# Youngest occurrences of rhomaleosaurid plesiosaurs indicate survival of an archaic marine reptile clade at high palaeolatitudes

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Rhomaleosaurid plesiosaurians were a common and ecologically significant component of Early Jurassic marine faunas, primarily as large-bodied predators. They declined in abundance and made their last fossil appearance in the Middle Jurassic. However, the geographic pattern of rhomaleosaurid extinction has thus far been obscured by spatial bias in the Middle Jurassic marine reptile fossil record, which is strongly focussed on low-latitude European assemblages. We report two rhomaleosaurid specimens from the Callovian (late Middle Jurassic) of the UK and Russia. Along with *Borealonectes* from Arctic Canada, these are the youngest-known occurrences of rhomaleosaurids. The UK specimen is the first identified from the Callovian of Europe, despite intensive fossil sampling over almost 200 years and the recovery of hundreds of other plesiosaurian specimens. Its discovery indicates that rhomaleosaurids were present, but extremely rare, at low palaeolatitudes of the Callovian. The Russian specimen is one of relatively few marine reptile specimens from its mid-palaeolatitude assemblage, as is also true of *Borealonectes*, which occurs in a high-palaeolatitude marine assemblage. Furthermore, we suggest that a mid latitude southern hemisphere occurrence from the Callovian of Argentina, previously referred to Pliosauridae, in fact represents a rhomaleosaurid. These findings suggest that rhomaleosaurids were actually common elements of mid-high palaeolatitude marine faunas, indicating a geographically staggered pattern of declining rhomaleosaurid abundance, and demonstrating the apparent persistence of an archaic marine reptile group in cool, mid–high latitude environments of the Middle Jurassic. It is therefore possible that sustained Middle–Late Jurassic global warming accelerated the ultimate extinction of rhomaleosaurids. Our findings suggest that widening the geographical breadth of fossil exploration could considerably enhance current knowledge of Jurassic marine reptile evolution.

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## Introduction

Plesiosauria was a long-lived group of secondarily aquatic reptiles with limbs modified to flippers. Plesiosaurs (i.e., members of Plesiosauria) attained a global distribution from shortly after their first definite appearance in the earliest Jurassic of Europe, until their last appearance more than 130 million years later at the end of the Cretaceous (Mulder et al. 2000; Ketchum and Benson 2010; Vincent et al. 2011;

Benson et al. 2012). However, much of the Jurassic fossil record of plesiosaurs, and of other Mesozoic marine reptiles, has come from a few highly productive, but geographically restricted European deposits (Benson et al. 2010). These exceptional assemblages have contributed substantially to our understanding of marine reptile evolution and diversity. However, we cannot assume that they are representative of a "global" marine fauna. Indeed, the lack of wider geographic sampling has so far limited our ability to discern biogeographic patterns, or to determine their implications
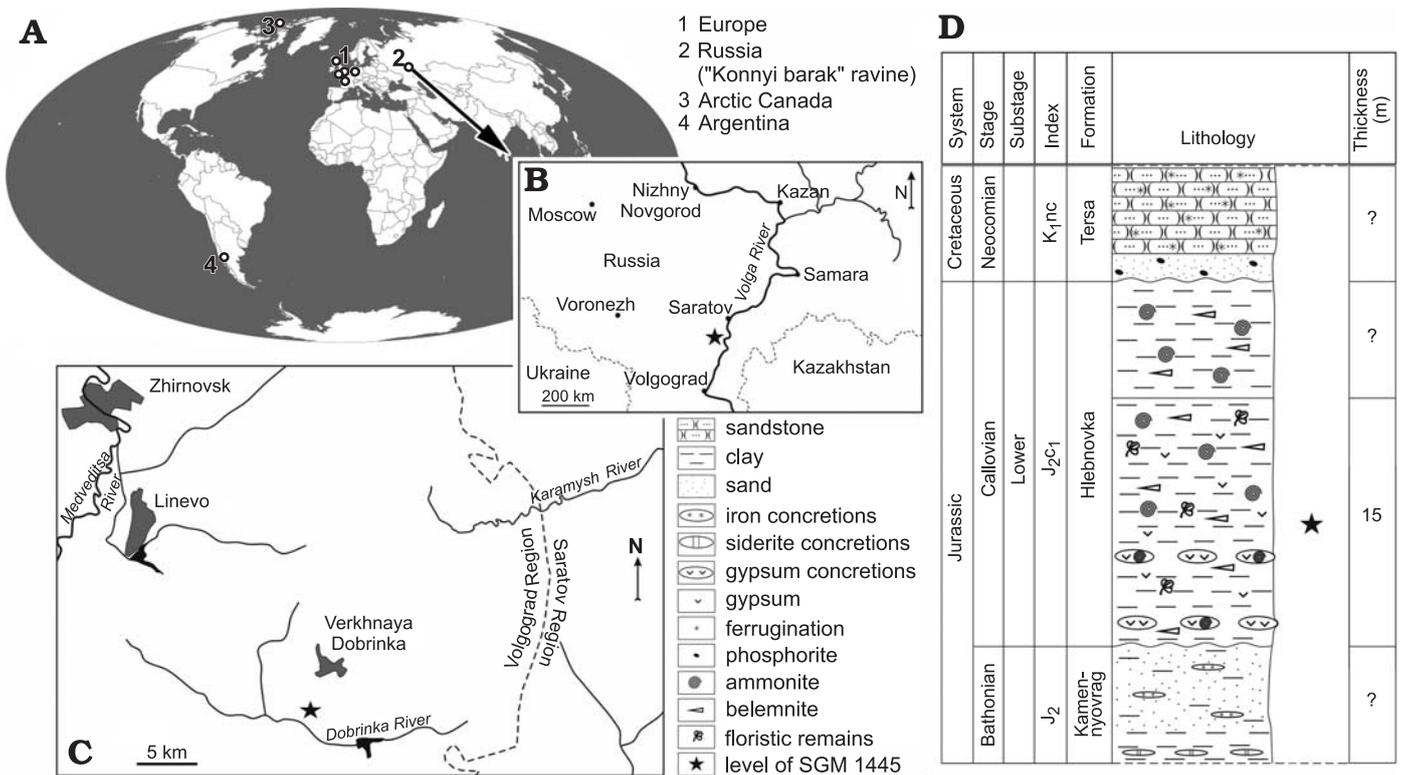
Fig. 1. Global map showing Callovian plesiosaurian localities (**A**), with further information on the geographic (regional map, **B**; local map, **C**) and stratigraphic (**D**) context of "Konnyi barak" ravine, from which SGM 1445-9–20, 97–120 was collected. Global map was constructed using https://paleobiodb.org.

for interactions between Jurassic marine reptiles and climatic evolution. This contrasts with our understanding of Late Cretaceous plesiosaur distributions, which indicate geographic heterogeneity in the taxonomic composition of assemblages at distinct latitudes (e.g., Otero et al. 2012; Vincent et al. 2013; Bardet et al. 2014).

The Peterborough Member of the UK has yielded one of the most intensively collected marine reptile assemblages of any time interval or geographic region (Andrews 1910, 1913). This late Callovian (Middle Jurassic) assemblage has so far yielded hundreds of individual specimens, revealing an ecologically diverse assemblage of thalassophonean pliosaurids and cryptoclidid plesiosauroids alongside other marine reptiles, fish and invertebrates that inhabited a warm, low latitude continental seaway (Martill and Hudson 1991). However, the abundance of Callovian marine reptile fossils in the UK, and their occurrence elsewhere in Europe (e.g., Sauvage 1873, 1914; Brunet 1969; Sachs 1997) contrasts with the near absence of discoveries from other global regions (see Gasparini and Spaletti 1993 for an exception), and especially from higher palaeolatitudes. One exception is a single specimen from the Hiccles Cove Formation of Arctic Canada, representing the youngest known rhomaleosaurid so far, *Borealonectes* (Russell 1993; Sato and Wu 2008). This occurrence seems highly incongruous. Although rhomaleosaurids were abundant in Early Jurassic marine faunas (e.g., Taylor 1992; Cruickshank 1994; Smith and Dyke 2008; Benson et al. 2012; Smith and Benson 2014; Smith 2015),

are present in Early Jurassic freshwater assemblages (Zhang 1985; Sato et al. 2003), and occurred in the earlier Middle Jurassic of Argentina (Gasparini 1997), until now they have not been reported from the late Middle Jurassic deposits of Europe, despite intensive fossil collection and study (e.g., Seeley 1869; Lydekker 1889; Arthaber 1906; Andrews 1910, 1913; Martill and Hudson 1991).

Here, we report two new likely rhomaleosaurid occurrences, from the Callovian Oxford Clay Formation of the UK, and Hlebnovka Formation of the Volgograd Region of Russia (Fig. 1). Furthermore, we identify a vertebral centrum from the Callovian of Argentina as likely also representing a rhomaleosaurid. These occurrences reveal that rhomaleosaurids were exceptionally rare in the low latitude marine faunas of late Middle Jurassic Europe, but might have been common in the mid-high latitude faunas represented in Russia, Argentina and Arctic Canada. This is the first clear evidence of geographic controls on Jurassic plesiosaur distributions and suggests that wider geographic sampling has considerable potential to enhance our knowledge of the evolution of Plesiosauria and other marine reptiles.

*Institutional abbreviations.*—CAMSM, Sedgwick Museum of Geology, Cambridge, UK; GSM Geological Survey Museum, Keyworth, UK; SGM, Verdansky State Geological Museum of the Russian Academy of Sciences, Moscow, Russia; MOZ, Museo "Professor Dr. Juan Olsacher", Zapala, Neuquén, Argentina; NHMUK, Natural History Museum, London, UK.
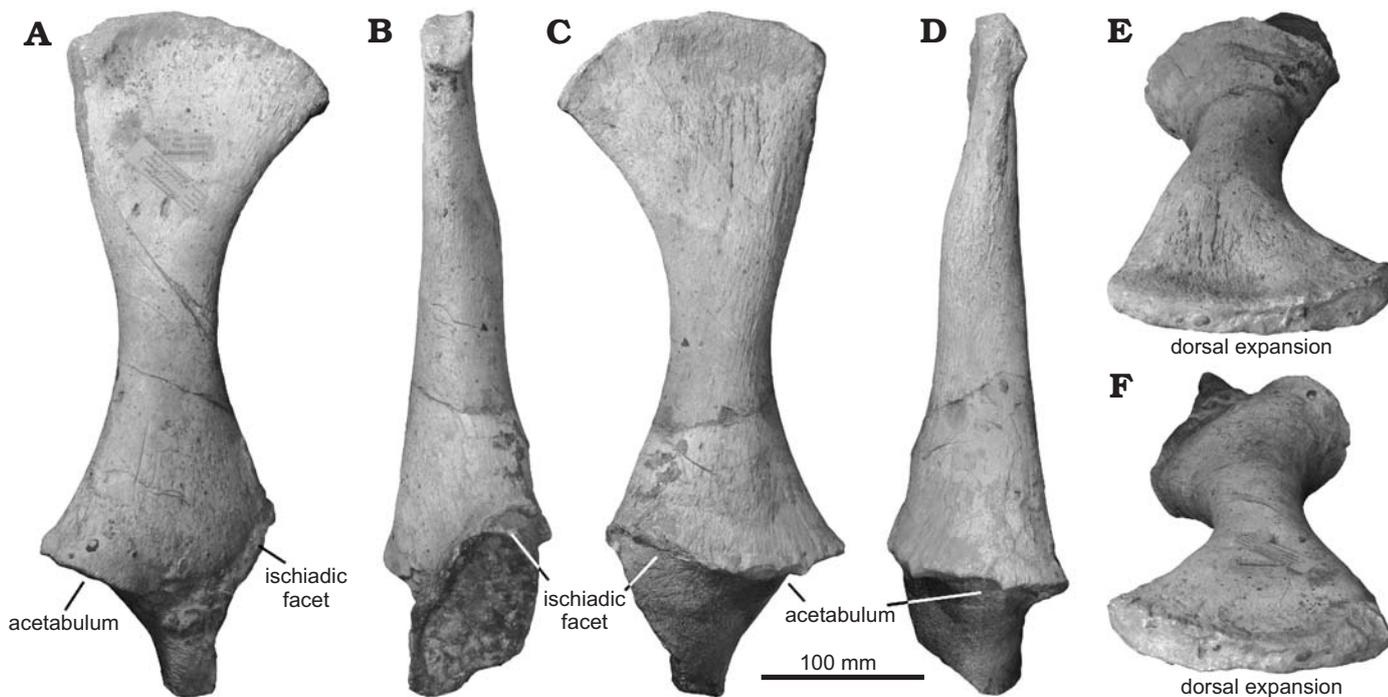
Fig. 2. Left ilium of the plesiosaur Rhomaleosauridae indet., CAMSM X.50215, from the Callovian Peterborough Member of Fletton, United Kingdom, in lateral (**A**), posterior (**B**), medial (**C**), anterior (**D**), dorsolateral (**E**), and dorsomedial (**F**) views.

# Systematic palaeontology

Sauropterygia Owen, 1860

Plesiosauria de Blainville, 1838

Rhomaleosauridae Kuhn, 1961

Genus et species indet.

Figs. 2–9.

*Material.*—CAMSM X.50215 comprises an associated left ilium and left ischium collected by Henry Keeping in 1898 from the Oxford Clay Formation at Fletton, Peterborough Member (Callovian), Peterborough, Cambridgeshire, United Kingdom. Evidence for the association of these bones is given by the fit between the iliac facet of the ischium, and matrix attached to the ventral surface of the ilium, covering its ischiadic facet, and part of the acetabulum. SGM 1445-9–20, 97−120 comprises a partial postcranial skeleton collected by Soviet geologist Eugeny Vladimirovich Milanovsky in the summer of 1920 during geological investigations in the basins of two small inflows of Medveditsa River; "Konnyi barak" ravine, flowing into the river Dobrinka on the left bank, located 3.2 km south of the village Verkhnaya Dobrinka, Zhirnovsk district, Volgograd region, Russia (Fig. 1). Currently a significant part of the ravine is recultivated (personal observation MSA). Bed J$_2$cl (after Milanovsky 1921; Pervushov et al. 1999; Fig. 2), *Cadoceras elatmae* Zone, Hlebnovka Formation, Lower Callovian (Mitta et al. 2012). Dark purplish-gray clay, including numerous gypsum crystals, sometimes forming ellipsoidal concretions, belemnites, fossil wood and the ammonites *Cadoceras elatmae*, *Chamoussetia chamousseti*, and *Keplerites* sp. also occur in this horizon.

*Description*

*CAMSM X.50215.—Ilium*: The ilium of CAMSM X.50215 is 375 mm long dorsoventrally (Fig. 2), and is large compared to cryptoclidid ilia (181–225 mm in *Muraenosaurus*; 172–200 mm in *Cryptoclidus*; Andrews 1910), but comparable in size to the ilia of some pliosaurids (116–206 mm in *Peloneustes*, 242–310 in "*Pliosaurus*" *andrewsi* [as *Peloneustes evansi*]; Andrews 1913; *Liopleurodon* is larger than *Peloneustes* or "*P.*" *andrewsi*, but no ilium is preserved). The ilium of CAMSM X.50215 comprises anteroposteriorly expanded proximal and distal ends, joined by a straight, constricted shaft, with a minimum anteroposterior diameter of 64 mm. The shaft cross section is suboval, and slightly mediolaterally compressed, with a mediolateral diameter of 54 mm at the point of minimum anteroposterior diameter. This morphology differs from that in cryptoclidids and most xenopsarians, in which the shaft is not straight, but curves anterodorsally (e.g., Andrews 1910; Wegner 1914; Sato 2002: character 170; Albright et al. 2007; Hampe 2013).

The ventral expansion of the ilium has a suboval outline in ventral view, which tapers posteriorly. It is 165 mm long anteroposteriorly, 95 mm wide mediolaterally, and is divided into two approximately flat facets; the ischiadic facet posteriorly, and the iliac portion of the acetabulum anteriorly. As in all plesiosaurians (Storrs 1991), the ilium lacks a pubic articular facet. The ischiadic facet faces posteroventrally, and is larger than the iliac portion of the acetablum, which faces ventrally. This morphology is similar to the condition
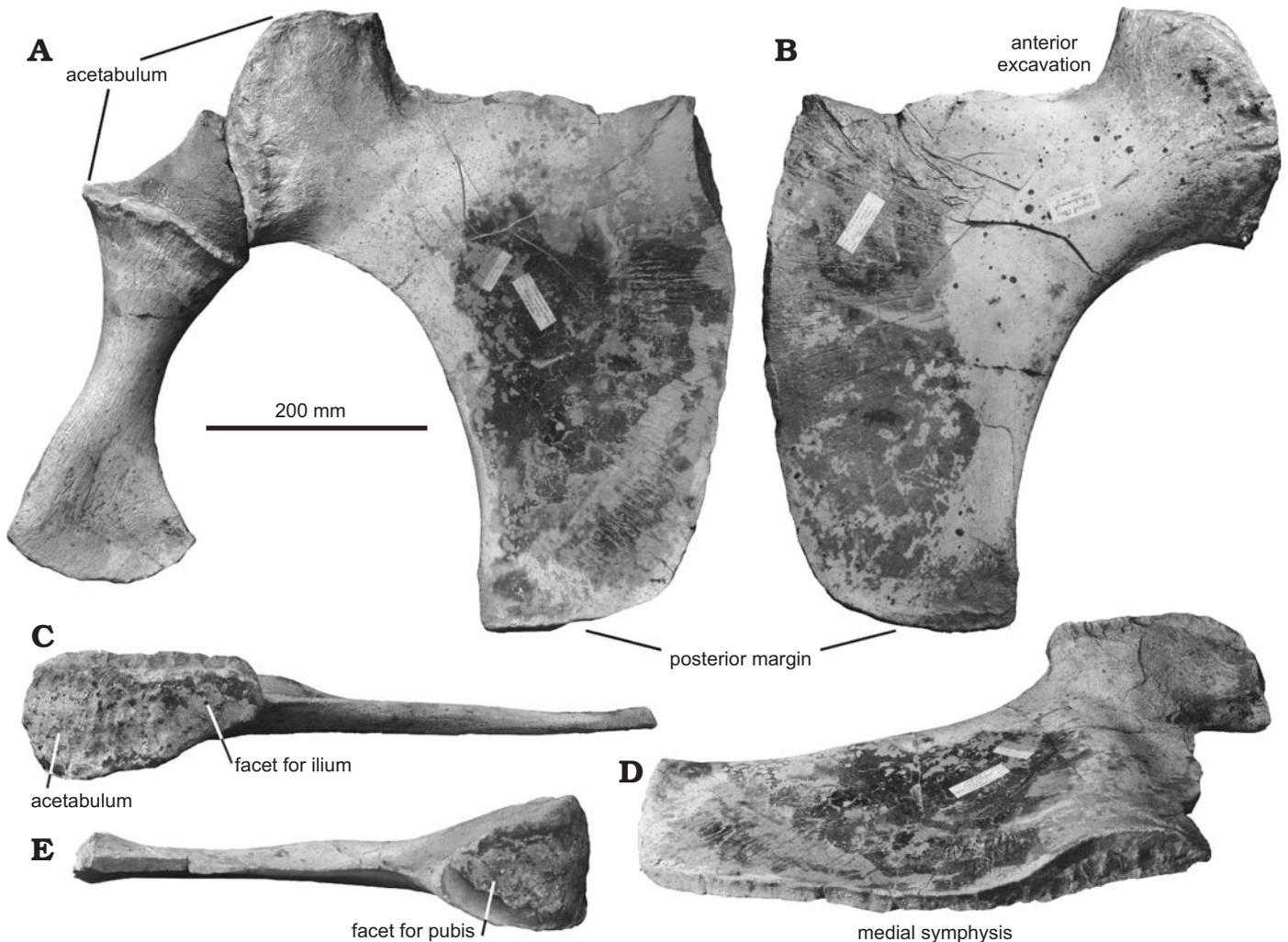
Fig. 3. Left ischium of the plesiosaur Rhomaleosauridae indet., CAMSM X.50215, from the Callovian Peterborough Member of Fletton, United Kingdom, in dorsal view (articulated with left ilium) (**A**), and ventral (**B**), lateral (**C**), dorsomedial (**D**), and anterior (**E**) views.

in Early Jurassic plesiosaurians, including rhomaleosaurids, microclidids and early pliosaurids (e.g., Fraas 1910; Bardet et al. 1999; Vincent 2011; Benson et al. 2012). However, it differs from the condition in thalassophonean pliosaurids (Andrews 1913; an ilium described as a scapula by Tarlo 1957; see Halstead 1989; Ketchum and Benson 2011), cryptoclidids (Andrews 1910) and xenopsarians (e.g., Wegner 1914), in which the ischiadic facet is located on the ventromedial surface of the ilium. Furthermore, in thalassophoneans the ventral end of the ilium is only slightly longer anteroposteriorly than it is mediolaterally (Andrews 1913; Ketchum and Benson 2011), and in cryptoclidids and many xenopsarians it is wider mediolaterally than it is long anteroposteriorly (Andrews 1910; Hampe 2013), further differing from CAMSM X.50215.

The dorsal portion of the ilium of CAMSM X.50215 is transversely narrow (maximum thickness = 32 mm; minimum = 19 mm), and expanded anteroposteriorly (170 mm) into a sheet-like dorsal expansion (Fig. 2). It extends further posterodorsally than anteriorly, and is therefore slightly asymmetrical in lateral view. This also occurs in

*Rhomaleosaurus* (Smith and Benson 2014), cryptoclidids, the early pliosaurid *Hauffiosaurus* (Vincent 2011), and some thalassophonean pliosaurids (*Peloneustes*, Andrews 1913; *Marmornectes*, Ketchum and Benson 2011). However, it is distinct from the almost symmetrical dorsal expansion seen in many early Jurassic plesiosaurians (e.g., *Thalassiodracon*, GSM 51235; *Eurycleidus*, NHMUK PV OR 2030* and associated material; *Stratesaurus*, Benson et al. 2012) and from the strongly asymmetrical conditions seen in more derived thalassophoneans such as "*Pliosaurus*" *andrewsi* (NHMUK R3891; Andrews 1913) and *Pliosaurus* (Tarlo 1957).

The plane of the dorsal expansion is rotated approximately 20° posterolaterally relative to that of the ventral expansion in CAMSM X.50215 (Fig. 2E, F). This is similar to the condition in many Early Jurassic plesiosaurians, including the rhomaleosaurids *Eurycleidus* (NHMUK PV OR 2030*) and *Rhomaleosaurus* (Smith and Benson 2014), but differs from that in thalassophoneans, cryptoclidids, and xenopsarians, in which the angle is 90° due to the position of the ischiadic facet on the ventromedial surface of the ilium (Benson et al. 2012: character 173).

*Ischium*: The ischium of CAMSM X.50215 is almost complete (Fig. 3), missing only its anteromedial process, which contacts the pubis in some plesiosaurians. The ischium is 550 mm long anteroposteriorly, from its posterior end to the anterior surface of the acetablum. It is 470 mm wide mediolaterally, from the acetabulum to the medial symphysis, and therefore has a length:width ratio of 1.17. This ratio is low compared to thalassophonean pliosaurids, which have anteroposteriorly elongate ischia (ratio = 1.7–2.0; Andrews 1913; Romer and Lewis 1959; Ketchum and Benson 2011), but is similar to the values seen in rhomaleosaurids (ratio = 1.0–1.5; *Meyerasaurus*, *Rhomaleosaurus*, *Macroplata*; Fraas 1910; Ketchum and Smith 2010; Smith and Vincent 2010; Benson et al. 2012; Smith and Benson 2014) and other Early Jurassic taxa, including pliosaurids (Bardet et al. 1999; Vincent 2011). It is also within the range of many plesiosauroids, including cryptoclidids (ratio ~1.1 in *Cryptoclidus* and *Muraenosaurus*, Andrews 1910; ratio = 1.4 in *Picrocleidus*, NHMUK R2739). The medial and lateral surfaces of the ischiadic blade are approximately parallel posteriorly, converging only weakly (Fig. 3A, B), and the posterior margin of the outline of the ischium in dorsal view is straight, with a truncated appearance. This is similar to the condition in rhomaleosaurids such as *Rhomlaeosaurus* (Andrews 1922; Smith and Benson 2014), *Meyerasaurus* (Fraas 1910; Smith and Vincent 2010) and *Eurycleidus* (NHMUK PV OR 2030*), but differs from the condition in most plesiosaurians, including Middle Jurassic taxa, in which the posterior margin of the ischium is convex, as seen in pliosaurids (*Peloneustes*, NHMUK R3318; *Simolestes*, NHMUK R3319; Andrews 1913), and most cryptoclidids (*Cryptoclidus*, NHMUK R2417; *Picrocleidus*, NHMUK R2739; Andrews 1910), although a specimen of *Muraenosaurus* (NHMUK R2863) was shown as having a straight posterior margin by Andrews (1910: text-fig. 65).

The acetabular process of the ischium is well preserved in CAMSM X.50215, with a dorsoventral height of 105 mm and anteroposterior length of 215 mm (Fig. 3). It shows prominent facets for the ilium (facing posterolaterally), acetabulum (facing laterally), and pubis (facing anteriorly). The lateral orientation of the iliac facet of CAMSM X.50215 is similar to that in *Rhomaleosaurus* (Andrews 1922; Smith and Benson 2014), but unlike the dorsolateral orientation seen in many other plesiosaurians, including in Early Jurassic taxa such as *Eurycleidus* (NHMUK PV OR 2030*) and *Microcleidus* (*Occitanosaurus*, Bardet et al. 1999), and in well-preserved Middle Jurassic pliosaurids (*Liopleurodon*, Andrews 1913: text-fig. 7) and cryptoclidids (*Muraenosaurus*, Andrews 1910: pl. 5; *Cryptoclidus*, NHMUK R2860).

The blade of the ischium of CAMSM X.50215 is dorsoventrally thin, with a minimum symphysial thickness of 18 mm. It attains its maximum symphysial thickness of 40 mm anteriorly, where the ischiadic symphysis rises anterodorsally. This thicker portion of the symphysis extends laterally as a low buttress that contacts the acetabular process and defines the anterior margin of a gentle depression on the dorsal
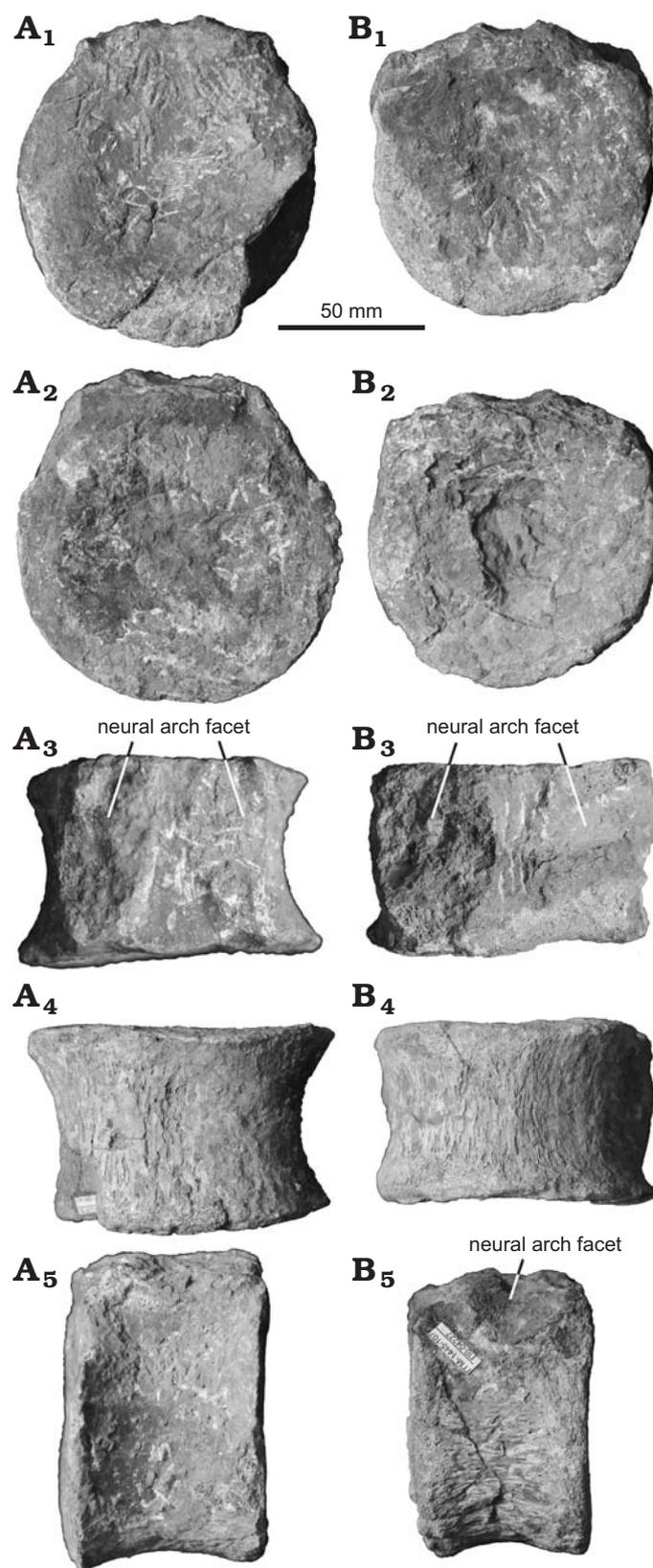


Fig. 4. Dorsal centra of the plesiosaur Rhomaleosauridae indet. from the Lower Callovian Hlebnovka Formation of "Konnyi barak" ravine, Russia. SGM 1445-108 (**A**) and SGM 1445-107 (**B**), in anterior ($A_1$, $B_1$), posterior ($A_2$, $B_2$), dorsal ($A_3$, $B_3$), ventral ($A_4$, $B_4$), left lateral ($A_5$), and right lateral ($B_5$) views.
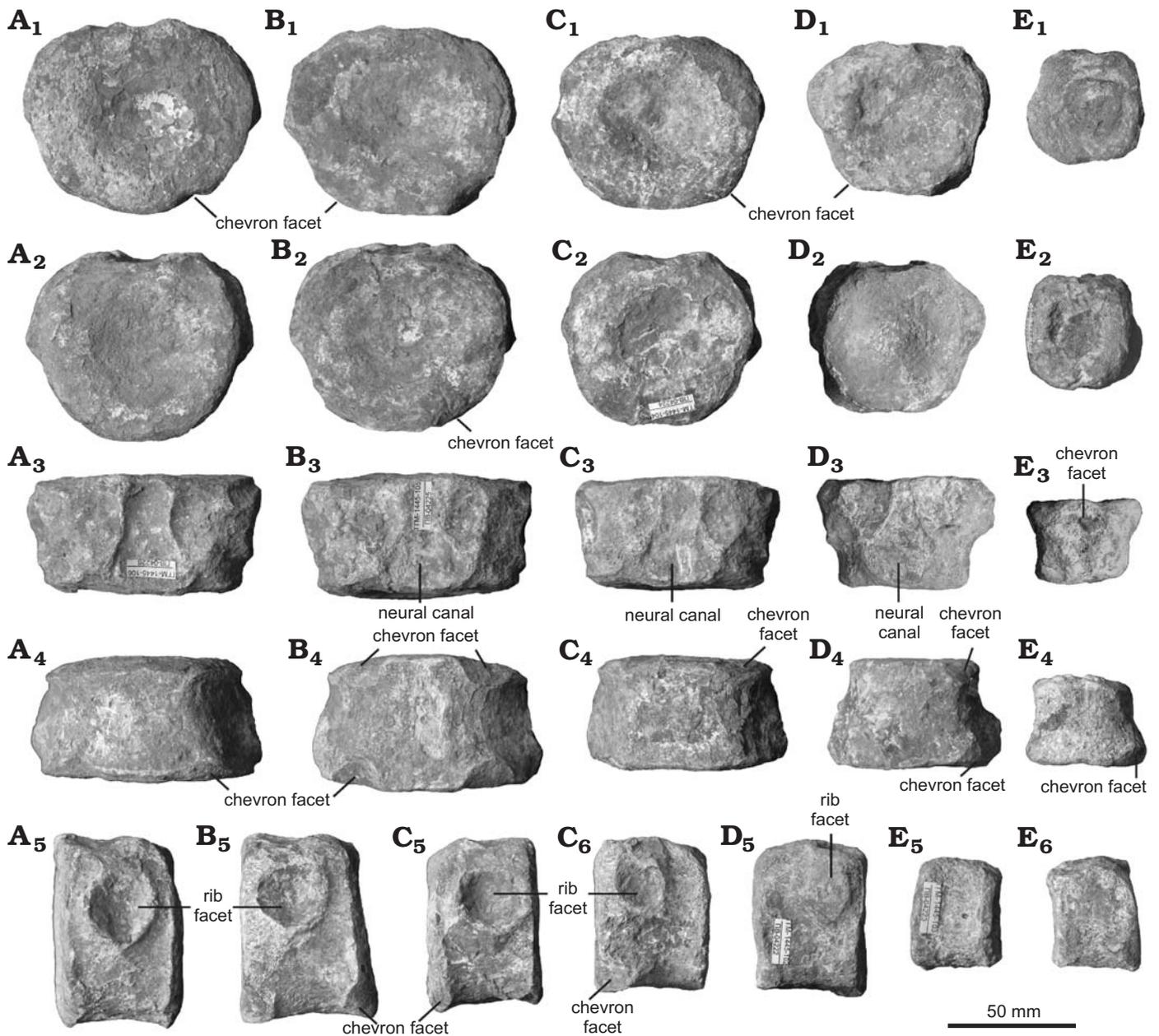
Fig. 5. Caudal centra of the plesiosaur Rhomaleosauridae indet. from the Lower Callovian Hlebnovka Formation of "Konnyi barak" ravine, Russia. SGM 1445-106 (**A**), SGM 1445-105 (**B**), SGM 1445-104 (**C**), SGM 1445-102 (**D**), and SGM 1445-103 (**E**), in anterior ($A_1$–$E_1$), posterior ($A_2$–$E_2$), dorsal ($A_3$–$E_3$), ventral ($A_4$–$E_4$), left lateral ($A_5$, $B_5$, $C_6$, $E_6$), and right lateral ($C_5$, $D_5$, $E_5$) views.

surface of the ischial blade. The ventral surface of the ischial blade is approximately flat.

The anterior and posterior borders of the ischial neck, connecting the acetabular process to the ischial blade, are dorsoventrally shallow and sharply edged. This cannot be attributed to postmortem compression, which appears to be absent. The neck of the ischium is relatively wide due to shallow excavations of anterior and posterior edges (the ischial neck:acetabular process ratio is ~0.73) as in most thalassophonean pliosaurids (ratio = 0.70 in *Liopleurodon*, NHMUK R 3536; 0.88 in *Peloneustes*, NHMUK R 3318; and ~1.0 in *Simolestes*, NHMUK R 3319 and *Marmornectes*; Andrews 1913; Ketchum and Benson 2011). This contrasts with the narrow ischial neck seen in rhomalesaurids, which is embayed by the deep anterior excavation of obturator foramen (ratio = 0.6 in *Rhomalesaurus thorntoni*, NHMUK R4853; Smith and Benson 2014; and 0.56 in *Eurycleidus arcuatus*, NHMUK R2230), or excavation of both the anterior and posterior margins (ratio = 0.5 in *Meyerasaurus victor*, SMNS 12478; Smith and Vincent 2010). In Early Jurassic pliosaurids (Vincent 2011) and Callovian cryptoclidids, the ischial neck is also relatively thin and mediolaterally elongated (*Cryptocleidus, Muraenosaurus*; Andrews 1910).

*SGM 1445-9–20, 97−120.*—The fragmented posterior part of the skeleton is preserved, including dorsal, sacral and

caudal vertebral centra and ribs, the pelvic girdle, and incomplete fragments of limbs. The bones are light gray-yellowish, and sometimes pyritized, with a covering of gypsum crystals.

*Dorsal vertebrae*: Two dorsal centra are preserved (Fig. 4; SGM 1445-108, 107). They have subcircular, weakly concave anterior and posterior articular surfaces that are approximately as wide mediolaterally as high dorsoventrally (Table 1). The central portions of the centra are slightly constricted between the articular surfaces. The centra are proportionally short anteroposteriorly, approximately 60% of their dorsoventral heights (Table 1), and have transversely convex ventral surfaces. The dorsal surfaces of the centra bear the neural arch facets and the floor of the neural canal, which is transversely narrowest anteriorly.

*Caudal vertebrae*: Five caudal centra are preserved (Fig. 5), forming a non-continuous sequence with specimens numbers listed here from anterior to posterior (SGM 1445-102−106). The centra are slightly wider mediolaterally than high dorsoventrally, and shorter anteroposteriorly than either their height or width (Table 1). One proximal caudal centrum (SGM 1445-105) has a ventral surface that is anteroposteriorly longer than its dorsal surface, conferring a wedge-like morphology (Fig. 5B$_5$) that does not result from taphonomic distortion. The outlines of the articular surfaces are suboval, with a subrectangular appearance due to ventrolateral expansion contributed by the chevron facets, especially in more posterior centra (SGM 1445-102, 103). Well-defined chevron facets are generally present both anteriorly and posteriorly on the ventral surfaces of the centra. They are semi-oval, and the anterior facets are generally larger than the posterior facets. Rib facets are present anterodorsally on the lateral surfaces of the centra, extending outwards from the lateral surface of the centrum (Fig. 5), and contacting the neural arch peduncle, as occurs in rhomaleosaurids, some pliosaurids, some leptocleidians, and Early Jurassic plesiosauroids (e.g., Benson et al. 2012; Smith 2013; Smith and Benson 2014). The articular surfaces of the rib facets are concave, and have suboval outlines in lateral view.

Paired subcentral foramina are present on the ventral surfaces of the caudal centra, as in many plesiosaurians (Storrs 1991), but differing from the condition in early xenopsarians, where often only a single, midline foramen is present (Benson and Druckenmiller 2013). The dorsal surfaces of the caudal centra bear the neural arch facets laterally, and the



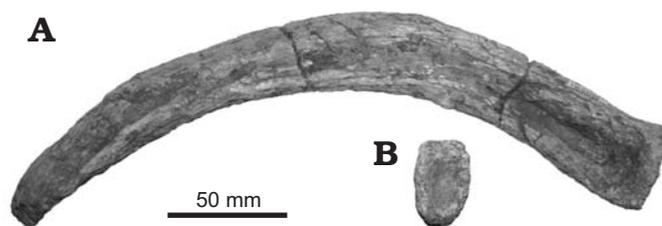Fig. 6. Dorsal rib of the plesiosaur Rhomaleosauridae indet., SGM 1445-100, from the Lower Callovian Hlebnovka Formation of "Konnyi barak" ravine, Russia, in ?anterior (**A**) and proximal (**B**) views.

ventral floor of the neural canal, centrally. The neural canal is mediolaterally narrower anteriorly than posteriorly, as it is constricted by the neural arch facets.

*Dorsal ribs*: One dorsal rib is completely preserved, with a length of 270 mm and a dumbbell-shaped cross section (Fig. 6). The proximal articular surface is oval, and measures 23 mm dorsoventrally. Other rib fragments are very small. Two of them might represent sacral ribs: they are double-headed, and 70 mm in length as preserved.

*Ilium*: The left ilium is well preserved (Fig. 7; SGM 1445-99), although it appears to have been plastically deformed, with the dorsal end bent over laterally. The ilium conforms well to the description of CAMSM X.50215 in most topological features: the orientations of the acetabular and ischiadic facets, the cross-section of the shaft, and the rotation of the dorsal expansion relative to the ventral end. These morphologies are consistent with affinities to an early-diverging group such as Rhomaleosauridae, but inconsistent with pliosaurid or cryptoclidid affinities (see comparisons above). However, SGM 1445-99 is smaller than CAMSM X.50215 with a dorsoventral length of 255 mm, and is proportionally more robust (the minimum anteroposterior diameter of the shaft is 60 mm, similar to that of CAMSM X.50215). The cross section of the shaft is suboval and its mediolateral diameter at the point of minimum anteroposterior diameter is 40 mm.

The dorsal portion of the ilium is expanded more posterodorsally than anteriorly, although the appearance of this morphology is exaggerated by plastic deformation (Fig. 7). The plane of the dorsal expansion is rotated approximately 35° posterolaterally relative to that of the ventral expansion. The ventral expansion is 115 mm long anteroposteriorly, with maximum mediolateral width of 60 mm. The ischiadic facet is subtriangular in outline and faces posteroventrally. It has an anteroposterior length is 55 mm, and maximal mediolateral width of 40 mm. The acetabular facet has a mediolateral and anteroposterior diameter of 60 mm.

*Ischium*: The ?left ischium is crushed and incomplete, and only two uninformative fragments are now present (Fig. 8C, D; SGM 1445-97). Measurements of the ischium recorded by Milanovsky (1921) report a mediolateral width of 300 mm, and a preserved anteroposterior length of 450 mm, noting that the posterior process was broken. Milanovsky estimated an original length of 600−650 mm (Milanovsky 1921). It is not clear that these measurements are reliable, or whether

Table 1. Measurements (in mm) of the preserved plesiosaurian vertebral centra of SGM 1445-9–20, 97−120.

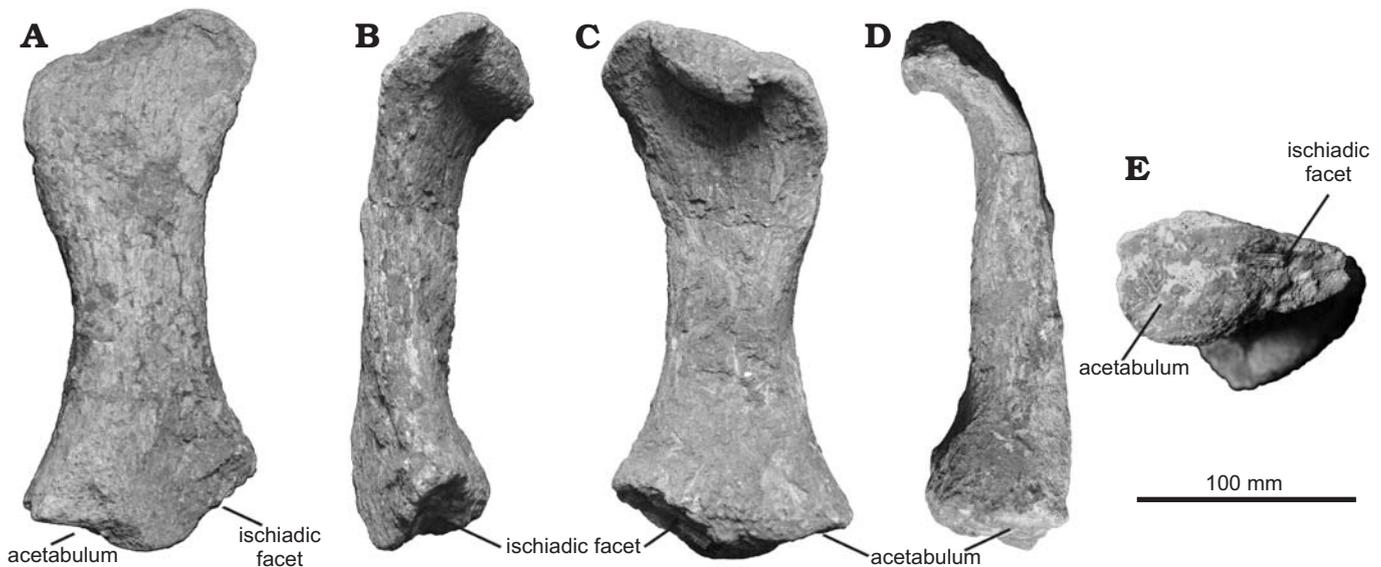| SGM no. | Type | Length | Anterior height | Anterior width | Posterior height | Posterior width |
|---|---|---|---|---|---|---|
| 1445-108 | dorsal | 65 | 110 | 110 | 110 | 105 |
| 1445-107 | dorsal | 60 | 90 | 95 | 95 | 90 |
| 1445-105 | caudal | 50 | 75 | 90 | 70 | 80 |
| 1445-106 | caudal | 45 | 75 | 90 | 70 | 75 |
| 1445-104 | caudal | 45 | 70 | 80 | 70 | 75 |
| 1445-102 | caudal | 43 | 60 | 65 | 58 | 54 |
| 1445-103 | caudal | 34 | 40 | 43 | 34 | 36 |

Fig. 7. Left ilium of the plesiosaur Rhomaleosauridae indet., SGM 1445-99, from the Lower Callovian Hlebnovka Formation of "Konnyi barak" ravine, Russia, in lateral (**A**), posterior (**B**), medial (**C**), anterior (**D**), and ventral (**E**) views.

the recorded mediolateral width represents a complete or incomplete specimen. Nevertheless, the length:width ratios resulting from these measurements range from 1.50–2.17, exceeding 1.17 seen in CAMSM X.50215, and overlapping with those of many other plesiosaurians, including rhomaleosaurids and pliosaurids (discussed above).

*Pubis*: Only the acetabular process of the left pubis is preserved (Fig. 8A, B), with a dorsoventral height of 95 mm and an anteroposterior length of 165 mm. It bears two flat slightly concave equal in size facets, one for the ischium, facing posteriorly and one for the acetabulum, facing laterally.
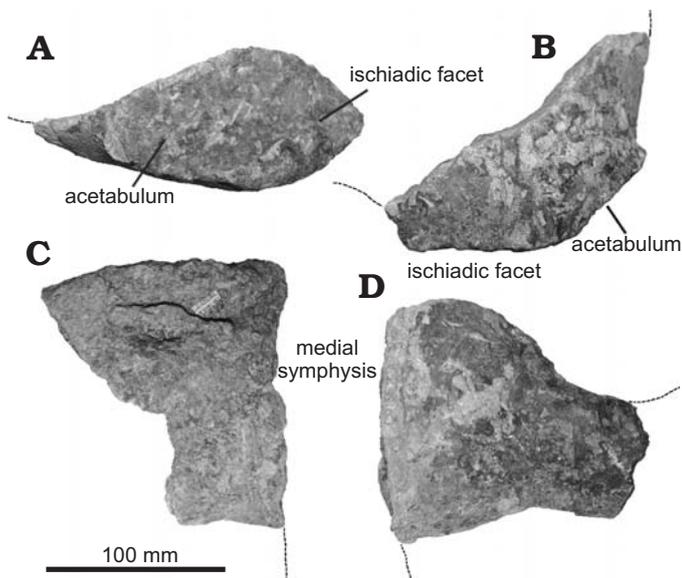


Fig. 8. Portions of the ?left pubis (A, B) and ischium (C, D) of the plesiosaur Rhomaleosauridae indet., SGM 1445-97, from the Lower Callovian Hlebnovka Formation of "Konnyi barak" ravine, Russia in lateral (**A**), dorsal (**B**), and ?dorsal (**C**, **D**) views.

*Hindlimb*: Five metatarsals and 17 phalanges are preserved (Fig. 9), probably representing the hindlimb, inferred from preservation of the pelvic girdle. The length of the metatarsals is 70 mm, with a proximal mediolateral width of 50 mm, and distal mediolateral width of 45−42 mm.

The phalanges are proportionally short, with proximodistal lengths that are generally less than twice their mediolateral width. They have rugose, approximately flat or weakly concave proximal and distal articular surfaces, which are dorsoventrally low compared to their mediolateral widths, and the central portions of the phalanges are mediolaterally constricted between these articular surfaces.

# Discussion

**Referral of CAMSM X.50215 and SGM 1445-9–20, 97−120 to Rhomaleosauridae.**—CAMSM X.50215 and SGM 1445-9–20, 97−120 possess several features seen primarily in Early Jurassic plesiosaurians, and discussed in the comparisons above. These features are absent in all thalassophonean pliosaurids and cryptoclidid plesiosauroids, suggesting that neither specimen can be referred to either of these groups, which otherwise occur abundantly from the Middle Jurassic–Early Cretaceous (Benson and Druckenmiller 2013). Both specimens possess features of the ilium that differ substantially from both thalassophoneans and cryptoclidids: (i) the ventral surface of the ilium is substantially wider anteroposteriorly than mediolaterally, with (ii) an ischiadic facet that faces posteroventrally instead of ventromedially, and (iii) the plane of the dorsal expansion of the ilium is only slightly rotated (20–35°) relative to the proximal end. Furthermore, the ischium of CAMSM X.50215 has a low ratio of anteroposterior length:mediolateral width (ratio = 1.17) compared to thalassophonean pliosaurids (1.7−2.0). We note that the
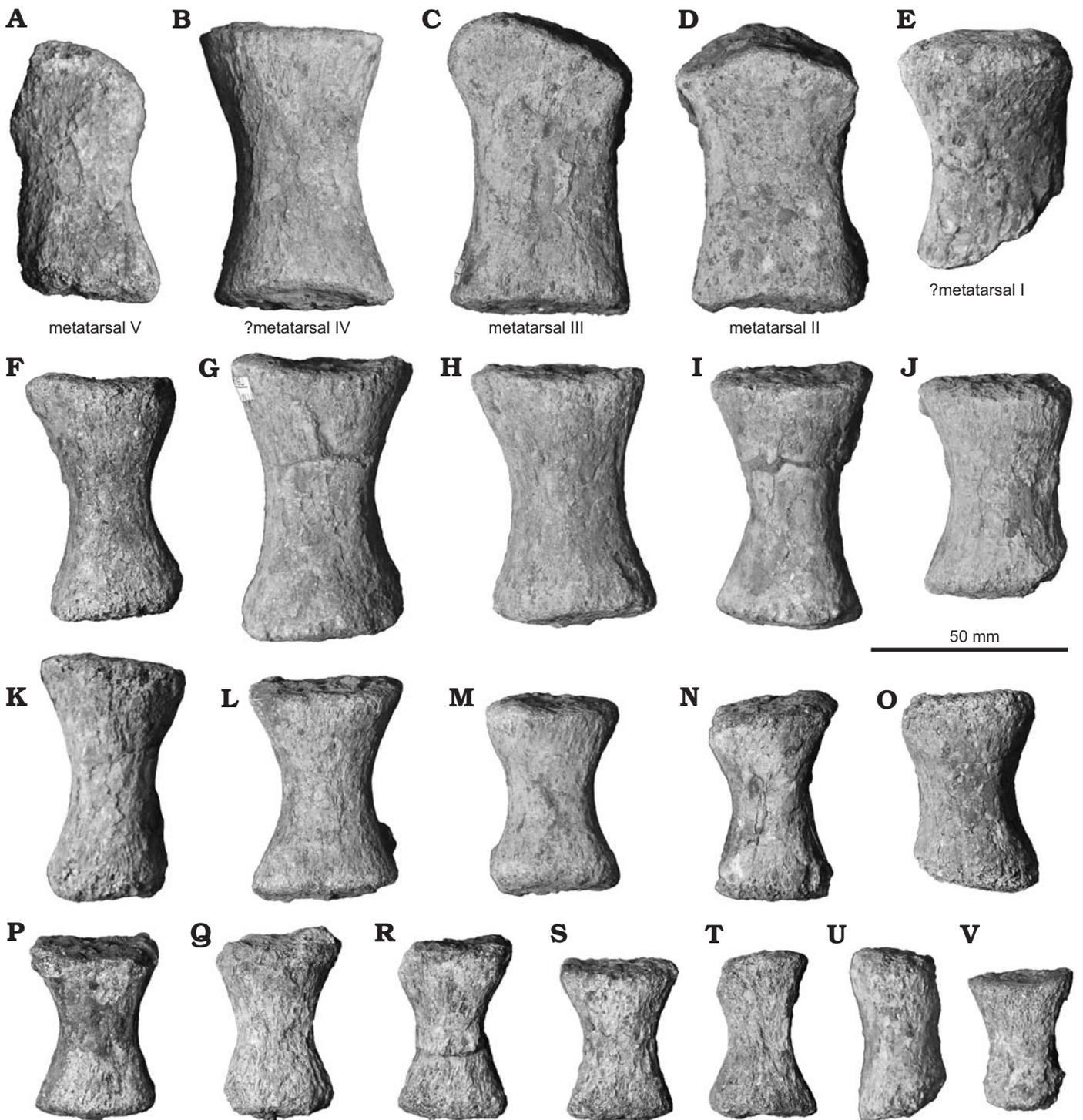
Fig. 9. Metatarsals (A–E) and phalanges (F–V) of the plesiosaur Rhomaleosauridae indet. from the Lower Callovian Hlebnovka Formation of "Konnyi barak" ravine, Russia, in ?dorsal view. **A**. SGM 1445-120. **B**. SGM 1445-115. **C**. SGM 1445-109. **D**. SGM 1445-114. **E**. SGM 1445-20. **F**. SGM 1445-118. **G**. SGM 1445-17. **H**. SGM 1445-116. **I**. SGM 1445-112. **J**. SGM 1445-117. **K**. SGM 1445-19. **L**. SGM 1445-111. **M**. SGM 1445-119. **N**. SGM 1445-18. **O**. SGM 1445-113. **P**. SGM 1445-10. **Q**. SGM 1445-11. **R**. SGM 1445-12. **S**. SGM 1445-14. **T**. SGM 1445-15. **U**. SGM 1445-13. **V**. SGM 1445-16. The arrangement of phalanges is not intended to represent their positions in life.

higher ratio of >1.5 that might have been present in SGM 1445-9–20, 97–120 based on the unpublished field notes of Milanovsky (1921), is unreliable as it is not clear whether his reported mediolateral width represents the complete, original width. The large size of both specimens is distinct from known cryptoclidids (the ilium of CAMSM X.50215 is 375 mm long, compared to that of the largest cryptoclidid: 225 mm; Andrews 1910) and the CAMSM X.50215 is larger than small pliosaurids such as *Peloneustes* and *Simolestes* (ilium length = 310 mm in "*Pliosaurus*" *andrewsi*; Andrews 1913).
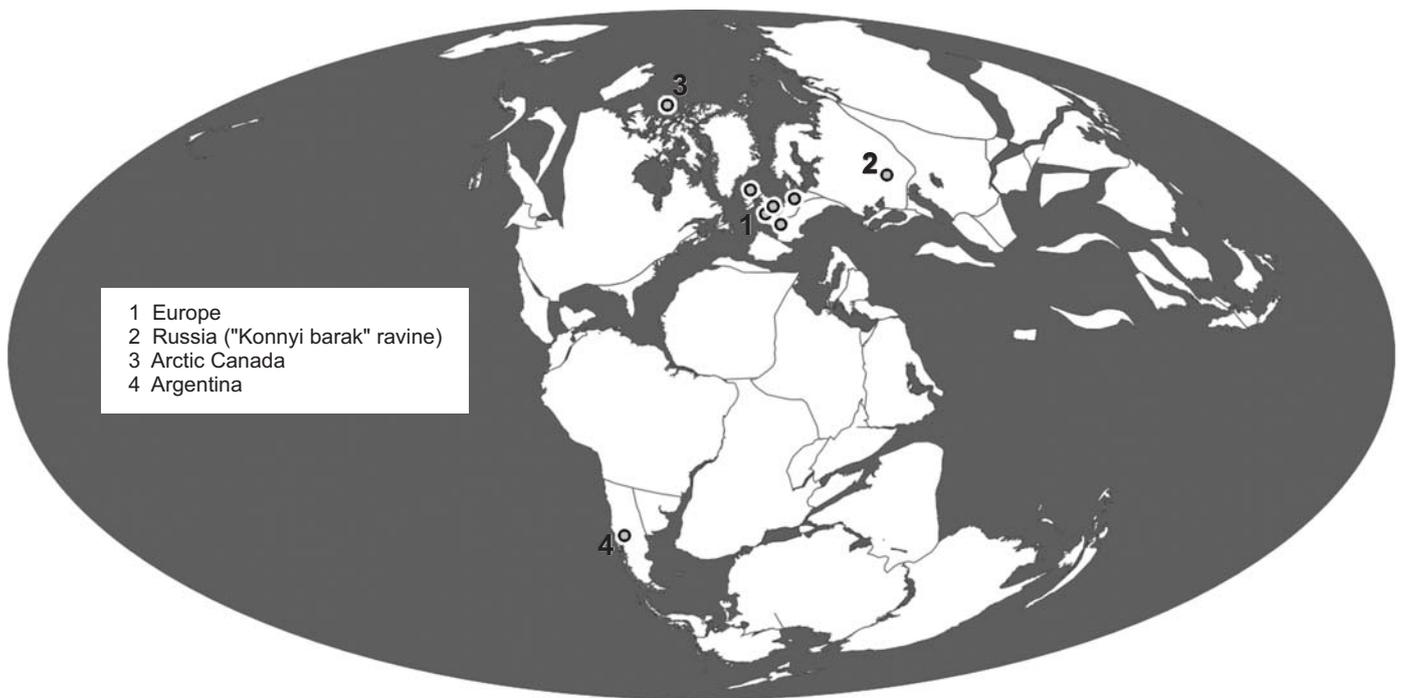
Fig. 10. Callovian palaeogeographic map (constructed by https://paleobiodb.org using plate rotations based on Wright et al. 2013) showing plesiosaur localities discussed in the text.

The straight shaft of the ilium in both specimens is distinct from the anterodorsally curving shaft in cryptoclidids and xenopsarians. Finally, the straight posterior margin of the ischium of CAMSM X.50215, with a "truncated" appearance in dorsal view, is uniquely shared with rhomaleosaurids (e.g., Andrews 1922; Fraas 1910; Smith and Vincent 2010; Smith and Benson 2014).

Together, these observations demonstrate that the CAMSM X.50215 and SGM 1455-9–20, 97−120 cannot be referred to either Thalassophonea or Cryptoclididae, and share more character states with Early Jurassic plesiosaurs. We are therefore confident in stating that they represent an early-diverging plesiosaurian clade. Referral specifically to Rhomaleosauridae is less secure in light of differences in the reported length:width ratio of the ischium of SGM 1445-9–20, 97−120, and in the presence of an anteroposteriorly thicker ischial neck in CAMSM X.50215 than those of Early Jurassic rhomaleosaurids. Nevertheless, we propose that referral to Rhomaleosauridae is conservative given the presence of the rhomaleosaurid *Borealonectes* in the Callovian of Arctic Canada (Sato and Wu 2008), and the presence of features shared uniquely with rhomaleosaurids among Early Jurassic plesiosaurian lineages, including (i) the posterior margin of the ischium has a "truncated" appearance in dorsal view, and (ii) the iliac facet of the ischium faces laterally, as in *Rhomaleosaurus* (Smith and Vincent 2010; Smith and Benson 2014). Nevertheless, further discoveries of more complete Callovian rhomaleosaurids are required to confirm our hypothesis that the specimens reported here represent rhomaleosaurids rather than a distinct, late-surviving clade of early-diverging plesiosaurs.

**Palaeobiogeographic implications**.—Previous plesiosaur discoveries from the Callovian of Europe represent exclusively cryptoclidid plesiosauroids and thalassophonean pliosaurids, and span a range of palaeolatitudes from 31°N (Migné-les-Lourdines locality of France; Brunet 1969) to 41°N (Flodigarry foreshore locality of Scotland, United Kingdom; Clark et al. 1993), although most discoveries are from localities in England, also in the United Kingdom, at approximately 35–36°N. The palaeolatitudes reported in this discussion were obtained from the Paleobiology Database (https://paleobiodb.org), and were computed using the "GPlates" rotations based on Wright et al. (2013).

*Borealonectes*, a rhomaleosaurid, is known from the Callovian of Cape Grassy, Melville Island, Arctic Canada, occurring at a high palaeolatitude of 62°N (Russell 1993; Sato and Wu 2008). Furthermore, fragmentary Callovian plesiosaur remains comprising vertebrae and epipodials were reported from higher southern latitudes at the Chacaico Sur locality (43°S) of Argentina by Gasparini and Spaletti (1993), and referred to Pliosauridae indet., and to the cryptoclidids *Cryptoclidus* and *Muraenosaurus*. The "pliosaurid" centrum (MOZ 6002; Gasparini and Spaletti 1993: pl. 1A–C) is anteroposteriorly short, with a length that is 0.54 times the dorsoventral height. A similar proportion is indeed seen in thalassophonean pliosaurids (Tarlo 1960). However, it is also present in rhomaleosaurids (e.g., Ketchum and Smith 2010; Smith and Vincent 2010; Smith and Benson 2014), including the Middle Jurassic taxa *Maresaurus*, from the Bajocian of Argentina (Gasparini 1997), and *Borealonectes*, from the Callovian of Arctic Canada (Sato and Wu 2008). The cervical centra of rhomaleosaurids differ from those of pliosaurids in

possessing a narrow, anteroposteriorly oriented ventral ridge on the ventral surface of the centrum between the subcentral foramina, and in the presence of a ventrally and laterally expanded rim around the intervertebral articular surfaces (compare pliosaurid centra in Tarlo 1960 with rhomaleosaurid centra in Smith and Benson 2014). These features are present in MOZ 6002, suggesting that it should be referred to Rhomaleosauridae indet., and not to Pliosauridae indet.

The specimens reported here add a rare occurrence of a likely rhomaleosaurid in the English localities, at 36°N, and a single occurrence of a likely rhomaleosaurid in the Volgograd Region ~42°N. These findings suggest that at the time of their last appearance, rhomaleosaurids were common components of mid–high palaeolatitude marine faunas, but were extremely rare at low latitudes, and had therefore escaped detection by palaeontologists, until now. This inference does not rest solely on the four datapoints representing Callovian global rhomaleosaurid occurrences, it also rests on the abundant occurrence of non-rhomaleosaurid plesiosaurians in the European, low latitude assemblage. If rhomaleosaurids are found to be common in other Callovian low latitude marine reptile assemblages, yet to be discovered, then our hypothesis will be shown to be incorrect. Whether our hypothesis is correct or not, then expanding the spread of palaeogeographic sampling, and undertaking further collection at existing mid–high palaeolatitude localities for the Middle and Late Jurassic could considerably extend our current knowledge of marine reptile evolution and biogeography.

**Extinction of Rhomaleosauridae**.—The apparent latitudinal gradient in Callovian rhomaleosaurid occurrences suggests that the last rhomaleosaurids were more abundant in cooler temperature faunas. A similar observation was recently made for the Late Jurassic ichthyosaur genus *Arthropterygius*, which is known only from high latitude occurrences in both the northern and southern hemispheres (Zverkov et al. 2015). Our observations may shed light on the final extinction of rhomaleosaurids, which currently make their last fossil appearances in the Callovian (Sato and Wu 2008; and herein). The Middle–Late Jurassic transition was marked by global warming that continued into the Early Cretaceous (e.g., Prokoph et al. 2008). If we are correct, then warming would progressively remove rhomaleosaurid-rich habitats, shifting rhomaleosaurid distributions to higher latitudes, reducing their geographic range, and rendering them vulnerable to extinction.

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