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Increased pliosaurid dental disparity across the Jurassic–Cretaceous transition

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Abstract

Pliosaurid marine reptiles played important roles in marine food chains from the Middle Jurassic to the ‘middle’ Cretaceous, frequently as apex predators. The evolution of pliosaurids during the later parts of the Early Cretaceous has recently been illuminated by discoveries from Russia (Hauterivian) and Colombia (Barremian). However, knowledge of pliosaurids representing the Jurassic–Cretaceous transition (late Tithonian–Valanginian), is still largely incomplete, especially during the earliest Cretaceous. As such, the effect on pliosaurids of hypothesized faunal turnover during the Jurassic–Cretaceous boundary interval is poorly understood. We report pliosaurid teeth from the upper Volgian (Tithonian, Upper Jurassic) of the Kheta river basin (Eastern Siberia, Russia), to the Berriasian and Valanginian (Lower Cretaceous) of the Volga region (European Russia). These assemblages yielded a series of distinct tooth morphotypes, including the first reports of conical-toothed pliosaurids from the latest Jurassic–earliest Cretaceous. This challenges the hypothesis that only one lineage of pliosaurids crossed

the Jurassic–Cretaceous boundary. It appears that conical-toothed pliosaurids co-existed with their trihedral-toothed relatives for at least 25 million years during the latest Jurassic and earliest Cretaceous. In fact, our quantitative analyses indicate that pliosaurids reached their maximal dental disparity during this interval, showing little evidence of turnover associated with the Jurassic–Cretaceous transition. Instead, disparity decreased later in the Early Cretaceous, with the disappearance of trihedral-toothed forms in the Barremian.

Key words: Pliosauridae, Thalassophonea, tooth enamel ornamentation, palaeoecology, Berriasian, Jurassic–Cretaceous transition.

INTRODUCTION

Thalassophonean pliosaurids were large marine amniotes with a short neck, a proportionally gigantic head and elongated jaws bearing large conical or trihedral teeth (Andrews 1913; White 1935; Tarlo 1960; Benson *et al.* 2013*a*; Benson & Druckenmiller 2014). They regulated the upper tiers of marine ecosystems as apex predators from the Middle Jurassic to early Late Cretaceous. As with many groups of Mesozoic marine reptiles (Benson *et al.* 2010), our knowledge of their evolutionary history is characterised by windows of high fossil abundance, separated by intervals of little or no knowledge (Hampe 2005; Fischer *et al.* 2015, 2017; Gómez-Pérez & Noè 2017). In particular, although many thalassophonean fossils are known from the upper Middle Jurassic, Upper Jurassic, and mid-Cretaceous, much less is known from the Jurassic–Cretaceous transitional interval.

Patterns of faunal turnover during the Jurassic–Cretaceous boundary interval are contentious, and potentially varied among different groups and environments (e.g. Fischer *et al.* 2012; Rogov 2013; Benson & Druckenmiller 2014; Tennant *et al*. 2017). In fact, the lack of consensus over the importance and severity of faunal turnover during this interval suggests that it does not represent a discrete mass extinction, and may not have differed from background patterns of turnover. For example, many squamate and mammalian genera are represented in both latest Jurassic and earliest Cretaceous assemblages (Benson *et al.* 2013*b*), and among marine reptiles, ichthyosaurs survived the transition relatively unscathed (Fischer *et al.* 2012; 2013). Marine and semi-aquatic crocodylomorphs, on the other hand, demonstrate high rates of extinction and turnover during this transition (Mannion *et al*. 2015; Tennant *et al*. 2016, 2017), and the same was hypothesized for plesiosaurs (Benson & Druckenmiller 2014). However, the hypothesized turnover among plesiosaurs could in part be explained by poor sampling: few plesiosaur specimens are known from this time interval. Despite this, at least one clade, Colymbosaurinae, whose members are abundant in the latest Jurassic, survived into the Cretaceous. Furthermore, a clade of typically Cretaceous plesiosaurs, Xenopsaria, likely originated in the Jurassic, though its early evolutionary history is still unclear (Benson & Druckenmiller 2014). Thalassophonean pliosaurids are the third clade of plesiosaurs that crossed the Jurassic–Cretaceous boundary, and earlier work suggested that only a single lineage did so (Benson & Druckenmiller 2014). Subsequent discoveries have improved our understanding of their diversity and disparity dynamics (Fischer *et al.* 2015, 2017), although fossils from this critical interval are not abundant.

Current knowledge of the dental morphology of pliosaurids comes mostly from several restricted time intervals and areas. Middle Jurassic pliosaurids are known predominantly from the Callovian Peterborough Member of the Oxford Clay Formation of England. This assemblage includes apex predators such as *Liopleurodon ferox* Sauvage, 1873 and *Simolestes vorax* Andrews, 1909 (see Andrews 1913; Tarlo 1960), alongside longirostrine taxa likely consuming smaller and softer prey: *Peloneustes philarchus* (Seeley, 1869), '*Pliosaurus*' *andrewsi* Tarlo, 1960, *Marmornectes candrewi* Ketchum & Benson 2011*a* and *Pachycostasaurus dawni* Cruickshank *et al.,* 1996 (see also Andrews 1913; Ketchum & Benson 2011*b*). All these taxa possessed conical teeth with distinctive shapes and patterns of enamel ornamentation that have been suggested to be diagnostic at the species level (Tarlo 1960; Noé 2001; Ketchum & Benson 2011*a*). Their phylogenetic position at or close to the base of the thalassophonean radiation

(Ketchum & Benson 2011*a*, *b*; Benson & Druckenmiller 2014) indicates that conical teeth represent the plesiomorphic condition for pliosaurid dentition.

Late Jurassic pliosaurids are mostly represented by the well-studied macropredatory taxon *Pliosaurus* Owen, 1841. This genus was geographically widespread, with occurrences reported from England (e.g. Owen 1841; Tarlo 1960; Benson *et al.* 2013*a*), France (e.g. Bardet *et al.* 1993), Germany (Wagner 1852), Norway (Svalbard; Knutsen *et al.* 2012), European part of Russia (e.g. Novozhilov 1948; Zverkov *et al.* 2017), Kazakhstan (Malakhov 1999) and Argentina (Gasparini & O'Gorman 2014; O'Gorman *et al.* 2018), and is characterised by subtrihedral-to-trihedral cross-sectional shape of its tooth crowns. The presence of trihedral teeth has been regarded a diagnostic feature uniting the Late Jurassic taxa attributed to *Pliosaurus* since early in the history of vertebrate palaeontology (e.g. Owen, 1869; Tarlo 1960; Knutsen 2012; Benson *et al*. 2013*a*; Zverkov 2015). However, other Late Jurassic pliosaurids (all Oxfordian in age) are still poorly known or incompletely described, which complicates the assessment of some of the aspects of their morphology, including the status of proposed dental apomorphies. These are *Gallardosaurus iturraldei* Gasparini, 2009 known from several cervical vertebra and incomplete skull with subtrihedral tooth crowns, *Anguanax zignoi* Cau & Fanti, 2015, known from incomplete skeleton that, among other elements, includes partial skull and several teeth with conical crowns, and '*Megalneusaurus rex*' (Knight, 1895) known from poorly-diagnostic postcranial remains (see Wahl *et al.* 2010).

Recent phylogenetic analyses reconstruct all Cretaceous thalassophoneans as a single clade, Brachaucheninae Benson & Druckenmiller, 2014, suggesting that only one thalassophonean lineage crossed the Jurassic-Cretaceous boundary (e.g. Benson *et al.* 2013*a*; Schumacher *et al.* 2013; Benson & Druckenmiller 2014; Fischer *et al.* 2015, 2017; Madzia 2016). Brachauchenine thalassophoneans from the relatively well-sampled Barremian–Turonian stages of the Cretaceous differ from Late Jurassic thalassophoneans in key diet-related morphological features. Many brachauchenines have more gracile rostra, possess isodont conical teeth, elongated snouts and several other features suggesting a diet of smaller prey (Williston 1903; Schumacher *et al.* 2013; Páramo-Fonseca *et al.* 2016), although this is not without exceptions (e.g. *Kronosaurus*; White 1935; Romer & Lewis 1959). However, this conspicuous difference between pliosaurid assemblages of the Late Jurassic and 'middle' Cretaceous may be due to a persistent hiatus in the fossil record of the early phases of the Early Cretaceous. This gap is gradually eroding thanks to new discoveries, especially from the Valanginian and Hauterivian of Russia (Fischer *et al.* 2015; Zverkov 2015; Fischer *et al*. 2017). Recently described peculiar pliosaurids *Makhaira rossica* Fischer *et al.*, 2015 and *Luskhan itilensis* Fischer *et al.*, 2017 from the upper Hauterivian of Russia, have subtrihedral or trihedral tooth crowns. These demonstrate that such morphology could actually have been retained plesiomorphically in the earliest brachauchenines, in spite of their otherwise long, gracile rostral characteristics (Fischer *et al.* 2015, 2017).

All hitherto described pliosaurid species of the Kimmeridgian to the Hauterivian possess trihedral and subtrihedral teeth with a smooth labial surface (Benson *et al*. 2013*a*; Fischer *et al.* 2015, 2017) while 'middle' Cretaceous and younger (Aptian–Turonian) pliosaurids have exclusively conical crowns with apicobasal ridges typically arranged around the entire circumference (Hampe 1992; Albright *et al.* 2007; Schumacher *et al.* 2013; Madzia 2016). Nevertheless, it remains unclear whether derived conical-toothed thalassophoneans originated in the Early Cretaceous from subtrihedral- to trihedral-toothed ancestors, whether several lineages of pliosaurids co-existed during the Late Jurassic–Early Cretaceous interval, each with distinct tooth morphologies, or whether trihedral teeth evolved more homoplastically among thalassophoneans of this interval.

New findings, reported herein, improve our knowledge of the evolution of pliosaurid teeth and demonstrate an unexpectedly high disparity of dental shapes among thalassophoneans from the Jurassic–Cretaceous transition. This observation is suggests higher rates of lineage survival among pliosaurids than were previously recognised (Benson & Druckenmiller 2014).

GEOLOGICAL SETTING

High levels of faunal provincialism have been observed among marine invertebrates during the latest Jurassic and earliest Cretaceous. This has led to use of independent regional marine stages that have proven to be difficult to correlate precisely on larger geographic scales. In the so-called Pan-Boreal Superrealm, Volgian and Ryazanian stages are used instead of Tithonian and Berriasian. Although the bases of the Tithonian and Volgian stages are approximately contemporaneous (Rogov 2010), their upper boundaries are not. Taking into account the results of recent voting of the Berriasian Working Group (which considered the base of the *Calpionella alpina* Biozone as a boundary level for the base of the Berriasian stage, and therefore for the top of the Tithonian stage) and results of magnetostratigraphic Boreal-Tethyan correlation (Houša *et al.* 2007; Bragin *et al.* 2013), the Tithonian–Berriasian boundary can be traced in the Pan-Boreal Superrealm, where it corresponds to a horizon within the Boreal *Craspedites* (*Taimyroceras*) *taimyrensis* Biozone (upper Volgian). This zone is nearly equivalent to the *C.* (*Trautscholdiceras*) *nodiger* Biozone of the Russian Platform (Rogov & Zakharov 2009).

Maryevka locality (N 53º06′59″, E 48º09′58″), Tsilninsky District, Ulyanovsk Oblast (Province), Russia (Fig. 1E). In several ravines located to the south and to the south-east of the village of Maryevka, there is a succession of Oxfordian–lower Valanginian deposits. The complete section of this locality was described by Rogov *et al*. (2015). The specimen SOIKM KP-28988 was discovered in Bed M24 (Fig. 1A), which is a 0.45 m thick bed of loosely cemented greensand, with local sandstone pockets. This layer forms the base of Ryazanian Stage and corresponds to *Riasanites rjasanensis* ammonite Zone (Rogov *et al*. 2015).

Kheta locality (N 70°32′15″, E 95°25′38″), Taymyr Dolgano-Nenets Autonomous Okrug, Krasnoyarsk Krai, Russia. The studied locality lies on the bank of the Kheta River (Fig. 1B, F; Section 22 in Sachs *et al*. 1969); it consists of greenish-brown silt with large (up to 2.5–3 m) concretions of carbonated and phosphatized siltstone, containing plant and animal fossils. The specimen TsNIGR 1/13307 was found within one of these concretions (see Fig. S1). Ammonites *Khetoceras* and poorly preserved *Craspedites* ex gr. *Craspedites okensis* were found in this locality, indicating it is entirely contained with the *Craspedites okensis* ammonite Zone of the upper Volgian (uppermost Jurassic; see e.g. Rogov & Zakharov 2009; Rogov 2014).

Rudnichnyi locality (59°31′44″N, 52°11′07″E), Verkhnekamsky District, Kirov Oblast (Province), Russia. Rudnichnyi was the mining centre of the Vjatka-Kama phosphate field. The quarries of Rudnichnyi mined Valanginian phosporites, in which isolated marine reptile bones are commonly found (see e.g. Arkhangelsky & Zverkov 2015). The Lower Cretaceous outcrops in this region are composed of the following succession, spanning from the Berriasian to the Hauterivian (Fig. 1C; Morozov *et al*. 1967):

(1) Coarse-grained quartz sandstones (up to 2.1 m), with the ammonite *Riasanites rjasanensis*, the belemnite *Acroteuthis russiensis*, and bivalves *Buchia volgensis* and *Buchia terebratuloides*. (2) Green medium-grained glauconitic sand with phosphorite nodules, containing nuclei of bivalves (*Buchia*) and the ammonite *Surites*, indicating a Ryazanian/Berriasian age. These sands are often cemented by phosphate and iron oxides. This horizon is up to 0.2 m thick.

(3) Dark-green glauconitic sands (up to 0.8 m thick) with phosphorite nodules containing ammonites *Nikitinoceras hoplitoides*, indicating an early Valanginian age.

(4) Dark grey glauconitic sands with phosphorite gravel and the ammonite *Prohomolsomites petschorensis* (0–1.5 m).

(5) Hauterivian grey silty clays up to 15 m thick.

According to the information on their labels and considering their state of preservation, the crowns NNGASU 740/5229 and NNGASU 740/5230 were collected from sands of the second lithological unit, and are therefore Ryazanian (Berriasian) in age. NNGASU 43/4577 was likely found in the third lithological unit, which is lower Valanginian.

TOOTH ANATOMICAL NOMENCLATURE

The terminology used to describe the morphology and outer enamel structures in the tooth crowns of pliosaurids varies from one paper to another. Below we propose a unified terminology and apply it throughout this paper.

Tooth orientation. We follow the tooth orientation terminology as widely used, and more recently summarised by Smith and Dodson (2003): apical, toward the apices of the tooth crown or the tooth root; basal, toward the base of the crown; mesial and distal, respectively, toward and away from the anterior margin of the symphysis; labial, toward the lips; lingual, toward the tongue (Fig. 2A).

Apicobasal ridges. Apicobasally oriented enamel ridges can be developed along the entire circumference of tooth crowns of plesiosaurs (i.e. they can be present on surfaces of any orientation). In the literature, the apicobasal ridges have also been called 'longitudinal ridges' (e.g. Ketchum & Benson 2011*a*, *b*; Fischer *et al.* 2015), 'enamel ridges' (e.g. Ketchum & Benson 2011*a*, *b*; Sassoon *et al.* 2012), and 'striations' (e.g. Albright *et al.* 2007; Schumacher 2008; Schumacher *et al*. 2013; Angst & Bardet 2016). The term 'striations', or 'striae', implies scratches, or other inwards-projecting structures such as grooves, and the raised areas between them. In fact, the primary, macroscopic linear structures on plesiosaur teeth are exclusively ridges (narrow, raised structures) and should not be referred to as 'striations'. The terms 'striae' and 'striations' have also been used for the description of distinct, smaller (constituting less than a half of ridge base width, and being less pronounced and sufficiently finer) raised, longitudinal structures on the enamel, as applied for example by Massare (1987) in teeth of *Liopleurodon*, and illustrated by Madzia (2016: Fig. 7).

We propose to refer to the larger longitudinal enamel structures as 'first order' as ridges (whatever their apicobasal extension), and to distinctly smaller longitudinal structures of 'second order', if they occur, as ridglets (Fig. 2A, G). The ridglets can be relatively rough, vermicular and developed throughout the crowns continuing apically and following an anastomosed pattern (see Madzia 2016: Fig. 7).

The apicobasal extent of the ridges varies widely: some ridges extend along the entire crown height, whereas others are developed only on a short basal segment. These additional shorter ridges, which appear between but do not contact of merge with to the 'main' longitudinal ridges are referred to here as 'inserted ridges' (Fig. 2A). The ridges on the mesial and labial surfaces of the crown tend to be apicobasally shorter, and more widely spaced than those of the distal and lingual surfaces.

Ridge undulations. The ridges of pliosaurid teeth are commonly straight or slightly sinuous and have triangular or semicircular cross-sections (see Tab. S1). Their external surface is usually straight, but sometimes the edges bear additional structural elements. These elements are described based on the shape of the ridge: (1) wavy, for low-amplitude and low frequency undulations of the profile of the ridge (Fig. 2B); (2) meandering, for high-amplitude and complex folding of the ridge, in external view (Figs 2C; 3F–G); (3) serrated, for low-amplitude and high frequency undulations of the profile of the ridge, forming denticle-like structures (Fig. 2D).

Ridge branching. The condition when two adjacent apicobasal ridges become confluent is usually termed ridge 'branching' (meaning that one ridge branches to produce two equal ridges basally) or ridge 'fusion' (meaning that two adjacent apicobasal ridges become confluent, forming a single ridge, apically). These terms only differ in the perceived direction of ridges extension (apically or basally), and therefore have identical meanings. However, the term 'branching' ridges is preferred here as it is more widely used (see e.g. Albright *et al*. 2007; Schumacher 2008; Schumacher *et al.* 2013; Angst & Bardet 2016; Madzia 2016; Madzia & Machalski 2017).

Carinae. The term carinae is used to describe more prominent, apicobasally oriented enamel ridges that are commonly exposed on the mesial and/or distal sides of the tooth crowns. These usually form cutting edges of the tooth crowns, especially in trihedral teeth, and differ from the apicobasal ridges in their limited number (up to three; e.g. Fischer *et al*. 2015) and more prominent relief. Pliosaurid carinae can be either serrated or not (Fischer *et al.* 2015).

Enamel bands and wrinkles. Undulose, wave-like enamel structures exposed on the unridged surface of the tooth crowns, oriented approximately perpendicular to the long axis of the crown were discussed in *Pliosaurus carpenteri* (BRSMG Cd6172) by Sassoon et al. (2012), and described as 'bands' and 'enamel rings'. These were hypothesized to possibly result from the tooth growth (Sassoon *et al.* 2012). Similar structures are present in a wide variety of Mesozoic predatory amniotes, including dinosaurs (e.g. Brusatte *et al.* 2007), crurotarsans (Brusatte *et al.* 2009; Andrade *et al.* 2010), mosasaurids (e.g. Buffeteaut & Bardet 2012; Harrell & Martin 2015) and some leptonectid neoichthyosaurs (Fischer *et al.* 2011). These enamel structural elements have been termed, for example, as 'enamel wrinkles' and 'bands' (e.g. Brusatte *et al.* 2007), 'transverse wrinkles' (Benson *et al.* 2008), 'transverse undulations' (Hendrickx *et al.* 2015*a*; 2015*b*), 'horizontal circular striations' (Fischer *et al.* 2011), or simply 'bands' (Andrade *et al.* 2010; Sasson *et al.* 2012; Fanti *et al.* 2014). Enamel bands appear in most of the crowns referable to *Pliosaurus* (see e.g. Sassoon *et al.* 2012) and could be also observed in some other pliosaurids (Fig. 2E, F). Additionally, the enamel surface of some pliosaurids became wrinkled near the carina (Fig. 2), in a manner similar to that of some theropod dinosaurs (e.g. Brusatte *et* *al.* 2007). In some cases, enamel surface is wrinkled near the base of ridges (Fig. 3G, H), probably contributing to undulations of their cutting profile.

METHODS

Fossil preparation and imaging

The crown SOIKM KP-28988 was found in loosely cemented sand and required minor preparation. SOIKM KP-28988 was studied in scanning microscope (TESCAN) at Borissiak Paleontological Institute of the Russian Academy of Sciences (PIN). A series of close-up images were taken of the labial, lingual, mesial and distal surfaces of the crown. A collage of photos was made for each view to achieve a high resolution of images (Fig. 3). Because of limits on the working chamber dimensions and characteristics of the microscope, the apical view of the crown was photographed using a digital camera, after being coated in ammonium chloride (Fig. 3C).

The specimen TsNIGR 1/13307 was enclosed in a dense, 10 cm wide siltstone concretion (Fig. S1). About a week of mechanical preparation was required to extract TsNIGR 1/13307 from the concretion. Being substantially larger than SOIKM KP-28988, TsNIGR 1/13307 could not enter the scanning microscope and was photographed using a digital camera, after being coated in ammonium chloride (Fig. 4).

Evolution of tooth size over time

We reconstructed the evolution of the maximum height and maximum diameter of pliosaurid tooth crowns over time using a phenogram. To do so, we estimated the ancestral heights and diameters for each node of a pliosaurid tree extracted from Fischer et al. (2017), using a maximum likelihood method developed in the package `phytools` v0.6-20 Revell 2012, adapting a script from Bell et al. (2017). Taxa for which crown diameter and/or crown height values could not be obtained were pruned from the tree. We selected the tree with the best Gap Excess Ratio index (calculated in Fischer et al. 2017) and we time-scaled it using an ‘equal’ optimisation of branch lengths using the `paleotree` package v2.7 (Bapst 2012). Taxa with crown size data but not considered in the phylogeny were added manually to the phenogram, notably the specimens described in this paper.

Principal coordinate analyses and cluster dendrograms

We gathered a series of continuous and categorical data that collectively summarise the morphology of pliosaurid teeth, including the finer details of their outer enamel structure. The dataset is resolved at the species level for taxonomy, and at the geological formation–ammonite zone level (or stage or substage when no more information is available) for stratigraphy. Measurements and ratios were derived from a single specimen for each operational taxonomical unit, usually from the largest referred specimen. For categorical observations, we observed multiple specimens per species, when possible (see Zverkov *et al*. 2018, documents~~table S1~~ and references therein). These data were gathered by personal observations on a series of specimens (for details see Zverkov *et al*. 2018, documents~~table S1~~) and were completed by measurements and analyses of pictures and descriptions of the following references: Phillips 1871; Andrews 1913; Tarlo 1960; Halstead 1971; Hampe 1992; Taylor & Cruickshank 1993; Carpenter 1996; Cruickshank *et al*. 1996; Noè 2001; Papazzoni 2003; Liggett *et al*. 2005; Albright *et al.* 2007; Schumacher 2008; Gasparini 2009; Ketchum & Benson 2011*a*, *b*; Sassoon *et al*. 2012; Benson *et al.* 2013*a*; Schumacher *et al*. 2013; Cau & Fanti 2014, 2016; Fischer *et al*. 2015, 2017; Zverkov 2015; Madzia 2016; Páramo-Fonesca *et al*. 2016; Madzia & Machalski 2017; Gómez-Pérez & Noè 2017 (see Zverkov *et al*. 2018, documents~~Supplementary table~~ for detailed account of each taxon included). In rare instances, we also used measurements of isolated crowns, especially when they occur at times of poorly documented pliosaurid evolution and when they exhibit a peculiar morphology. Nevertheless, we then applied a 50% completeness threshold to remove the influence of highly incomplete taxa for which pairwise distances cannot be estimated correctly due to abundant missing data.

We used the following metrics (~~Table S1~~see Zverkov *et al*. 2018, documents):

1. Absolute crown height of the largest tooth (a crucial determinant in the diet of odontocete cetaceans; e.g. Ridgway & Harrison 1999). This character is used from Fischer *et al.* (2017) and adapted from Fischer *et al*. (2016). For more than a half of the taxa considered, this metric is known thanks to a good fossil record (see ~~table S1~~Zverkov *et al*. 2018, documents). However, some of the taxa we considered are known by only a small number of teeth. This introduces some biases as these teeth are probably not the largest among the population. Nevertheless, where possible we have been consistent and selective in the data we used, solely considering teeth from the middle or anterior part of the jaw, where all the large teeth are located. Taxa for which the assessable teeth were much smaller than the largest in the jaw, as suggested by the size of preserved dental alveoli, were scored as NA (e.g. *Acostasaurus*). Another potential source of error for this metric lies in the breakage and apical wear (such as in *Pliosaurus kevani*, Morphotype 3 NNGASU and GFMSU h-216) as well as measuring from the photographs (e.g. *Brachauchenius lucasi*). Again, crowns that were obviously broken were not considered; we posit that the potential errors introduced by slight apical wear and the distortion of photograph are outweighed by the gain of widely sampling across pliosaurid taxa.

2. Crown shape (crown height divided by the basal diameter of the crown, of the largest tooth). This character is used from Fischer *et al.* (2016; 2017). This ratio is susceptible to similar source of errors as the metric 1, thereby poorly known taxa were scored with NA.

3. Number of carinae. 0, 1, 2, or 3. New character.

4. Shape of the enamel ridges, in cross-section. 0: semicircular, 1: triangular. New character.

5. Ridge branching in the middle and apical parts of the crown. 0: absent, 1: present. New character.

6. Crown section. 0: subcircular, 1: subtrihedral, 2: trihedral. Character obtained from Benson & Druckenmiller (2014: Char. 139).

7. Ornamentation of the labial surface. 0: ridged, 1: smooth. New character.

8. Density of apical ridges. 0: densely packed (more than four ridges reach the apex), 1: medium (*c*. 4 ridges reach the apex), 2: rare or absent (3 or less ridges reach the apex). New character.

9. Density of basal ridges. 0: all ridges reach the base of the crown, but are not densely packed, 1: not all ridges reach the base of the crown, 2: all ridges reach the base of the crown and are densely packed. New character. The ridges are considered to be densely packed (2) when the distance between the bases of adjacent ridges is shorter than the width of the ridge base (see e.g. Fig. 3E); in the state (0) the distance between the bases of adjacent ridges is wider than the width of the ridge base.

10. Enamel surface. 0: smooth, 1: ridglets and wrinkles, 2: 'glassy' texture. Smooth enamel is enamel devoid of ridges and other visible structures, such as striations and wrinkles; 'glassy' enamel texture was described by Noè (2001) and only for *Simolestes*, it is extremely smooth state of outer enamel with characteristic lustre, so that enamel in other pliosaurids appears comparatively matte. New character.

11. Apical wear score. 0: apical wear absent, 1: apical wear frequent, 2: apical wear and spalling present. Scored as NA for specimens/taxa with too few apices preserved and where the character is thus too difficult to assess. New character.

Data were scaled to equal variance and a mean of zero by subtracting the mean value for each feature and then dividing each feature by the standard deviation. We then created a distance matrix with this data, using the Gower metric, which is better suited for datasets mixing continuous and categorical variables (Gower 1971; Stubbs & Benton 2016), using the `cluster` v2.0.6 package in the R statistical environment (v3.4.1). We submitted this distance matrix to a cluster dendrogram analysis using the `stats` package, using the Ward.D2 method. We also visualised the tooth shape disparity and convergences in between taxa and over time via principal coordinate analyses of the same dataset, applying the Cailliez correction for negative eigenvalues and using the `ape` package (v4.1) (Paradis *et al*. 2004).

Binning methods

We discuss pliosaurid dental evolution in context of four temporal assemblages:

(1) The 'Middle Jurassic' assemblage is represented exclusively by conical-toothed pliosaurids of Callovian age. This assemblage comprises pliosaurids mostly from the Peterborough Member of the Oxford Clay Formation. It is therefore more restricted than the other proposed assemblages in both temporal and spatial coverage. Nevertheless, it is essential in establishing a 'baseline' for pliosaurid dental evolution. Furthermore, this interval samples large diversity of pliosaurids, both at the generic and specific levels, and there is currently no evidence from other Middle Jurassic finds (e.g. isolated teeth) that a temporally longer/geographically wider bin sample could change the broad pattern we recover (e.g. only conical teeth are known in the wider record of pliosaurids from the Bajocian of France [Godefroit 1994] and the Bathonian and Callovian of Russia [Efimov & Efimov 2011; Zverkov *et al.* 2017]). (2) The Late Jurassic assemblage is marked by the appearance of subtrihedral- to trihedral-toothed pliosaurids in the Oxfordian (Gasparini, 2009) and their dominance in the Kimmeridgian and Tithonian (Benson *et al.* 2013*a*). Two assemblages not corresponding to epochs were used for the Cretaceous pliosaurids: (3) Berriasian–Barremian and (4) Aptian–Turonian. Such division is applied with regard to the disappearance of trihedral-toothed pliosaurids in the Barremian and presence of exclusively conical-toothed morphotypes from the Aptian onwards. This division results in all four temporal assemblages under consideration characterised by comparable taxonomic diversity and number of morphotypes (6, 8, 7, 8), as well as temporal coverage (3 or 4 stages covered for all, except for the 'Middle Jurassic' assemblage).

Institutional abbreviations

BRSMG, Geology Collections, Bristol City Museum and Art Gallery, UK; GIN, Geological Institute, Russian Academy of Sciences, Moscow, Russia; GFMSU, Geological Faculty of

Lomonosov Moscow State University, Museum at the academic base named after Prof. A.A. Bogdanov, Bakhchisaray district, Crimea, Russia; NNGASU, Museum of Nizhny Novgorod State University of Architecture, Building and Civil Engineering, Nizhny Novgorod, Russia; PIN, Borissiak Paleontological Institute of Russian Academy of Sciences; SGM, V.I. Vernadsky State Geological Museum of the Russian Academy of Sciences, Moscow, Russia; SOIKM, Samara Regional History and Local Lore Museum named after P.V. Alabin, Samara, Russia; TsNIGR, Central scientific research geological survey museum named after Academician F.N. Chernyshev, St Petersburg, Russia; VSEGEI, A.P. Karpinsky Russian Geological Research Institute, St Petersburg, Russia.

SYSTEMATIC PALAEONTOLOGY

Sauropterygia Owen, 1860

Plesiosauria de Blainville, 1835

Pliosauridae Seeley, 1874

Thalassophonea Benson & Druckenmiller, 2014

Thalassophonea indet.

Morphotype 1

Figure 3

Material. SOIKM KP-28988, an isolated tooth crown (height of the preserved part = 28 mm).

Occurrence. SOIKM KP-28988 was found by Prof. Andrey Yu. Guzhikov during the field trip of The International Scientific Conference on the Jurassic–Cretaceous Boundary (Samara, September 2015) in the bank of a ravine near Maryevka village (Tsilninsky district, Ulyanovsk region, Russia). SOIKM KP-28988 originates from Bed M24 (Rogov *et al.* 2015), which forms the base of Ryazanian Stage and corresponds to the *Riasanites rjasanensis* Biozone (Fig. 1A; Rogov *et al.* 2015).

Description

The preserved crown is broken at its base and lacks the apex. Even though the apex is incomplete, the morphology of the apical parts of the labial ridges suggests that it was hardly worn (Fig. 3 B, C, E). The height of the preserved part of the crown (measured on its labial surface) is 28 mm. The weak curvature of the crown and its relatively high stoutness value (1.87; see Massare 1987 and ~~Table S1~~Zverkov *et al*. 2018, documents) indicate that it originates from the anterior or middle position of the jaw.

The crown is conical (circular in cross-section) (Fig. 3C). It is ornamented with robust apicobasal ridges. The ridges on the labial surface are more widely spaced than those on the lingual surface; the distance between the bases of adjacent ridges is wider than the width of the ridge base (Fig. 2D); lingual ridges are densely packed (Fig. 3E). Many ridges (12 out of 42) extend to the apex and some of them are branching (Fig. 3C). Ridge branching occurs near the base, in the middle and near the apex of the crown, as in *Brachauchenius* and *Megacephalosaurus* (Albright *et al.* 2007; Schumacher *et al.* 2013). Ridges become more widely spaced towards the apex as a result of fusions and the termination of inserted ridges.

None of the ridges could be regarded as a true carinae. Thus, the morphology differs from trihedral or subtrihedral teeth of some thalassophoneans (Benson *et al.* 2013*a*; Fischer *et al.* 2015). However, each ridge forms a distinct cutting edge. The edge meanders (irregularly folds) (Fig. 3F, G), recalling the morphology seen in some teleosaurid crocodyliforms (Young *et al.* 2015). The amplitude of these folds reduces basally, forming a serrated edge (Fig. 3A, B, D). The presence of meandering ridges is unique for SOIKM KP-28988. Wave-like serrations have been described for the carinae of *Makhaira rossica* (Fischer *et al.* 2015), but these structures appear distinct from those of SOIKM KP-28988. In other documented pliosaurid teeth, the ridges are straight or slightly undulating (wavy) (e.g. Sassoon *et al.* 2012; Benson *et al.* 2013*a*; and pers. obs. of the authors).

Remarks on the affinities of SOIKM KP-28988

All the specimens discussed in this paper have relatively large and robust crowns, have tapered apices, and bear ornamentation, with robust widely-spaced apicobasal ridges. Given the spatiotemporal setting, these features are uniquely found in thalassophonean pliosaurids (e.g. Tarlo 1960; Madzia 2016). Nevertheless, the peculiarities of SOIKM KP-28988 merit additional discussion.

Besides pliosaurids, strata from the Berriasian have also yielded xenopsarians (Benson & Druckenmiller 2014; Hornung *et al.* 2013; Sachs *et al.* 2016), rare ichthyosaurs (Fernández & Aguirre-Urreta 2005; Fernández 2007; Ensom *et al.* 2009; Fischer *et al.* 2012; Green & Lomax 2014), and thalattosuchians (e.g. Young *et al*., 2014). The lack of carinae in SOIKM KP-28988 would be unusual for thalattosuchians. Among Tithonian and Berriasian representatives of that group, this feature is only found in some *Machimosaurus* teeth (Young *et al*. 2014). However, the crowns of *Machimosaurus* differ substantially from SOIKM KP-28988 and are highly distinctive in having blunt apices and an anastomosed pattern of the enamel surface in the apical region. Therefore, SOIKM KP-28988 is likely not a thalattosuchian.

The ornamentation pattern of neoichthyosaurian tooth crowns is commonly composed of numerous tightly packed ridges, which are semicircular in cross-section, even in large predatory forms (Fischer *et al.* 2016, Fischer 2016) of the Late Jurassic and the Cretaceous. After the disappearance of *Temnodontosaurus* during the late Toarcian (Martin *et al.* 2012), no ichthyosaur is known to possess carinae or protruding ridges (e.g. Massare 1987, Godefroit 1993). This strongly suggests that SOIKM KP-28988 is not an ichthyosaur either. Many derived ichthyosaurs also have plicidentine, but this structure can however be reduced or absent in some platypterygiine ophthalmosaurids (Scheyer & Moser 2011; Maxwell *et al.* 2011).

Some derived xenopsarians from younger deposits, such as the early polycotylid *Edgarosaurus muddi* from the Albian of the USA (Druckenmiller 2002) and polycotyline *Polycotylus latipinnis* Cope, 1869, from the Santonian–Campanian of the USA (see also Schumacher & Martin 2016) are characterised by a relatively robust dentition. The largest crowns of *Edgarosaurus* are 50 mm high and have 15 mm in diameter (Druckenmiller 2002). This is almost twice the apicobasal height of SOIKM KP-28988. However, the teeth of *Edgarosaurus* are more slender, having the stoutness ratio of 3.3, and their outer enamel surface was described as bearing 'numerous wavy, longitudinal and in some cases bifurcating striations' (Druckenmiller 2002: 38). Even though such appearance might seem similar to the condition of SOIKM KP-28988, the apicobasal ridges of *Edgarosaurus* (and of polycotylids in general, when present) are fine in comparison to the strongly protruding ridges of SOIKM KP-28988 (N.G.Z. and R.B.J.B. examination of photographs provided by H. Ketchum, pers. comm. October 2009). Early xenopsarians known so far from the Berriasian are characterised by slender teeth and fine ridges (Wegner 1914; Hampe 2013). Thereby, considering the morphology of SOIKM KP-28988 (even compared to some other pliosaurids), its referral to Pliosauridae is robust.

Thalassophonea indet.

Morphotype 2

Figure 4

Material. TsNIGR 1/13307, a nearly complete tooth (height of the preserved part = 64 mm).

Occurrence. TsNIGR 1/13307 was found by Mikhail A. Rogov (GIN) in upper Volgian (uppermost Tithonian to lowermost Berriasian) deposits of Siberia during the expedition of VSEGEI in summer 2015, on the bank of the Kheta River (Section 22 in Sachs *et al*. 1969). TsNIGR 1/13307 was found along with ammonites typical for the *Craspedites okensis* Biozone of the upper Volgian (uppermost Jurassic; see e.g. Rogov 2014).

Description

The apex is worn and so terminates in a flat, circular surface (Fig. 4E). The crown is curved and circular in cross-section, as in early thalassophoneans and derived brachauchenines (Andrews 1913; Tarlo 1960; Schumacher *et al.* 2013; Madzia 2016) (Fig. 4). All apicobasal ridges are straight, as in *Simolestes* and '*Polyptychodon*' (Tarlo 1960; Madzia 2016). The ridges are semicircular in cross-section all over their length, unlike the triangular cross-sections of enamel ridges in most thalassophoneans (see Discussion and Zverkov *et al*. 2018, documentssupplementary table S1). Most of the ridges (about 25) reach the apex of the crown, where they become wider and nearly confluent. This morphology is likely due to the substantial apical wear. Shorter inserted ridges, which extend from one fifth (Fig. 4B) up to three fifths of the apicobasal length of the crown, are present between the main apicobasal ridges. Labial ridges are widely spaced (the distance between the bases of adjacent ridges is nearly three times their transverse width) and do not reach the base of enamel layer, as in *Simolestes* (Tarlo 1960) and *Marmornectes* (Ketchum & Benson 2011a). However, in *Marmornectes,* this condition occurs not only labially but also on two other surfaces (Ketchum & Benson 2011a). Lingual ridges of TsNIGR 1/13307 are closely spaced due to numerous inserted ridges (Fig. 4C, E).

Thalassophonea indet.

Morphotype 3

Figure 5

Material. NNGASU 740/5229, 740/5230 and 43/4577, three conical tooth crowns. NNGASU 740/5229 and 740/5230 are incomplete conical crowns free of matrix; the height of both is 75 mm. NNGASU 43/4577 is a fragmentary tooth enclosed in a solid phosphorite matrix; the height of the preserved part is 142 mm.

Occurrence. NNGASU specimens were collected from quarries of Vyatka-Kama phosphorite field. NNGASU 740/5229 and 740/5230 were found by Yu. S. Rubtsov in 1995. According to information from the specimen label, and considering their state of preservation, these crowns were collected from the Ryazanian (Berriasian) sands (the second lithological unit; see Fig. 1C) exposed at the Rudnichnyi quarries. NNGASU 43/4577 was found by N. A. Abramychev in 1973; it is enclosed in a phosphorite cemented matrix, typical for the Valanginian strata of the Rudnichnyi quarry (the third lithological unit; see Fig. 1C for details).

Description

The crowns are conical, curved, and sculpted by numerous ridges around their entire circumference. The enamel ornamentation is similar to that of *Liopleurodon* and *Peloneustes* (Tarlo 1960; Ketchum & Benson 2011b). Each ridge forms a cutting edge, resulting in its triangular cross-section. However, apically most of the ridges become smoother and semicircular in cross-section, which is possibly due to wear. There are more ridges on the lingual surface (Fig. 5B, D) than on the labial surface (Fig. 5A, E). All ridges originate at the base of the crown, but only few of them reach the apex. Ridge branching is absent. The apical part of the labial surface in NNGASU 740/5229 lacks ridges as all except for two terminate well below the apex (Fig. 5A). In NNGASU 740/5229, the ridges are serrated similarly to SOIKM KP-28988 (Fig. 5K).

RESULTS

Evolution of the size and shape of the pliosaurid teeth through time

We estimated the evolution of both the apicobasal height and the diameter of the largest crowns of pliosaurids through time, within (Fig. 6B–C) and without (Fig. 6A) a phylogenetic context. The evolution of these two metrics is generally similar, but we hypothesise that the evolution of the crown diameter (Fig. 6C) is a better proxy for general tooth size than the apicobasal height (Fig. 6B), because the latter is probably more affected by diet-related changes in the crown shape at the specific level (i.e. stouter or more elongate crowns). Figure 6 also shows the evolution of the cross-sectional shape of pliosaurid crowns over time.

Maximum likelihood estimation of ancestral states suggests that pliosaurids steadily and rapidly increased their crown size (both in terms of diameter and height) during the Middle Jurassic, which is consistent with patterns of their body size evolution (Benson *et al*. 2013*a*). Non-thalassophonean pliosaurids such as *Anguanax*, *Marmornectes* and *Pachycostasaurus* are characterised by small crowns. Crown size (both apicobasal height and diameter) increases continuously during the early evolution of thalassophoneans up to the appearance of *Pliosaurus* in the Late Jurassic. The first appearance of *Pliosaurus* marks three important events in the evolution of pliosaurid teeth: (1) the evolution of the largest crowns (in terms of apicobasal length, up to 130 mm) – with the species *P. rossicus* (Halstead 1971); (2) the first decrease of crown size in pliosaurids, notably with the species *P. kevani* (Benson *et al.* 2013*a*); and (3) the acquisition of trihedral and subtrihedral crowns (e.g. Owen 1869; Benson *et al.* 2013*a*). The early evolution of Brachaucheninae is characterised by a marked decrease of tooth size (similar or smaller than those of the smallest-crowned *Pliosaurus*, *P. kevani*), with taxa like *Makhaira*, *Luskhan* and *Stenorhynchosaurus* (Páramo-Fonesca *et al*. 2016; Fischer *et al.* 2017).

This interval of generally small crown sizes during the Berriasian–Barremian is somewhat altered by the morphotypes we reported in the descriptions above. Although SOIKM KP-28988 and GFMSU h-216 from the Valanginian of Crimea (Zverkov 2015) accentuate this decrease, Morphotype 2 (TsNIGR 1/13307) from the latest Jurassic and Morphotype 3 (NNGASU specimens) from the Berriasian and Valanginian suggest the continued presence of larger-toothed pliosaurids across and after the Jurassic-Cretaceous boundary, with a crown height close to 80 mm and diameter of 40 mm in the Berriasian NNGASU specimens (or even bigger, possibly up to 100 mm in height and *c*. 50 mm in diameter, in the poorly preserved Valanginian NNGASU specimen). Nevertheless, the pliosaurids of the first half of the Early Cretaceous have smaller teeth than their Late Jurassic and ‘middle’ Cretaceous counterparts.

This diminution of crown sizes is not correlated with a reduction of the disparity of pliosaurid crown morphologies: a wide range of crown sizes is still present, with the co-occurrence of the major pliosaurid dental types: conical, trihedral and subtrihedral.

Pliosaurids re-evolved very large crowns by the start of the 'middle' Cretaceous, with the appearance of derived brachauchenines, most notably with *Kronosaurus queenslandicus*, which has crown sizes similar to those of the largest-crowned pliosaurids of the Late Jurassic (crown height up to 100 mm and basal diameter *c*. 50 mm). The last brachauchenines have disparate crown sizes: *Megacephalosaurus eulerti* has thick and quite large crowns while *Brachauchenius lucasi* possesses some of the smallest crowns among Thalassophonea, both in absolute and relative size (~~see Table S1 and~~ Fig. 6B, C; Fischer *et al*. 2017; Zverkov *et al.* 2018, documents). This rise and later fluctuation of crown sizes of 'middle' Cretaceous pliosaurids is associated with a strong reduction of tooth shape disparity: only simple, conical crowns are known from the Aptian onwards.

Multivariate analyses

The cluster dendrogram indicates the presence of two main tooth morphotypes in pliosaurids: one group contains most subtrihedral and trihedral-toothed forms, and the other group is composed mostly of conical-toothed forms. The cross-sectional shape of the tooth thus appears to be associated with a series of other dental features. Our PCoA clearly separates these groups by the first principal coordinate axis (PCo1): all subtrihedral and trihedral-toothed forms are located on the negative side of the axis and clearly separated from conical-toothed forms (Fig. 7A, B). In the cluster dendrogram analysis, the 'conical cluster' is also associated with three small-sized, crowns that are similar in some aspects to the trihedral-toothed taxa: conical crowns of '*Pliosaurus*' *andrewsi*, MWGUW 009761 and trihedral crown GFMSU h-216. A series of finer groups can be distinguished within the 'conical cluster', each comprising Jurassic and

Cretaceous taxa. The morphotypes described in the present paper are distributed across all of these groups (Fig. 7C).

Most importantly, the new morphotypes we report herein considerably expand the dental morphospace occupation of Late Jurassic and Berriasian–Barremian pliosaurids, resulting in wide, partially overlapping morphospaces between these two temporal assemblages (Fig. 7A, B). The Late Jurassic group has expanded its morphospace occupation exclusively by the discovery of Morphotype 2 (TsNIGR 1/13307), which falls within conical-toothed morphospace, whereas other Late Jurassic taxa form a rather compact group of strictly trihedral-toothed forms. Morphotype 1 (SOIKM KP-28988) is an important outlier among Early Cretaceous morphotypes, demonstrating the highest positive value on the axis 1 (Fig. 7A, B), which further emphasises its uniqueness.

Our multivariate analyses reveal the close morphospace occupation of Middle Jurassic and post-Barremian taxa. This suggests that these distantly related taxa convergently evolved similar dental features. Phylogenetic heritage might be more important for the 'trihedral cluster' because the taxa bearing these crowns are also closely related phylogenetically (see also Fischer *et al.* 2015). Our results thus suggest that convergence combined with phylogenetic heritage shaped patterns of dental evolution in pliosaurids.

DISCUSSION

Crown shape, enamel ornamentation, carinae and their taxonomic and ecological implications in pliosaurids

As shown above, pliosaurids are characterised by a wide range of crown morphologies, notably regarding the ornamentation of the enamel (see also Zverkov *et al.* 2018, documents~~Table S1~~). The labial surface of the crown in many pliosaurids, including conical-, subthrihedral- and trihedral-toothed taxa, lacks enamel ridges. Such a condition occurs in *Liopleurodon*, *Simolestes* and *Pachycostasaurus* among conical-toothed pliosaurids of the Jurassic (Tarlo 1960;

Cruickshank *et al*. 1996; Noè, 2001). However, the presence of labial ridges is variable intraspecifically in Callovian pliosaurids (Tarlo 1960; Noè, 2001). In trihedral-toothed pliosaurids of the Late Jurassic and Early Cretaceous, the labial surface is always unridged, even in small posterior 'ratchet' teeth (Taylor & Cruickshank 1993; Sassoon *et al.* 2012). This configuration (i.e. trihedral tooth with flat and smooth labial surface) is considered as a macropredatory specialisation (e.g. Massare 1987). By contrast, taxa possessing small to medium-sized crowns with fine longitudinal ridges and a circular cross-section are commonly regarded as generalists that feed on small cartilaginous and bony fish, soft cephalopods and/or belemnoids (Massare 1987; Ciampaglio *et al.* 2005). However, the largest known pliosaurids, *Kronosaurus queenslandicus* and '*Kronosaurus*' *boyacensis* (see Benson *et al*. 2013*a*), bear conical teeth ornamented by fine longitudinal ridges around the entire circumference. At the same time, they demonstrate other cranial macropredatory adaptations, such as anisodont dentition and symphysial shortening (Hampe 1992; McHenry 2009; Fischer *et al.* 2017).

The evolutionary history of pliosaurid dentition could thus be summarised as follows: macropredatory conical-toothed taxa appeared in the Middle Jurassic and were replaced by carinate, trihedral-toothed taxa that dominate the Late Jurassic. Conical-toothed macropredators then reappeared in the Cretaceous (Fig. 6), while trihedral-tooth forms seemingly vanished after the Hauterivian. These back-and-forth switches in the crown shape of macropredators appears intriguing and are not unique to pliosaurids. Indeed, roughly comparable patterns of dental evolution could be observed in some other groups of marine amniotes. Ichthyosaurians evolved large macropredatory forms with carinate tooth morphology independently three times and form conical-tooth ancestors, during the Middle Triassic, the Late Triassic, and the Early Jurassic (Massare 1987; McGowan 1996; Motani *et al*. 1999; Fröbisch *et al*. 2013). As with the geologically youngest pliosaurids, all the large predatory ichthyosaurs from the Middle Jurassic onwards possess simple conical crowns of large size (Fischer *et al*. 2014, 2016; Fischer 2016). While most derived thalattosuchians, including macropredatory forms, are characterised by carinate teeth (e.g. Andrade *et al*. 2010), representatives of *Machimosaurus* evolved macropredatory traits whilst still possessing approximately conical crowns (Young *et al.* 2014; Fanti *et al.* 2016). Many derived macropredatory cetaceans, including modern forms, have simple conical crowns and uniform dentition as well (e.g. Ridgway & Harrison 1999; Lambert *et al*. 2010), whereas earlier forms possess more disparate and complex dentitions, including the somewhat carinate incisors and canines of some 'archaeocetes' and stem-odontocetes (e.g. Fahlke 2012; Lambert *et al.* 2017). All examples above support the idea that tetrapods bearing sufficiently large conical teeth can colonise macropredatatory niches in marine ecosystems. Carinate teeth, however, do not guarantee occupation of macropredatory niches over very long evolutionary timescales.

The increased complexity of the cutting edge clearly impacts on the efficient puncturing and gripping of a prey (Abler 1992), hence its independent evolution in many lineages of macropredatory vertebrates (e.g. Sander 1999; Young *et al.* 2013; Brink & Reisz 2014; Brink *et al.* 2015; Fischer *et al*. 2015). Undulation of the carinae and ridges in pliosaurids is one of the ways to produce complex cutting edge via additional folding of epithelium during amelogenesis. Wavy and at least weakly serrated ridges are observable already in the earliest thalassophoneans of the Callovian, such as *Liopleurodon* (see Massare 1987). 'Finely crenulated carinae' of the teeth in the Late Jurassic *Pliosaurus carpenteri* (BRSMG Cd6172) were noted by Sassoon *et al*., (2012: 746). However, no detailed figures of them were provided. The first thorough description and illustration of 'complex serrations' in a pliosaurid were provided by Fischer *et al.* (2015) for the Hauterivian *Makhaira rossica.*

The complex enamel ornamentation of SOIKM KP-28988 is unlike that of other aquatic tetrapods, and is therefore difficult to interpret in terms of possible optimal function, notably because so few remains are currently known of this pliosaurid. The crown (SOIKM KP-28988) lacks carinae, but every ridge has well-developed cutting edge. The crown demonstrates a conspicuous apical wear facet on its lingual surface (Fig. 3C, E) and wear is also visible on the apical portions of the meandering ridges. The sinuosity of the ridges makes them suboptimal for piercing flesh, but the complexity and size of ridges would strengthen the resistance of the tooth under apicobasal loading, by giving it a corrugated-like structure.

The evolution of dental disparity of pliosaurids through time

Recent studies illuminated the evolutionary history of pliosaurids during the Early Cretaceous (Fischer *et al.* 2015, 2017; Páramo-Fonseca *et al.* 2016; Gómez-Pérez & Noè 2017). Nevertheless, latest Tithonian and Berriasian pliosaurids remained hitherto unknown. The youngest Jurassic pliosaurids known to date were Tithonian *Pliosaurus rossicus* (middle Volgian, *Dorsoplanites panderi* Biozone), *Pliosaurus funkei* (middle Volgian, *Dorsoplanites maximus* Biozone), *Pliosaurus patagonicus* (middle Tithonian, *Pseudolissoceras zitteli* Biozone) and *Pliosaurus almanzaensis* (upper Tithonian, *Substeueroceras koeneni* Biozone), all characterised by trihedral teeth (Novozhilov 1948; Halstead 1971; Knutsen *et al*. 2012; Gasparini & O'Gorman 2014; O'Gorman *et al.* 2018). Several finds of isolated teeth from the upper middle Volgian (*Virgatites virgatus* and *Epivirgatites nikitini* biozones) of European Russia demonstrate the presence of trihedral tooth morphology in this spatiotemporal setting as well (Zverkov *et al.* 2017). Previously reported Valanginian, Hauterivian and Barremian pliosaurids, including the early brachauchenines *Luskhan itilensis* and *Stenorhynchosaurus munozi*, demonstrate subtrihedral-trihedral tooth crowns as well, suggesting that such a morphology is widespread among the Late Jurassic to Early Cretaceous pliosaurids, including even basal brachauchenines (Zverkov 2015; Fischer *et al*. 2015, 2017).

The conical-toothed specimens described herein show that several pliosaurid taxa with different crown morphotypes were present during the Jurassic-Cretaceous transition (in the late Tithonian, Berriasian and Valanginian) (Fig. 6A). As shown by our morphospace analyses (Figs 7A, B), these specimens considerably expand the dental morphospace occupation of Late Jurassic and Berriasian–Barremian pliosaurids, resulting in sufficient morphospace overlap between these two assemblages (Fig. 7A, B). Unexpectedly, the range of morphologies occupied by Late Jurassic forms is smaller than the range occupied by their Berriasian–Barremian relatives. This implies a similar or slightly increased disparity of pliosaurid tooth shape and size across the Jurassic-Cretaceous transition.

On one hand, the positions of pliosaurid taxa in our hierarchical cluster dendrogram analysis (Fig. 7C) are distinct from their phylogenetic relationships (Benson & Druckenmiller 2014; Fischer *et al*. 2017), especially for Middle Jurassic and post-Barremian forms. This implies that convergences in shape and enamel ornamentation of teeth took place during the evolution of pliosaurids. On the other hand, of all of the variables we considered, the trihedral/conical character appears to polarize the results of our morphological analyses most strongly, suggesting that the cross-sectional shape of pliosaurid teeth is associated with a series of other features, possibly forming a pair of discrete peaks in the adaptive landscape. Because of this, it is possible that distinct pliosaurid lineages evolved similar tooth shapes independently. While the phylogenetic results of Fischer *et al.* (2015, 2017) suggested a relatively simple history for teeth in pliosaurids, the novel specimens we described above complicate this narrative by revealing shapes not seen in the *Gallardosaurus* + *Pliosaurus* + Brachaucheninae clade. Thus, several possible scenarios of thalassophonean dental evolution could be proposed:

1. Trihedral teeth originated several times in pliosaurids as macropredatory specialization, and the underlying rate of transitions from conical to trihedral tooth morphologies is high. Reversal rates back to conical morphologies may also be high.

2. A trihedral-toothed morphology characterises the most recent common ancestor of Late Jurassic and Early Cretaceous pliosaurids, from which conical-toothed pliosaurids originated one or more times (as found by Fischer *et al*. 2015 using maximum-likelihood optimisation of dental morphology to pliosaurid phylogeny).

3. Lineages of conical-toothed and trihedral-toothed pliosaurids co-existed during the Late Jurassic and Early Cretaceous from ancestors that occurred earlier.

The first scenario proposes that crown shape can readily vary from lineage to lineage. This scenario is challenged by the existence of subtrihedral- to trihedral-toothed piscivorous taxa *Luskhan itilensis* and *Stenorhynchosaurus munozi* in the Early Cretaceous. Subtrihedral (or even trihedral) and carinate teeth of *Luskhan itilensis* and *Stenorhynchosaurus munozi* may represent plesiomorphic retention (Fischer *et al.* 2017). Even when occupying novel ecomorphospace (inferred from craniomandibular morphology), these thalassophoneans retained their trihedral ancestral condition.

Subtrihedral- and trihedral-toothed pliosaurids are first recorded with certainty in the Oxfordian (Gasparini 2009; Benson *et al.* 2013*a*) (Fig. 6A). A fragmental crown figured by Hermann [1907] might extend this range to the middle Callovian. Subtrihedral- and trihedral-toothed pliosaurids co-existed with conical-toothed pliosaurids for a while: the youngest hitherto known Jurassic conical-toothed pliosaurids were *Liopleurodon*-like specimens from the lower Oxfordian of Poland (Lomax 2015), upper Oxfordian to lower Kimmeridgian of Russia (Kiprijanow 1883; Zverkov *et al.* 2017) and Kimmeridgian of France (Lennier, 1887) and Mexico (Barrientos-Lara *et al*. 2015). The absence of conical-toothed pliosaurids from the fossil record during the Tithonian and early stages of the Early Cretaceous, and their re-appearance in the late Early Cretaceous among derived brachauchenines (Fischer *et al.* 2015) could previously have been taken as evidence for Scenario 2 above. Our new data demonstrate in fact that large, conical-toothed pliosaurids co-existed with trihedral-toothed pliosaurids during the latest Jurassic–earliest Cretaceous as well (Fig. 6). The late Tithonian specimen TsNIGR 1/13307 from Siberia indirectly supports the presence of *Simolestes*-like pliosaurids in the late Tithonian, sharing a series of features with *Simolestes* (crown is conical and ornamented with numerous fine and straight apicobasal ridges; labial ridges do not reach the base of enamel layer; Tarlo 1960; Noè 2001). Recently, Sachs *et al*. (2017) described a mandible of a large, likely macropredatory, ‘pliosauromorph’ from the Berriasian of Germany, which has a short symphysial rosette similar to that of ‘*Simolestes indicus*’, known from a partial symphysis found in Tithonian to Lower Cretaceous Umia Formation of western India (Lydekker 1877; Bardet *et al.* 1991; Fürsich *et al.* 2013; Rana *et al*. 2015). Considering the insufficient data on both these fragmentary mandibles, and absence of preserved teeth, the identification of these specimens as pliosaurids should be regarded as plausible, but nevertheless tentative. More complete specimens are required to test the hypothesis that these specimens indicate the presence of macropredatory pliosaurids, similar in their symphysial rosette and teeth to *Simolestes* in the Tithonian–Berriasian. If this hypothesis turns out to be correct, the diversity of pliosaurids across the Jurassic–Cretaceous transition would be further increased, providing more evidence in support of Scenario 3.

At present, Scenario 2 seems to be the most plausible explanation of thalassophonean dental evolution. There are no unambiguous examples of conical-toothed pliosaurids repeatedly evolving macropredatory adaptation via trihedral and carinate crown morphology, and trihedral-toothed macropredatory pliosaurids have been reported exclusively from pre-Barremian strata. Furthermore, SOIKM KP-28988 and NNGASU specimens provide evidence for an alternative macropredatory adaptation via enlargement and serration of the ridges. While the feeding ecology of SOIKM KP-28988 will remain speculative until more complete specimens are recovered, its unexpected combination of features couples with unusual dental features seen in recently described Early Cretaceous thalassophoneans of Russia (*Makhaira rossica* and *Luskhan itilensis*; see Fischer *et al*. 2015; 2017) to significantly broaden the dental disparity, and, probably, ecological diversity of pliosaurids across and after the Jurassic-Cretaceous transition.

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DATA ARCHIVING STATEMENT

Data for this study are available in the Morphobank:

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SUPPORTING INFORMATION

Additional Supporting Information can be found in the online version of this article:

~~Table S1. Characteristic of pliosaurid tooth morphology~~

Figure S1. Field photography of TsNIGR 1/13307

Figure S2. SOIKM KP-28988 photographed without coating

Figure S3. TsNIGR 1/13307 photographed without coating

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Figure captions

FIG. 1. Spatiotemporal setting of the studied specimens. A–C, stratigraphic sections for Maryevka (A), Kheta, section 22 (B) and Rudnichnyi (C) localities. D, general geographic position of the localities and detailed maps with the localities indicated by asterisks: Maryevka (E), Kheta, section 22 (F) and Rudnichnyi (G). Abbreviations: Albid. - Albidum Biozone; Pand. – Panderi Biozone; Tzikw. – Tzikwinianus Biozone.

FIG. 2. Pliosaurid tooth anatomical orientation and enamel structures. A, generalized pliosaurid tooth crown demonstrating anatomical orientation and main structures. B–D, type of ridge undulations: wavy (B), meandering (C), and serrated (D) ridges. E, F, band-like structures. G, ridges, ridglets and wrinkles on tooth crown of *Pliosaurus carpenteri*. Figured specimens: B, PIN 5477/3574; C, SOIKM KP-28988; D, F, NNGASU 740/5229; E, PIN 5477/3577; G, BRSMG Cd6172. Scale bars represent 10 mm.

FIG. 3. Thalassophonea indet. Morphotype 1, SOIKM KP-28988. A, B, mesial or distal views. C, apical view. D, labial view. E, lingual view. F, magnified apical region of the crown in labial view. G, magnified region of the same. H, magnified apical region of the crown in lingual view. Scale bars represent 10 mm (A–E) and 1 mm (F–H).

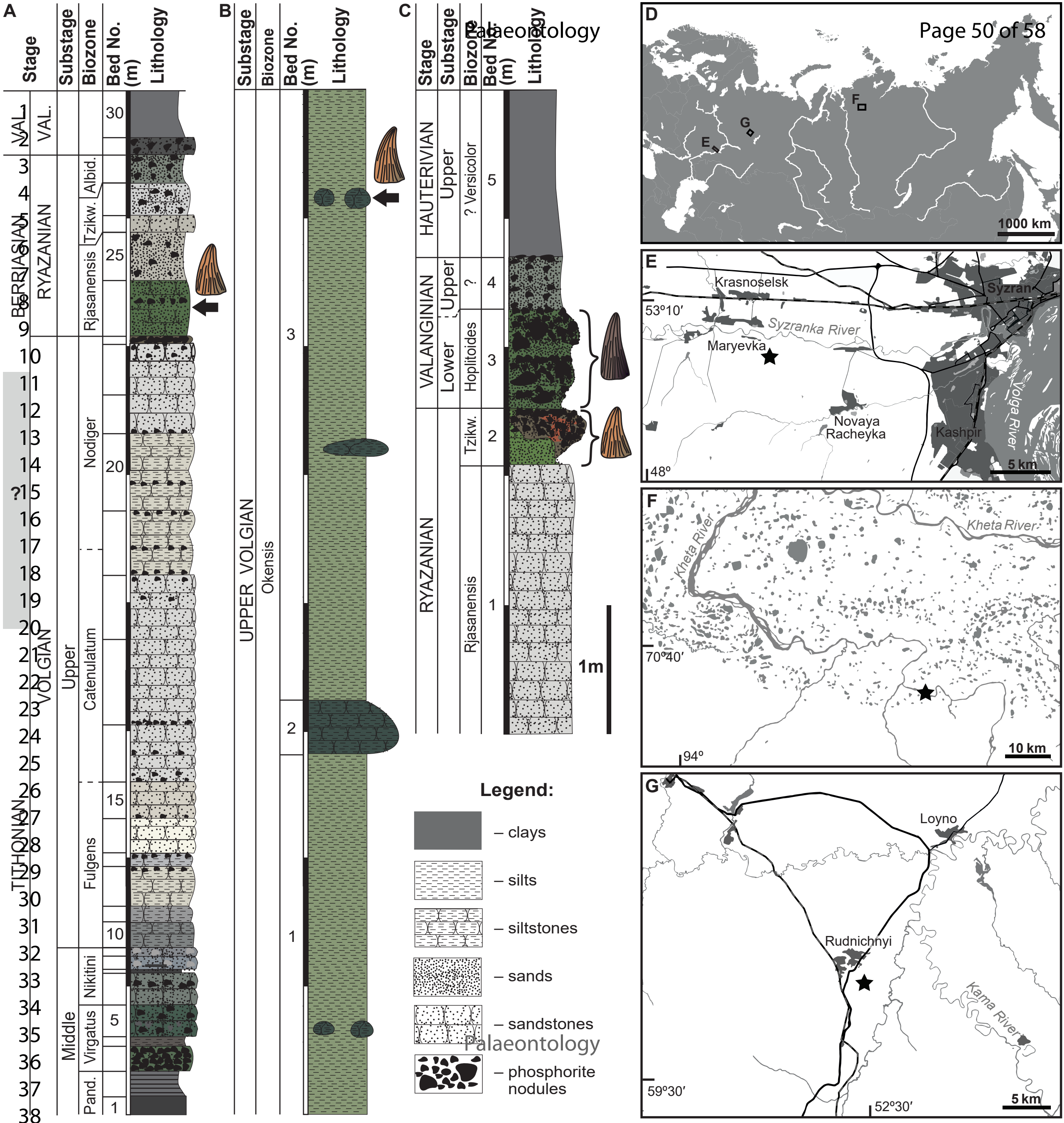
FIG. 4. Thalassophonea indet. Morphotype 2, isolated crown, TsNIGR 1/13307. A, labial view. B, D, mesial or distal views. C, lingual view. E, apical view. Scale bar represents 20 mm.

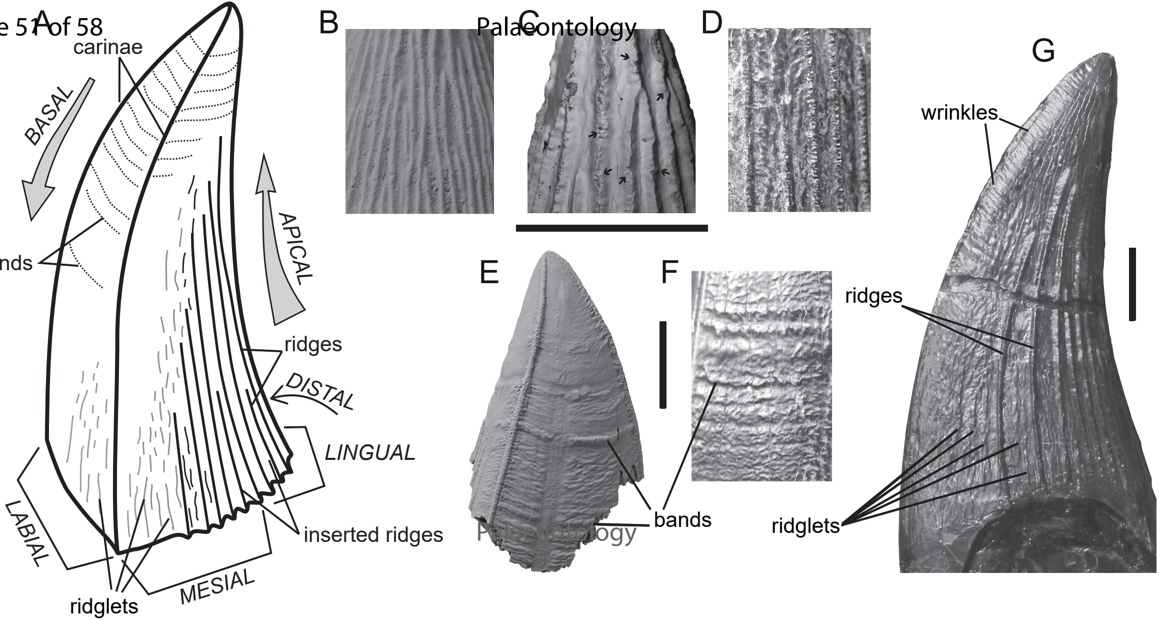
FIG. 5. Thalassophonea indet. Morphotype 3, isolated crowns NNGASU 740/5229 (A–C, J, K), 740/5230 (D–F) and 43/4577 (G, H, I). A, E, labial views. B, D, lingual views. C, F, H, apical views. G, I, mesial or distal views. J, basal section of NNGASU 740/5229. K, serrated ridges of NNGASU 740/5229. The unridged area on the labial surface of the crow is emphasized with dashed line. Scale bars represent 50 mm (A–G), 20 mm (H–I) and 5 mm (J–K).

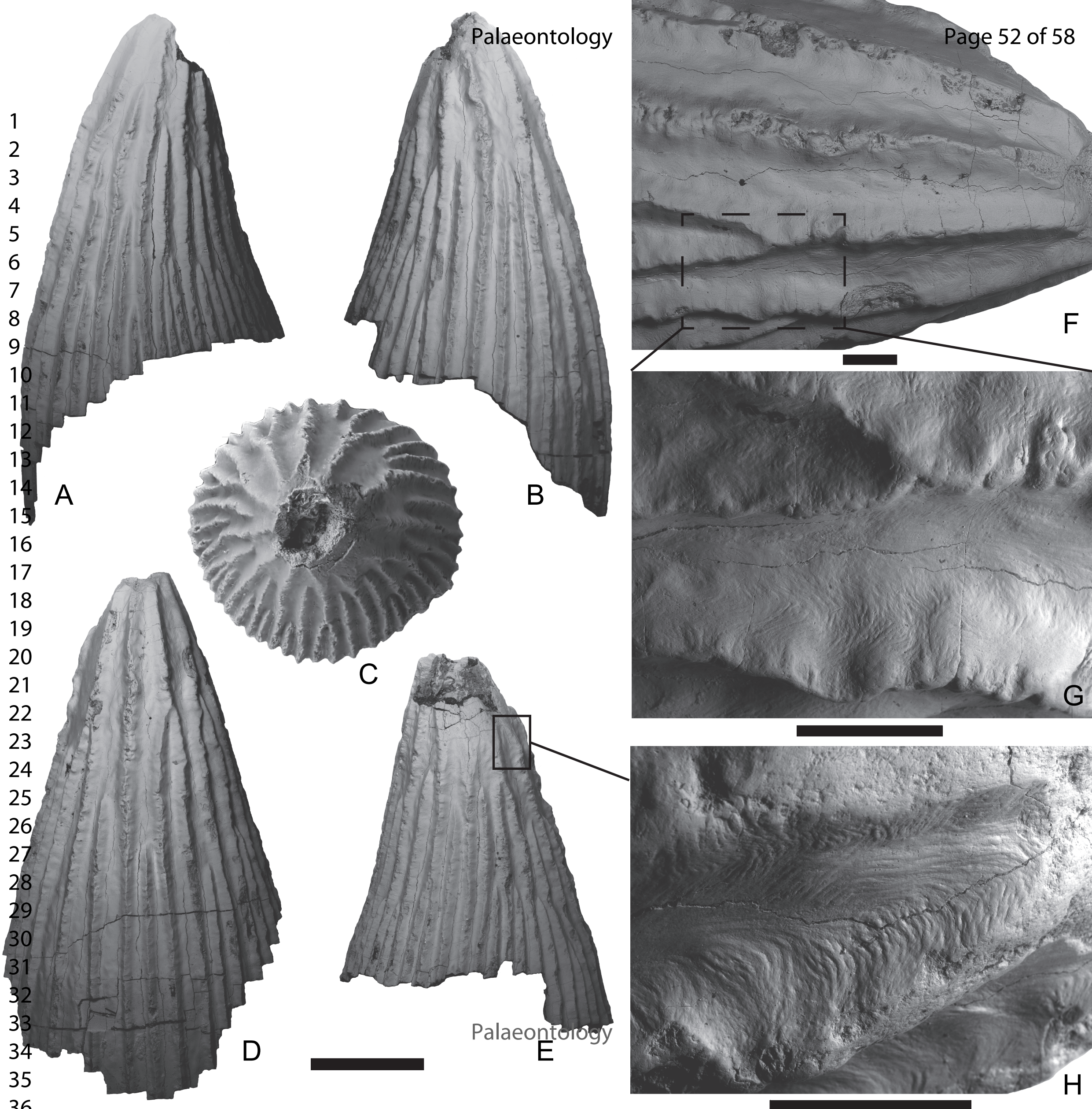
FIG. 6. Temporal distribution of pliosaurid tooth morphotypes. A, general representation of pliosaurid tooth crown size and shape distribution. Dashed line on the Barremian–Aptian boundary indicates declining dental disparity in pliosaurids, solid line on the Turonian–

Coniacian boundary indicates the last occurrence of pliosaurids in the Turonian. Crown outlines that have no centre marked represent the specimens with crowns poorly preserved for precise measurements. C, evolution of pliosaurid crown height (B) and diameter (C) over time, in phylogenetic context and with likelihood from Fischer *et al.* (2017).

FIG. 7. A, B, occupation of the dental morphospace of pliosaurids in the Middle Jurassic and Late Jurassic (A) and in the Early Cretaceous and Late Cretaceous (B), visualised using principal coordinates 1 and 2. C, hierarchical cluster dendrogram analysis of the tooth morphological dataset.


A
Stage
Substage
Biozone
Bed No.
(m)
Lithology
VAL.
BERRIASIAN
RYAZANIAN
TITHONIAN
VOLGIAN
Upper
Middle
Albid.
Tzikw.
Rjasanensis
Nodiger
Catenulatum
Fulgens
Nikitini
Virgatus
Pand.
B
UPPER VOLGIAN
Okensis
C
HAUTERIVIAN
VALANGINIAN
Lower
? Versicolor
?
Hoplitoides
1m
Legend:
– clays
– silts
– siltstones
– sands
– sandstones
– phosphorite nodules
D
1000 km
E
Krasnoselsk
Syzran
53°10′
Syzranka River
Maryevka
Novaya Racheyka
Kashpir
Volga River
48°
5 km
F
Kheta River
70°40′
94°
10 km
G
Loyno
Rudnichnyi
Kama River
59°30′
52°30′
5 km


A
carinae
BASAL
bands
APICAL
ridges
DISTAL
LINGUAL
LABIAL
MESIAL
ridglets
inserted ridges
B
C
D
E
F
bands
G
wrinkles
ridges
ridglets


A
B
C
D
E
F
G
H

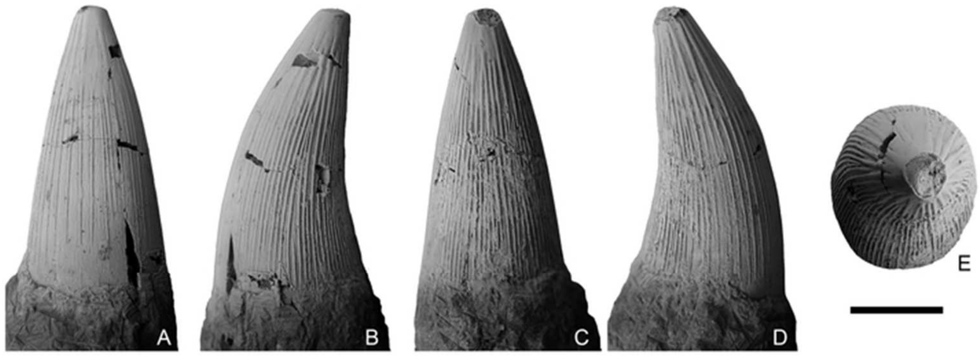
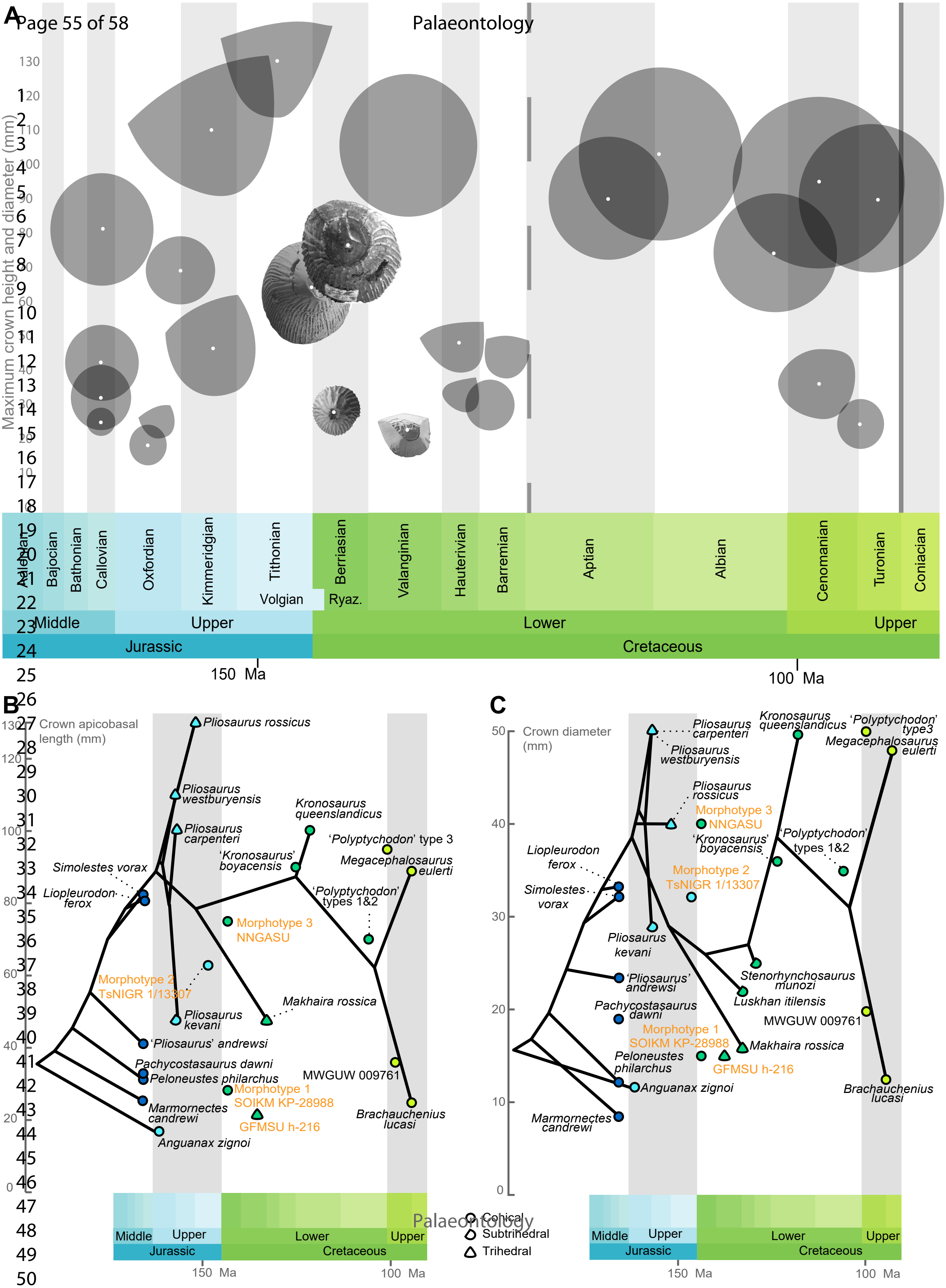


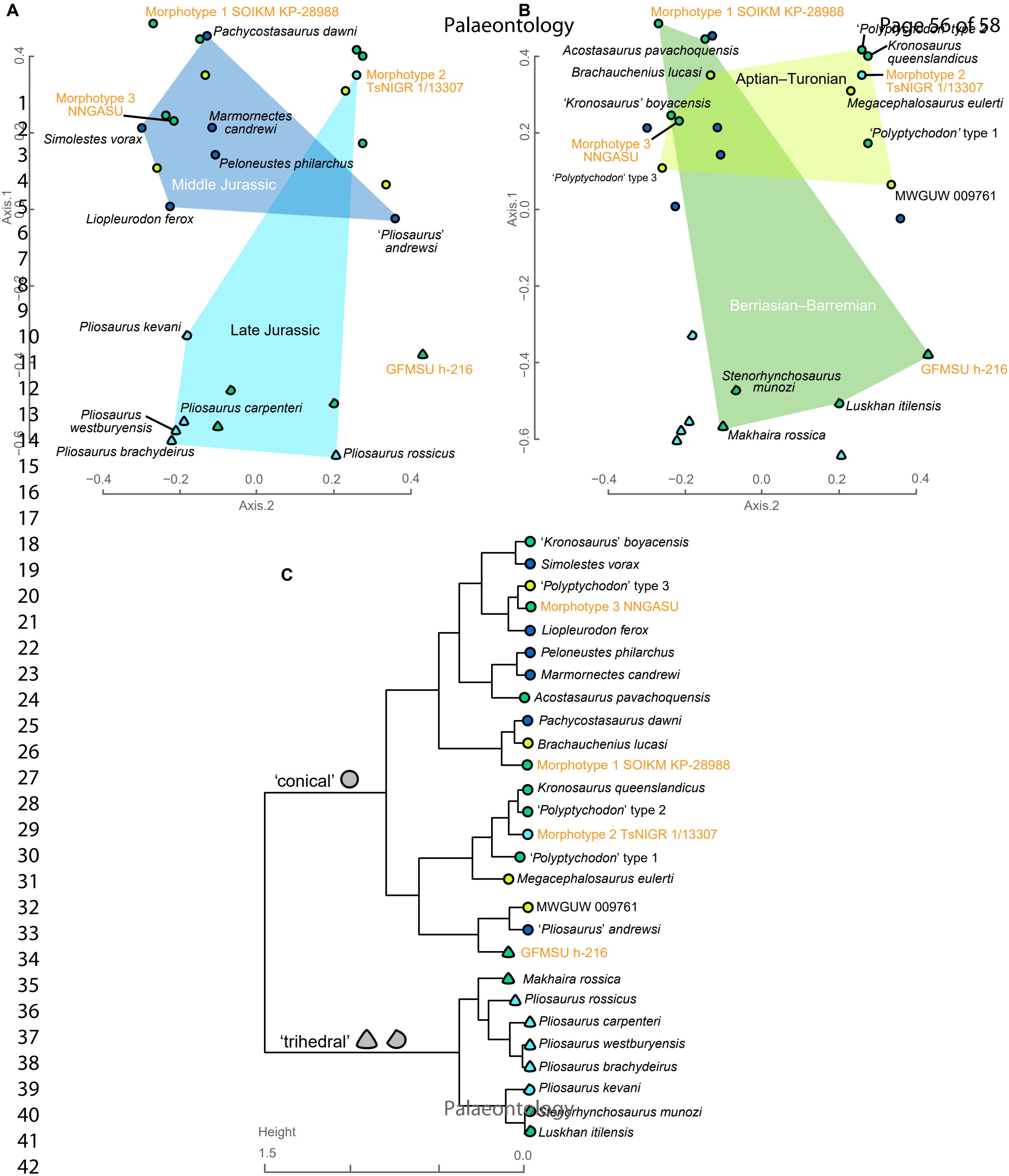
FIG. 4. Thalassophonea indet. Morphotype 2, isolated crown, TsNIGR 1/13307. A, labial view. B, D, mesial or distal views. C, lingual view. E, apical view. Scale bar represents 20 mm.

61x22mm (300 x 300 DPI)

FIG. 5. Thalassophonea indet. Morphotype 3, isolated crowns NNGASU 740/5229 (A–C, J, K), 740/5230 (D–F) and 43/4577 (G, H, I). A, E, labial views. B, D, lingual views. C, F, H, apical views. G, I, mesial or distal views. J, basal section of NNGASU 740/5229. K, serrated ridges of NNGASU 740/5229. The unridged area on the labial surface of the crow is emphasized with dashed line. Scale bars represent 50 mm (A–G), 20 mm (H–I) and 5 mm (J–K).

121x88mm (300 x 300 DPI)


A
Maximum crown height and diameter (mm)
130
120
110
100
90
80
70
60
50
40
30
20
10
0
Aalenian
Bajocian
Bathonian
Callovian
Oxfordian
Kimmeridgian
Tithonian
Volgian
Berriasian
Ryaz.
Valanginian
Hauterivian
Barremian
Aptian
Albian
Cenomanian
Turonian
Coniacian
Middle
Upper
Lower
Upper
Jurassic
Cretaceous
150 Ma
100 Ma
B
Crown apicobasal length (mm)
Pliosaurus rossicus
Pliosaurus westburyensis
Pliosaurus carpenteri
Kronosaurus queenslandicus
'Polyptychodon' type 3
'Kronosaurus' boyacensis
Megacephalosaurus eulerti
Simolestes vorax
Liopleurodon ferox
'Polyptychodon' types 1&2
Morphotype 3 NNGASU
Morphotype 2 TsNIGR 1/13307
Makhaira rossica
Pliosaurus kevani
'Pliosaurus' andrewsi
Pachycostasaurus dawni
Peloneustes philarchus
MWGUW 009761
Morphotype 1 SOIKM KP-28988
Marmornectes candrewi
GFMSU h-216
Brachauchenius lucasi
Anguanax zignoi
C
Crown diameter (mm)
50
40
30
20
10
0
Pliosaurus carpenteri
Pliosaurus westburyensis
Kronosaurus queenslandicus
'Polyptychodon' type3
Megacephalosaurus eulerti
Pliosaurus rossicus
Morphotype 3 NNGASU
'Kronosaurus' boyacensis
'Polyptychodon' types 1&2
Liopleurodon ferox
Simolestes vorax
Morphotype 2 TsNIGR 1/13307
Pliosaurus kevani
'Pliosaurus' andrewsi
Stenorhynchosaurus munozi
Luskhan itilensis
Pachycostasaurus dawni
MWGUW 009761
Morphotype 1 SOIKM KP-28988
Makhaira rossica
Peloneustes philarchus
GFMSU h-216
Anguanax zignoi
Brachauchenius lucasi
Marmornectes candrewi
Conical
Subtrihedral
Trihedral


A
Morphotype 1 SOIKM KP-28988
Pachycostasaurus dawni
Morphotype 2 TsNIGR 1/13307
Morphotype 3 NNGASU
Marmornectes candrewi
Simolestes vorax
Peloneustes philarchus
Middle Jurassic
Liopleurodon ferox
'Pliosaurus' andrewsi
Pliosaurus kevani
Late Jurassic
GFMSU h-216
Pliosaurus carpenteri
Pliosaurus westburyensis
Pliosaurus brachydeirus
Pliosaurus rossicus
Axis.1
Axis.2
B
Acostasaurus pavachoquensis
'Polyptychodon' type 2
Kronosaurus queenslandicus
Brachauchenius lucasi
Aptian–Turonian
Megacephalosaurus eulerti
'Kronosaurus' boyacensis
'Polyptychodon' type 1
'Polyptychodon' type 3
MWGUW 009761
Berriasian–Barremian
Stenorhynchosaurus munozi
Luskhan itilensis
Makhaira rossica
C
'conical'
'trihedral'
Height
1.5
0.0

SUPPLEMENTARY FIGURES

Figure S1. Field photography of TsNIGR 1/13307. Photo by F.A. Trikolidi.

Figure S2. SOIKM KP-28988 in labial, distal and lingual views. Scale bar represents 10 mm.

Figure S3. TsNIGR 1/13307 in labial, mesial or distal and lingual views. Scale bar represents 20 mm.