* as dispersal route. *Arthropterygius* could penetrate in the Tethys basin though the Brest (Pripyat) Strait or through the Norwegian–Greenland Seaway (Fig. 10). But the lack of *Arthropterygius* remains in the well-studied Upper Jurassic deposits of Western Europe, however, indirectly contradicts such a variant of distribution.

Undorosaurus (European Russia) and ‘*Cryopterygius*’ (Svalbard, Central Europe), being synonymous genera (for discussion, see Arkhangelsky and Zverkov 2014; Zverkov and Efimov 2019), demonstrate a strong relation between the Polish, Middle Russian and the Arctic seas during the late middle Volgian (Fig. 10a; Zverkov and Efimov 2019).

The genus *Ophthalmosaurus* mainly known from the Callovian and Oxfordian of the North-West Europe (UK) was also found in the Oxfordian deposits in the western USA, in the Tithonian of Mexico and possibly Argentina (Buchy 2010; Fernandez and Maxwell 2012), as well as in European Russia (Zverkov et al. 2015a; Arkhangelsky et al. 2018), which demonstrates migration between the faunas inhabiting the Panboreal palaeobiogeographic superrealm and Tethys–Panthalassa superrealm (Table 2). This

interrelation is supported by finds of the genus *Grendelius* both in Russia (Efimov 1998; Arkhangelsky 1997, 1998, 2000, 2001; Zverkov et al. 2015b), and in Europe (McGowan 1976, 1997) and possibly even in Mexico (Buchy and López Oliva 2009). It is probable that *Grendelius* penetrated the Middle Russian Sea in the middle Volgian through the Brest Strait until its closure in the late middle Volgian. The medium-sized ichthyosaur *Aegirosaurus* is typical for Europe (Bardet and Fernandez 2000; Fischer et al. 2011) and has been identified in the Neuquén Basin (Gasparini et al. 2015). The “Boreal” and “Hispanic” routes could be possibly used for migration of *Ophthalmosaurus* and *Aegirosaurus*. Connection in the Boreal and Tethys basins could take place by the Brest (Pripyat) Strait and by the Norwegian–Greenland Seaway.

Available data on plesiosaur distribution are incomparably scarcer. The genus *Pliosaurus* was widely spread in the Boreal areas. Representatives of this genus are common in Western Europe (England, France, ?Germany). Numerous remains of this genus have been found in the Volgian deposits of Svalbard and European Russia (Bogolubov 1911; Rozhdestvensky 1947; Novozhilov 1948; Gerasimov et al. 1995; Knutsen et al. 2012a, b), and isolated records are known from Kazakhstan (Malakhov 1999) (Table 2). This confirms herpetofauna exchanges between the Boreal and Tethyan basins. Findings of *Pliosaurus* in Mexico and Argentina (Table 2) may indicate their distribution through the “Hispanic Corridor” (Fig. 10).

Presently, authentic remains of *Colymbosaurus* have been found in Western Europe (UK, France), Svalbard and European Russia (see Table 2). Russian specimens of *Colymbosaurus* complement existing data on the composition of the Late Jurassic Boreal marine herpetofauna associations of the Northern Eurasia.

In conclusion, the main herpetofauna exchange between the Tethyan and Boreal basins in the late Kimmeridgian and early Tithonian occurred through the Brest (Pripyat) Strait. Herpetofauna of the NW Europe (consisting *Pliosaurus*,

Table 2 Stratigraphical and geographical distribution of some widespread Kimmeridgian and Tithonian (Volgian) ichthyosaur and plesiosaur genera

Age	Oxfordian	Kimmeridgian	Tithonian (for Tethys)		Ber
Geogr.	Lower	Upper	Lower	Upper	
	Volgian (for Boreal Basin)				
	Lower	Middle	Upper		
NW Europe (UK; France; Germany)	–	<i>Ophthalmosaurus</i> (Etches and Clarke 1999; Moon, Kirtin 2018) <i>Pliosaurus</i> (Benson et al. 2013) <i>Colymbosaurus</i> (Benson and Bowdler 2014)	<i>Brachypterygius</i> (McGowan and Motani 2003) <i>Ophthalmosaurus</i> (Mansell-Pleydell 1890; Sauvage 1899; Delair 1958; Moon, Kirtin 2018) <i>Pliosaurus</i> (Delair 1958; Clarke, Etches 1992; Bardet et al. 1993; Sauvage 1899, 1911; Benson et al. 2013)	<i>Ophthalmosaurus</i> (Bardet et al. 1997) <i>Grendelius</i> (McGowan 1976) <i>Aegirosaurus</i> (Bardet and Fernández 2000) <i>Colymbosaurus</i> (Etches and Clarke 1999)	<i>Colymbosaurus</i> (Sauvage 1888; Delair 1958) <i>Pliosaurus</i> (Sauvage 1888, 1899)
Boreal basins	Middle Russian Sea	<i>Ophthalmosaurus</i> (Arkhangelsky et al. 2018)	–	<i>Undorosaurus</i> (Efimov 1999) <i>Grendelius</i> (Arkhangelsky 1997–2001; Zverkov et al. 2015b) <i>Arthropterygius</i> (Zverkov et al. 2015a; Zverkov and Prilepskaya 2019) <i>Pliosaurus</i> (Bogolubov 1911; Rozhdestvensky 1947; Novozhilov 1948; Gerasimov et al. 1995; Malakhov 1999) <i>Colymbosaurus</i> (Bogolubov 1911; herein) <i>Undorosaurus</i> (Druckenmiller et al. 2012; Zverkov and Efimov 2019) <i>Arthropterygius</i> (Zverkov and Prilepskaya 2019) <i>Colymbosaurus</i> (Knutsen et al. 2012a) <i>Pliosaurus</i> (Knutsen et al. 2012d)	<i>Undorosaurus</i> (Efimov 1999) <i>Ophthalmosaurus</i> (Zverkov et al. 2015a)
Svalbard (Norway)	–	–	–	–	–
Melville Island (Canada)	–	<i>Arthropterygius</i> (Maxwell 2010)	–	–	–
Neuquén Basin (Argentina)	–	–	–	<i>Arthropterygius</i> (Fernández and Maxwell 2012), <i>Aegirosaurus</i> (Gasparini et al. 2015), <i>Ophthalmosaurus</i> (McGowan and Motani 2003; Fernández and Maxwell 2012); <i>Pliosaurus</i> (Gasparini and O’Gorman 2014; O’Gorman et al. 2018)	–
Sundance Sea (USA)	–	<i>Ophthalmosaurus</i> (Gilmore 1905) <i>Megadneusaurus</i> (Knight 1898; Wahl et al. 2007) <i>Gallardosaurus</i> (Gasparini 2009)	–	–	–
Caribbean region (Cuba and Mexican Gulf)	–	<i>Pliosaurus</i> (Buchy et al. 2003)	<i>Ophthalmosaurus</i> (Buchy 2010)	<i>?Grendelius</i> (Buchy and López Oliva 2009)	–

Colymbosaurus, *Ophthalmosaurus*, *Grendelius*) presumably used this migrational pathway, entering the Boreal Middle Russian Sea and spreading northward into the Arctic through the Mezen–Pechora strait system. However, the West European marine reptiles could use the Norwegian–Greenland Seaway, so they could penetrate directly the Boreal basin bypassing the Middle Russian Sea. Further, their penetration into the Middle Russian Sea from the polar waters could occur through the Mezen–Pechora strait system.

Large and small colymbosaurines in the Volgian of European Russia

The colymbosaurinae specimens from the Volgian of European Russia are represented by two size classes. The large colymbosaurines have been recovered exclusively from the Dorsoplanites panderi Ammonite Zone; younger specimens distributed in the Virgatites virgatus and Epivirgatites nikitini zones are all represented by small-sized but mature individuals; thereby, we concluded that they could be a distinct *Colymbosaurus* species, or even a distinct colymbosaurine genus, and therefore referred them to as Colymbosaurinae indet., despite the fact that their propodial bones demonstrate a suit of traits characteristic of *Colymbosaurus* (extensive posterodistal expansion bearing a postaxial facet equal in size to the epipodial facets and a prominent anteroposteriorly orientated ridge on the distal articular facets). This size disparity is unlikely due to sexual dimorphism, because of the lack of temporal overlap between the two morphs. However, the fragmentary nature of the material available prohibits the assignation of the material to lower taxonomic levels; thereby, the hypothesis of the presence of at least two different colymbosaurine taxa in the Middle Russian Sea during the Volgian should be considered instead.

The fact that large *Colymbosaurus* disappear in the Middle Russian Sea after the Panderi Chron and that small *Colymbosaurus*-like colymbosaurines are dominate since then is of certain interest as it correlates with the Brest (Pripyat) Strait closure and consequent isolation of the Middle Russian Sea from the Tethys (see above). Probably, this isolation was a driver for colymbosaurine evolution in the Middle Russian Sea.

Conclusions

Our reappraisal of some historical plesiosaur specimens from the Volgian of European Russia supports their original identification as *Colymbosaurus* (Bogolubov 1911) contra previous revisions (Storrs et al. 2000; Arkhangelsky and Sennikov 2008). Additionally, we provided descriptions of several specimens referable to as *Colymbosaurus* sp. and Colymbosaurinae indet. from the Volgian of European Russia.

At least two colymbosaurine taxa existed in the Middle Russian Sea during the Volgian. Large *Colymbosaurus* inhabited the Middle Russian Sea during the Panderi Chron when the connections with other basins were intense. Since the isolation of the Middle Russian Sea from the Tethys during the Virgatus Nikitini chronos, exclusively small *Colymbosaurus*-like colymbosaurines occur in the Middle Russian Sea.

The specimens from Russia expand the geographical range of the genus *Colymbosaurus*. Found only in the Upper Jurassic of NW Europe, Svalbard and European Russia, this plesiosaur genus is the unifying element of the herpetofauna for the listed basins, supporting active herpetofauna exchange in aquatories of Panboreal superrealm during the Kimmeridgian and early middle Volgian.

Acknowledgements We thank Yu.K. Volodina and O.E. Borodina (YKM), I.A. Starodubtseva (SGM), A.I. Klukina and P.V. Bogdanov (SDM) and M. Riley (CAMSM) for the opportunity to study the museum materials and their help that make our research as easy as possible. Attentive reviews of Espen Knutsen, Aubrey Roberts, Richard Forrest and an anonymous reviewer helped us sufficiently improve this work.

Funding information This research was supported by the state programs no. 0135-2018-0035 (Geological Institute, Russian Acad. Sci.; N. Zverkov and M. Rogov) and partly supported by the Russian Foundation for Basic Research, project nos. 18-05-01070 (MAR) and 18-35-00221 (NGZ) and by the Basic Research Program of the Presidium of RAS no. 8, project no. 0135-2018-0042 (MAR and NGZ).

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

- Andrews, C. W. (1910). *A descriptive catalogue of the marine reptiles of the Oxford Clay, based on the Leeds Collection in the British Museum (Natural History). London. Part I.* British Museum: London.
- Andrews, C. W. (1913). *A descriptive catalogue of the marine reptiles of the Oxford Clay based on the Leeds Collection in the British Museum (Natural History). London. Part II.* British Museum: London.
- Arkhangelsky, M. S. (1997). On a new ichthyosaurian genus from the Lower Volgian substage of the Saratov, Volga region. *Paleontological Journal*, 31(1), 87–90.
- Arkhangelsky, M. S. (1998). On the ichthyosaurian fossils from the Volgian Stage of the Saratov region. *Paleontological Journal*, 32(2), 192–196.
- Arkhangelsky, M. S. (2000). On the ichthyosaur *Otschevia* from the Volgian Stage of the Volga region. *Paleontological Journal*, 34(5), 549–552.
- Arkhangelsky, M. S. (2001). On a new ichthyosaur of the genus *Otschevia* from the Volgian Stage of the Volga region near Ulyanovsk. *Paleontological Journal*, 35(6), 629–634.
- Arkhangelsky, M. S., & Sennikov, A. G. (2008). Subclass Synaptosauria. In M. F. Ivakhnenko & E. N. Kurochkin (Eds.), *Fossil vertebrates of*

- Russia and neighboring countries. Fossil reptiles and birds. Part 1 (pp. 224–243). GEOS: Moscow [In Russian].
- Arkhangelsky, M. S., & Zverkov, N. G. (2014). On a new ichthyosaur of the genus *Undorosaurus*. *Proceedings of the Zoological Institute RAS*, 318(3), 187–196.
- Arkhangelsky, M. S., Zverkov, N. G., Spasskaya, O. S., & Evgrafov, A. V. (2018). On the first reliable find of ichthyosaur *Ophthalmosaurus icenicus* Seeley, 1874 from the Oxfordian-Kimmeridgian of European Russia. *Paleontological Journal*, 52(1), 49–57.
- Baraboshkin, E.J. (2002). Early Cretaceous seaways of the Russian platform and the problem of Boreal/Tethyan correlation. In J. Machalik (Ed.), *Tethyan/Boreal Cretaceous correlation. Mediterranean and Boreal Cretaceous paleobiogeographic areas in 19 Central and Eastern Europe* (pp. 39–78) r. Bratislava: VEDA, Slovak Academy of Sciences.
- Baraboshkin, E. J. (2003). Early Cretaceous straits of the Russian plate. *Bylleten MOIP Otd. geol.*, 78(4), 35–48 [In Russian].
- Baraboshkin, E.E. (2017). *Gastrochaenolites* isp. borings in phosphorite concretions of Dorsoplanites panderi zone (Volgian Stage, Upper Jurassic) of Moscow and the vicinities of Moscow. In M. A. Rogov, & V. A. Zakharov (Eds.) *Jurassic deposits of the southern part of the Moscow Syneclise and their fauna. Transaction of the Geological Institute*. 615, 320–325. Moscow: GEOS [in Russian, English summary].
- Bardet, N., & Fernández, M. (2000). A new ichthyosaur from the Upper Jurassic lithographic limestones of Bavaria. *Journal of Paleontology*, 74, 503–511.
- Bardet, N., Mazin, J.-M., & Martin, M. (1993). Une mandibule de *Pliosaurus brachyspondylus* (Reptilia, Sauropterygia) dans le Kimméridgien du Boulonnais (France). *Neues Jahrbuch für Geologie und Paläontologie Monatshefte*, 385–392.
- Bardet, N., Duffaud, S., Martin, M., Mazin, J.-M., Pereda-Suberbiola, X., & Vidier, J.-P. (1997). Découverte de l'ichthyosaure *Ophthalmosaurus* dans le Tithonien (Jurassique supérieur) du Boulonnais, Nord de la France. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 205, 339–354.
- Bardet, N., Falconnet, J., Fischer, V., Houssaye, A., Jouve, S., Pereda Suberbiola, X., Pérez-García, A., Rage, J.-C., & Vincent, P. (2014). Mesozoic marine reptile palaeobiogeography in response to drifting plates. *Gondwana Research*, 26, 869–887.
- Benson, R., Evans, M., Smith, A. S., Sassoon, J., Moore-Faye, S., Ketchum, H. F., & Forrest, R. (2013). A giant pliosaurid skull from the Late Jurassic of England. *PLoS One*, 8(5), e65989. <https://doi.org/10.1371/journal.pone.0065989>.
- Benson, R., & Bowdler, T. (2014). Anatomy of *Colymbosaurus* (Reptilia, Plesiosauroidea) from the Kimmeridge Clay Formation of the U.K., and high diversity among Late Jurassic plesiosauroids. *Journal of Vertebrate Paleontology*, 34(5), 1053–1071.
- Blakey, R.C. & Colorado Plateau Geosystems, Inc. (2011): *Reconstructing the ancient Earth*, <http://cpgeosystems.com>
- Bogolubov, N. N. (1911). *On the history of plesiosaurs in Russia*. Moscow: Tipografia Imperatorskogo Moskovskogo Universiteta [In Russian].
- Bogolubov, N.N. (1909). Sur quelques restes de deux reptiles (*Cryptodidus simbirskensis* n. sp. et *Ichthyosaurus steleodon* n. sp.), trouvés par M. le Profes. A. P. Pavlov sur les bords de la Volga dans les couches mésozoïques de Simbirsk. *Annuaire Géologique et Minéralogique de la Russie*, 11, 42–64.
- Bragin, V. Y., Dzyuba, O. S., Kazansky, A. Y., & Shurygin, B. N. (2013). New data on the magnetostratigraphy of the Jurassic–cretaceous boundary interval, Nordvik Peninsula (northern East Siberia). *Russian Geology and Geophysics*, 54(3), 335–348.
- Brown, D. S. (1981). The English Upper Jurassic Plesiosauroidea (Reptilia) and a review of the phylogeny and classification of the Plesiosauroidea. *Bulletin of the British Museum (Natural History), Geology*, 35(4), 253–347.
- Brown, D. S. (1984). Discovery of a specimen of the plesiosaur *Colymbosaurus trochanterius* (Owen) on the island of Portland. *Proceedings of the Dorset Natural Historical and Archaeological Society*, 105, 170.
- Buchy, M.-C. (2010). First record of *Ophthalmosaurus* (Reptilia: Ichthyosauria) from the Tithonian (Upper Jurassic) of Mexico. *Journal of Paleontology*, 84(1), 149–155.
- Buchy, M.-C., & López Oliva, J. G. (2009). Occurrence of a second ichthyosaur genus (Reptilia: Ichthyosauria) in the Late Jurassic Gulf of Mexico. *Boletín de la Sociedad Geológica Mexicana*, 61(2), 233–238.
- Buchy, M.-C., Frey, E., Stinnesbeck, W., & López-Oliva, J. G. (2003). First occurrence of a gigantic pliosaurid plesiosaur in the late Jurassic (Kimmeridgian) of Mexico. *Bulletin de la Société géologique de France*, 174(3), 271–278.
- Buitrón, B.E. (1984). Late Jurassic bivalves and gastropods from Northern Zacatecas, Mexico, and their biogeographic significance. In G.E.G. Westermann (Ed.) *Jurassic-Cretaceous biochronology and paleogeography of North America: Geological Association of Canada, Special Papers*, 27, 89–98.
- Bulot, L. G., Frau, C., & Wimbledon, W. A. P. (2014). New and poorly known Perisphinctoidea (Ammonitina) from the Upper Tithonian of Le Chouet (Drôme, SE France). *Volumina Jurassica*, XII(1), 113–128.
- Carpenter, K., Sanders, F., Reed, B., Reed, J., & Larson, P. (2010). Plesiosaur swimming as interpreted from skeletal analysis and experimental results. *Transactions of the Kansas Academy of Science*, 113(1/2), 1–34.
- Caldwell, M. W. (1997). Limb osteology and ossification patterns in *Cryptoclidus* (Reptilia: Plesiosauroidea) with a review of sauropterygian limbs. *Journal of Vertebrate Paleontology*, 17(2), 295–307.
- Casey, R. (1973). The ammonite succession at the Jurassic-Cretaceous boundary in eastern England. In R. Casey & P.F. Rawson (Eds.) Special Issue, *The Boreal Lower Cretaceous. Geological Journal* 5, 193–266.
- Cecca, F. (1999). Palaeobiogeography of Tethyan ammonites during the Tithonian (latest Jurassic). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 147, 1–37.
- Clarke, J.B. & Etches, S.M. (1992). Predation amongst Jurassic marine reptiles. *Proceedings - Dorset Natural History and Archaeological Society*, 113, 202–205.
- Cope, J. C. W. (1993). The Bolonian stage: an old answer to an old problem. *Newsletters on Stratigraphy*, 28, 151–156.
- Cope, J. C. W. (2013). Stage nomenclature in the uppermost Jurassic rocks of Britain. *Geoscience in South-West England*, 13, 216–221.
- Cope, J. C. W., Duff, K. L., Parsons, C. F., Torrens, H. S., Wimbledon, W. A., & Wright, J. K. (1980). A correlation of Jurassic rocks in the British Isles. Part two: Middle and Upper Jurassic. *Geological Society of London, Special Report*, 15, 1–109.
- Damborenea, S. E., & Manceñido, M. O. (1979). On the palaeogeographical distribution of the Pectinid genus *Weyla* (Bivalvia, Lower Jurassic). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 27, 85–102.
- Delair, J. B. (1958). The Mesozoic reptiles of Dorset: Part two. *Proceedings of the Dorset Natural Historical and Archaeological Society*, 80, 52–90.
- Delsett, L.L., Novis, L.K., Roberts, A.J., Koevoets, M.J., Hammer, Ø., Druckenmiller, P.S., & Hurum, J.H. (2016). The Slottsmøya marine reptile Lagerstätte: depositional environments, taphonomy and diagenesis. In B.P. Kear, J. Lindgren, J. H. Hurum, J. Milán & V. Vajda (Eds.) *Mesozoic biotas of Scandinavia and its Arctic territories. Geological Society, London, Special Publications*, 434, 165–178, <https://doi.org/10.1144/SP434.2>
- Druckenmiller, P. S., Hurum, J. H., Knutsen, E. M., & Nakrem, H. A. (2012). Two new ophthalmosaurids (Reptilia: Ichthyosauria) from

- the Agardhfjellet Formation (Upper Jurassic: Volgian/Tithonian), Svalbard, Norway. *Norwegian Journal of Geology*, 92, 311–339.
- Efimov, V. M. (1998). An ichthyosaur, *Otschevia pseudoscythyca* gen. et sp. nov. from the Upper Jurassic strata of the Ulyanovsk region. *Paleontological Journal*, 32(2), 187–191.
- Efimov, V. M. (1999). A new family of ichthyosaurs, the Undorosauridae fam. nov. from the Volgian Stage of the European part of Russia. *Paleontological Journal*, 33(2), 174–181.
- Etches, S., & Clarke, J. (1999). *Steve Etches' Kimmeridge collection illustrated catalogue*. Published privately by J Clarke.
- Fernández, M. S. (1997). A new ichthyosaur from the Tithonian (Late Jurassic) of the Neuquén Basin, northwestern Patagonia, Argentina. *Journal of Paleontology*, 71, 479–484.
- Fernández, M. S., & Maxwell, E. E. (2012). The genus *Arthropterygius* Maxwell (Ichthyosauria: Ophthalmosauridae) in the Late Jurassic of the Neuquén Basin, Argentina. *Geobios*, 45, 535–540.
- Fischer von Waldheim, G. F. (1846). Notice sur quelques sauriens fossils du Gouvernement de Moscou. *Bulletin de la Société impériale des Naturalistes de Moscou*, 19, 90–107.
- Fischer, V., Clément, A., Guiomar, M., & Godefroit, P. (2011). The first definite record of a Valanginian ichthyosaur and its implication for the evolution of post-Liassic Ichthyosauria. *Cretaceous Research*, 32, 155–163.
- Gallois, R. W. (2011). A revised description of the lithostratigraphy of the Kimmeridgian-Tithonian and Kimmeridgian-Volgian boundary beds at Kimmeridge, Dorset, UK. *Geoscience in South-West England*, 12, 288–294.
- Gasparini, Z. (1992). Marine reptiles from the circum-Pacific region. In G. E. G. Westermann (Ed.), *The Jurassic of the circum Pacific. World and regional Geology* 3, 361–364. Cambridge: Cambridge University Press.
- Gasparini, Z. (2009). A new Oxfordian pliosaurid (Plesiosauria, Pliosauridae) in the Caribbean Seaway. *Palaeontology*, 52, 661–669.
- Gasparini, Z., & Fernández, M. (1997). Tithonian marine reptiles of the eastern Pacific. In J. Callaway, & E. Nicholls (Eds.), *Ancient marine reptiles* (pp. 435–450). Academic press.
- Gasparini, Z., & Fernández, M. (2005). Jurassic marine reptiles of the Neuquén Basin: records, faunas and their palaeobiogeographic significance. In G. D. Veiga, L. A. Spalletti, J. A. Howell, E. Schwarz (Eds.), *The Neuquén Basin, Argentina: a case study in sequence stratigraphy and basin dynamics*. Geological Society, London, *Special Publications*, 252, 279–294.
- Gasparini, Z., & Iturralde-Vinent, M. (2006). The Cuban Oxfordian herpetofauna in the Caribbean Seaway. *Neues Jahrbuch für Mineralogie und Paläontologie Abhandlungen*, 240(3), 343–371.
- Gasparini, Z., & O'Gorman, J. (2014). A new species of *Pliosaurus* (Sauropterygia, Plesiosauria) from the Upper Jurassic of northwestern Patagonia, Argentina. *Ameghiniana*, 51, 269–283.
- Gasparini, Z., & Spalletti, L. (1993). First Callovian plesiosaurs from the Neuquén Basin, Argentina. *Ameghiniana*, 30(3), 245–254.
- Gasparini, Z., Bardet, N., & Iturralde-Vinent, M. (2002). A new cryptoclidid plesiosaur from the Oxfordian (Late Jurassic) of Cuba. *Geobios*, 35(2), 201–211.
- Gasparini, Z., Fernández, M.S., De La Fuente, M., Herrera, Y., Codomiú, L., & Garrido, A. (2015). Reptiles from lithographic limestones of the Los Catutos Member (middle–upper Tithonian), Neuquén Province, Argentina: an essay on its taxonomic composition and preservation in an environmental and geographic context. *Ameghiniana*, 52(1), 1–28. <https://doi.org/10.5710/AMGH.14.08.2014.2738>.
- Gerasimov, P. A., Mitta, V. V., & Kochanova, M. D. (1995). *Fossils of the Volgian Stage of Central Russia*. VNIGNI: Moscow [In Russian].
- Gilmore, C. W. (1905). Osteology of *Baptanodon* (Marsh). *Memoirs of the Carnegie Museum*, 2(2), 77–129.
- Hillebrandt, A., Smith, P., Westermann, G. E. G., & Callomon, J. H. (1992). Ammonite zones of the circum-Pacific region. In G. E. G. Westermann (Ed.), *The Jurassic of the Circum-Pacific* (pp. 247–272). Cambridge: University Press.
- Houša, V., Pruner, P., Zakharov, V. A., Kostak, M., Chadima, M., Rogov, M. A., Šlechtá, S., & Mazuch, M. (2007). Boreal-Tethyan correlation of the Jurassic-Cretaceous boundary interval by magneto- and biostratigraphy. *Stratigraphy and Geological Correlation*, 15(3), 63–75.
- Huene, F. von (1922). *Die Ichthyosaurier des Lias und ihre Zusammenhänge*. Berlin: Verlag von Gebrüder Borntraeger.
- Hulke, J. W. (1870). Note on some plesiosaurian remains obtained by J.C. Mansel Esq., F.G.S., in Kimmeridge Bay, Dorset. *Quarterly Journal of the Geological Society of London*, 26, 611–622.
- Imlay, R. W. (1961). Late Jurassic ammonites from the western Sierra Nevada, California. *Geological Survey Professional Paper*, 374-D, 1–30.
- Imlay, R. W., & Jones, D. L. (1970). Ammonites from the Buchia zones in northwestern California and southwestern Oregon. *United States Geological Survey Professional Paper*, 647-B, 1–29.
- Kiprijanow, W. (1883). Studien über die fossilen Reptilien Russlands: 3. Gruppe Thaumatosauria n. aus der Kreide-Formation und dem Moskauer Jura. *Mémoires de l'Académie Impériale des Sciences de St.-Petersbourg*, VII séries, XXXI (6), 1–57.
- Kiselev, D. N., Rogov, M. A. & Zakharov, V. A. (2018). The Volgidiscus singularis Zone of the terminal horizons of the Volgian stage of European Russia and its significance for interregional correlation and paleogeography. *Stratigraphy and Geological Correlation*, 26(2), 206–233.
- Knight, W. C. (1898). Some new Jurassic vertebrates from Wyoming. *American Journal of Science*, 4, 378–381.
- Knutsen, E. M., Druckenmiller, P. S., & Hurum, J. H. (2012a). Redescription and taxonomic clarification of '*Tricleidus*' svalbardensis based on new material from the Agardhfjellet Formation (middle Volgian). *Norwegian Journal of Geology*, 92, 175–186.
- Knutsen, E. M., Druckenmiller, P. S., & Hurum, J. H. (2012b). Two new species of long-necked plesiosaurs (Reptilia: Sauropterygia) from the Upper Jurassic (middle Volgian) Agardhfjellet Formation of central Spitsbergen. *Norwegian Journal of Geology*, 92, 187–212.
- Knutsen, E. M., Druckenmiller, P. S., & Hurum, J. H. (2012c). A new plesiosauroid (Reptilia: Sauropterygia) from the Agardhfjellet Formation (middle Volgian) of central Spitsbergen, Norway. *Norwegian Journal of Geology*, 92, 213–234.
- Knutsen, E. M., Druckenmiller, P. S., & Hurum, J. H. (2012d). A new species of *Pliosaurus* (Sauropterygia: Plesiosauria) from the middle Volgian of central Spitsbergen, Norway. *Norwegian Journal of Geology*, 92, 235–258.
- Lydekker, R. (1888). *Catalogue of the fossil Reptilia and Amphibia in the British Museum (Natural History)*. Part II. The orders Ichthyopterygia and Sauropterygia. British Museum (Natural History). London.
- Malakhov, D. V. (1999). Giant pliosaur (Reptilia: Sauropterygia) from the Late Jurassic of Kazakhstan and some remarks on the systematics of Pliosauridae. *Russian Journal of Herpetology*, 6(3), 241–246.
- Mansell-Pleydell, J.C. (1890). Memoir upon a new ichthyopterygian from the Kimmeridge Clay of Gillingham, Dorset, *Ophthalmosaurus pleydelli*. *Proceedings of the Dorset Natural History and Antiquarian Field Club*, 11, 7–15.
- Matyja, B. A., & Wierzbowski, A. (2016). *Ammonites and ammonite stratigraphy of the uppermost Jurassic (Tithonian) of the Owadów-Brzezinki quarry (central Poland)* (pp. 65–122). XIV: Volumina Jurassica.
- Maxwell, E. E. (2010). Generic reassignment of an ichthyosaur from the Queen Elizabeth Islands, Northwest Territories, Canada. *Journal of Vertebrate Paleontology*, 2(30), 403–415.

- Maxwell, E. E., Scheyer, T. M., & Fowler, D. A. (2014). An evolutionary and developmental perspective on the loss of regionalization in the limbs of derived ichthyosaurs. *Geological Magazine*, 151, 29–40.
- McGowan, C. (1976). The description and phenetic relationships of a new ichthyosaur genus from the Upper Jurassic of England. *Canadian Journal of Earth Sciences*, 13, 668–683.
- McGowan, C. (1997). The taxonomic status of *Grendelius mordax*: a preliminary report. *Journal of Vertebrate Paleontology*, 17, 428–430.
- McGowan, C., & Motani, R. (2003). *Ichthyopterygia*. In H.-D. Sues (Ed.) *Handbook of paleoherpetology*. München: Verlag. Dr. Friedrich Pfeil.
- Mesezhnikov, M. S., Alekseev, S. N., Dzhinoridze, N. M., Krasnov, S. G., & Yakovleva, S. P. (1987). Volgian deposits of the Lake Inder. *Doklady AN SSSR*, 292(3), 685–689 [In Russian].
- Mesezhnikov, M. S., & Zakharov, V. A. (1974). On paleozoogeography of North Eurasia during the Volgian time. In A. S. Dagus & V. A. Zakharov (Eds.), *Mesozoic paleobiogeography of the North of Eurasia* (pp. 87–100). Novosibirsk: Nauka, Siberian Branch [In Russian].
- Mitta, V. V. (1984). On a new finds of ichthyosaurs and plesiosaurs in Moscow region. *Bylleten MOIP. Otd. geol.*, 59(3), 131 [In Russian].
- Moon, B. C. & Kirton, A. M. (2018). Ichthyosaurs of the British Middle and Upper Jurassic Part 1. *Monographs of the Palaeontographical Society*, 170(647), 1–84.
- Muscutt, L. E., Dyke, G., Weymouth, G. D., Naish, D., Palmer, C., & Ganapathisubramani, B. (2017). The four-flipper swimming method of plesiosaurs enabled efficient and effective locomotion. *Proceedings of the Royal Society B: Biological Sciences*, 284(1861), 20170951. <https://doi.org/10.1098/rspb.2017.0951>.
- Mutterlose, J., Brumsack, H., Flogel, S., Hay, W., Klein, C., Langrock, U., Lipinski, M., Ricken, W., Soding, E., Stein, R., & Swientek, O. (2003). The Greenland-Norwegian Seaway: a key area for understanding Late Jurassic to Early Cretaceous paleoenvironments. *Paleoceanography*, 18(1), 1–26. <https://doi.org/10.1029/2001PA000625>.
- Nikitin, S. (1890). Carte géologique générale de la Russie, Feuille 57. *Memoires du Comité Géologique*, 5, Saint-Petersburg [In Russian].
- Novozhilov, N. I. (1948). Two new pliosaurs from the Lower Volgian Stage of the Volga region (right bank). *Doklady AN SSSR*, 60, 115–118 [In Russian].
- O’Gorman, J., Gasparini, Z., & Spalletti, L. (2018). A new *Pliosaurus* species (Sauropterygia, Plesiosauria) from the Upper Jurassic of Patagonia: new insights on the Tithonian morphological disparity of mandibular symphyseal morphology. *Journal of Paleontology*, 92, 1–14.
- O’Keefe, F. R., & Carrano, M. T. (2005). Correlated trends in the evolution of the plesiosaur locomotor system. *Paleobiology*, 31(4), 656–675.
- O’Keefe, F. R., & Street, H. P. (2009). Osteology of the cryptocleidoid plesiosaur *Tatenectes laramiensis* from the Upper Sundance Formation of the Bighorn Basin, Wyoming. *Journal of Vertebrate Paleontology*, 29, 48–57.
- Ogg, J. G., & Hinnov, L. A. (2012). Jurassic. In F. M. Gradstein, J. G. Ogg, M. Schmitz, & G. Ogg (Eds.), *The geologic time scale* (pp. 731–791). Elsevier.
- Owen, R. (1840). Report on the British fossil reptiles. Part 1. *Report of the ninth meeting of the British Association for the Advancement of Science*, Birmingham, 1839. London, UK, 43–126.
- Owen, R. (1841a). Odontography. In R. Owen (Ed.), part 2. *Hippolyte Bailliere, foreign booksellers to the Royal College of Surgeons*, London, UK, 282–284.
- Owen, R. (1841b). Report on British fossil reptiles part 2. Report of the Eleventh Meeting for the British Association for the Advancement of Science, 60–204.
- Owen, R. (1869). Monographs on the British fossil Reptilia from the Kimmeridge Clay III: contains *Pliosaurus grandis*, *Pliosaurus trochanterius*, and *Pliosaurus portlandicus*. *Palaeontographical Society Monographs*, 22(98), 1–12.
- Pardo Pérez, J., Frey, E., Stinnesbeck, W., Fernández, M. S., Rivas, L., Salazar, C., & Leppe, M. (2012). An ichthyosaurian forefin from the Lower Cretaceous Zapata Formation of Southern Chile: implications for morphological variability within *Platypterygius*. *Palaeobiodiversity and Palaeoenvironments*, 92(2), 287–294.
- Persson, P. O. (1962). Plesiosaurs from Spitsbergen. *Norsk Polarinstittut*, 62–68.
- Pervushov, E. M., Arkhangelsky, M. S., & Ivanov, A. V. (1999). *Catalogue of localities of marine reptiles in the Jurassic and Cretaceous beds of the Lower Volga region*. Kolledzh: Saratov [in Russian].
- Roberts, A. J., Druckenmiller, P. S., Sætre, G.-P., & Hurum, J. H. (2014). A new Upper Jurassic ophthalmosaurid ichthyosaur from the Slottsmøya member, Agardhfjellet formation of Central Spitsbergen. *PLoS ONE*, 9(8), e103152. <https://doi.org/10.1371/journal.pone.0103152>.
- Roberts, A. J., Druckenmiller, P. S., Delsett, L. L., & Hurum, J. H. (2017). Osteology and relationships of *Colymbosaurus* Seeley, 1874, based on new material of *C. svalbardensis* from the Slottsmøya member, Agardhfjellet formation of Central Spitsbergen. *Journal of Vertebrate Paleontology*, 37(1). <https://doi.org/10.1080/02724634.2017.1278381>.
- Rogov, M. A. (2010a). A precise ammonite biostratigraphy through the Kimmeridgian–Volgian boundary beds in the Gorodischi section (middle Volga area, Russia), and the base of the Volgian Stage in its type area. *Volumina Jurassica*, 8, 103–130.
- Rogov, M. A. (2010b). New data on ammonites and stratigraphy of the Volgian Stage in Spitzbergen. *Stratigraphy and Geological Correlation*, 18, 505–531.
- Rogov, M. A. (2012). Latitudinal gradient of taxonomic richness of ammonites in the Kimmeridgian–Volgian in the northern hemisphere. *Paleontological Journal*, 46(2), 148–156.
- Rogov, M. A. (2013a). Ammonites and infrazonal subdivision of the Dorsoplanites panderi zone (Volgian Stage, Upper Jurassic) of the European part of Russia. *Doklady Earth Sciences*, 451(2), 803–808.
- Rogov, M. A. (2013b). The end-Jurassic extinction. In *Grzimek’s animal life encyclopedia. Extinction*. (pp. 487–495). Gale/Cengage Learning: Detroit.
- Rogov, M. (2014a). Infrazonal subdivision of the Volgian Stage in its type area using ammonites and correlation of the Volgian and Tithonian stages. *STRATI 2013. First International Congress on Stratigraphy. At the Cutting Edge of Stratigraphy*. Springer Geology, 577–580.
- Rogov, M. A. (2014b). *Khetoceras* (Craspeditidae, Ammonoidea)—a new genus from the Volgian Stage of Northern Middle Siberia, and parallel evolution of Late Volgian Boreal ammonites. *Paleontological Journal*, 48, 457–464.
- Rogov, M. A., & Poulton, T. P. (2015). Aulacostephanid ammonites from the Kimmeridgian (Upper Jurassic) of British Columbia (western Canada) and their significance for correlation and palaeobiogeography. *Bulletin of Geosciences*, 90, 7–20.
- Rogov, M., & Zakharov, V. (2009). Ammonite- and bivalve-based biostratigraphy and Panboreal correlation of the Volgian Stage. *Science in China, Series D, Earth Sciences*, 52, 1890–1909.
- Rogov, M., Zakharov, V., & Kiselev, D. (2008). *Molluscan immigrations via biogeographical ecotone of the Middle Russian Sea during the Jurassic* (pp. 143–152). VI: Volumina Jurassica.
- Rosanov, A. (1906). Sur la question de la subdivision des couches à Virgati dans les environs de Moscou. *Annuaire géologique et minéralogique de la Russie*, VIII(6-7), 198–210.
- Rozhdestvensky, A. (1947). A new finding of a huge pliosaur from the TransVolga region. *Doklady AN SSSR*, 56(2), 197–199 [In Russian].

- Sasonova, I. G., & Sasonov, N. T. (1967). Paleogeography of the Russian Platform during Jurassic and Cretaceous period. *Trudy VNIGNI*, 62, 1–260 [In Russian].
- Sauvage, H.-E. (1888). Sur les Reptiles trouvés dans le Portlandien supérieur de Boulogne-sur-Mer. *Bulletin de la société géologique de France. 3rd séries*, 16, 623–632.
- Sauvage, H.-E. (1899). Catalogue des reptiles trouves dans le terrain Jurassique superieur du Boulonnais. *Comptes rendus de l'Association française pour l'avancement des sciences*, 1, 416–419.
- Sauvage, H.-E. (1911). Les plésiosaures du terrain Jurassique du Boulonnais. *Bulletin de la Société académique de l'arrondissement de Boulogne-sur-Mer*, 9, 186–215.
- Seeley, H.G. (1869). *Index to the fossil remains of Aves, Ornithosauria, and Reptilia in the Woodwardian Museum of the University of Cambridge*. Deighton, Bell and Co., Cambridge, U.K.
- Seeley, H. G. (1874). On the pectoral arch and fore limb of *Ophthalmosaurus*. *The Quarterly Journal of the Geological Society of London*, 30, 696–707.
- Schumacher, B. A., & Martin, J. E. (2015). *Polycotylus latipinnis* Cope (Plesiosauria, Polycotylidae), a nearly complete skeleton from the Niobrara Formation (Early Campanian) of southwestern South Dakota. *Journal of Vertebrate Paleontology*, 36(1), e1031341. <https://doi.org/10.1080/02724634.2015.1031341>.
- Smellie, W. R. (1917). Chapter XIX. *Apractocleidus teretipes*: a new Oxfordian Plesiosaur in the Hunterian Museum, Glasgow University. *Transactions of the Royal Society of Edinburgh*, 51, 609–629.
- Sokolova, E. I. (1939). To the stratigraphy of the Upper Jurassic deposits of the Uralo-Emba region. *Transactions of the Geological Oil Institute, Serie A Fascicle*, 114, 1–47 [In Russian].
- Stanley, G. (1994). Late Paleozoic and Early Mesozoic reef-building organisms and paleogeography: the Tethyan-North American connection. *Courier Forschungsinstitut Senckenberg*, 172, 69–75.
- Stinnesbeck, W., Frey, E., Rivas, L., Pardo Pérez, J., Cartes, M. L., Soto, C. S., & Lobos, P. Z. (2014). A Lower Cretaceous ichthyosaur graveyard in deep marine slope channel deposits at Torres del Paine National Park, southern Chile. *Geological Society of America Bulletin*, 126, 1–24. <https://doi.org/10.1130/b30964.1>.
- Storrs, G. W., Arkhangelsky, M. S., & Efimov, V. M. (2000). Mesozoic marine reptiles of Russia and other former Soviet republics. In M. J. Benton, M. A. Shishkin, D. M. Unwin, & E. N. Kurochkin (Eds.), *The age of dinosaurs in Russia and Mongolia* (pp. 187–210). Cambridge: Cambridge Univ. Press.
- Tarlo, L.B. (1960). A review of the Upper Jurassic pliosaurs. *Bulletin of the British Museum (Natural History), Geology Series*, 4, 147–189.
- Trautschold, H. (1860). Recherches géologiques aux environs de Moscou. Couche Jurassique de Galiowa. *Bulletin de la Société impériale des naturalistes de Moscou*, XXXIII(4), 338–361.
- Villaseñor, A. B., Olóriz, F., Palomino, I. L., & López-Caballero, I. (2012). Updated ammonite biostratigraphy from Upper Jurassic deposits in Mexico. *Revue de Paléobiologie*, 11, 249–267.
- Wagner, G. P., & Gauthier, J. A. (1999). 1,2,3 = 2,3,4: a solution to the problem of the homology of the digits in the avian hand. *PNAS*, 96(9), 5111–5116.
- Wahl, W. R., Ross, M., & Massare, J. A. (2007). Rediscovery of Wilbur Knight's *Megalneusaurus rex* site: new material from an old pit. *Paludicola*, 6(2), 94–104.
- Wang, Z., Young, R. L., Xue, H., & Wagner, G. P. (2011). Transcriptomic analysis of avian digits reveals conserved and derived digit identities in bird. *Nature*, 477, 583–586.
- Welles, S.P. (1962). *A new species of elasmosaur from the Aptian of Columbia and a review of the Cretaceous plesiosaurs*. University of California Publications, 44.
- Wimbledon, W.A. (1984). The Portlandian, the terminal Jurassic stage in the Boreal realm. In O. Michelsen and A. Zeiss (Eds.) *International symposium on Jurassic stratigraphy Erlangen*, 2, 533–549.
- Wimbledon, W. A. P. (2008). The Jurassic-Cretaceous boundary: an age-old correlative enigma. *Episodes*, 31(4), 423–428.
- Zakharov, V. A., & Rogov, M. A. (2003). Boreal-Tethyan mollusk migrations at the Jurassic-Cretaceous boundary time and biogeographic ecotone position in the Northern Hemisphere. *Stratigraphy and Geological Correlation*, 11(2), 152–171.
- Zakharov, V. A., & Kasumzade, A. A. (2005). On the Boreal genus *Buchia* (Bivalvia) from the Tithonian of the Lesser Caucasus. *Stratigraphy and Geological Correlation*, 13(6), 606–612.
- Zell, P., Beckmann, S., & Stinnesbeck, W. (2013). Late Jurassic-earliest Cretaceous belemnites (Cephalopoda: Coleoidea) from northeastern Mexico and their palaeobiogeographic implications. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 270(3), 325–341.
- Zverkov, N. G., & Efimov, V. M. (2019). Revision of *Undorosaurus*, a mysterious Late Jurassic ichthyosaur of the Boreal realm. *Journal of Systematic Palaeontology*, 17, 963–993. <https://doi.org/10.1080/14772019.2018.1515793>.
- Zverkov, N. G. & Prilepskaya, N.E. (2019). A prevalence of *Arthropterygius* (Ichthyosauria: Ophthalmosauridae) in the Late Jurassic—earliest Cretaceous of the Boreal Realm. *PeerJ*, 7, e6799. <https://doi.org/10.7717/peerj.6799>
- Zverkov, N. G., Arkhangelsky, M. S., Pardo Pérez, J. M., & Beznosov, P. A. (2015a). On the Upper Jurassic ichthyosaur remains from the Russian North. *Proceedings of the Zoological Institute RAS*, 319(1), 81–97.
- Zverkov, N. G., Arkhangelsky, M. S., & Stenshin, I. M. (2015b). A review of Russian Upper Jurassic ichthyosaurs with an intermedium/humeral contact. Reassessing *Grendelius* McGowan, 1976. *Proceedings of the Zoological Institute RAS*, 319(4), 558–588.
- Zverkov, N.G., Shmakov, A. S., & Arkhangelsky, M. S. (2017). Jurassic marine reptiles of Moscow and surroundings. In M. A. Rogov, & V. A. Zakharov (Eds.) *Jurassic deposits of the southern part of the Moscow Syneclyse and their fauna*. *Transaction of the Geological Institute* 615, 230–263. Moscow: GEOS [in Russian, English summary].

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.