

ARTICLE

Received 12 Aug 2015 | Accepted 22 Jan 2016 | Published 8 Mar 2016

DOI: 10.1038/ncomms10825

OPEN

Extinction of fish-shaped marine reptiles associated with reduced evolutionary rates and global environmental volatility

Valentin Fischer^{1,2}, Nathalie Bardet³, Roger B.J. Benson¹, Maxim S. Arkhangelsky^{4,5} & Matt Friedman¹

Despite their profound adaptations to the aquatic realm and their apparent success throughout the Triassic and the Jurassic, ichthyosaurs became extinct roughly 30 million years before the end-Cretaceous mass extinction. Current hypotheses for this early demise involve relatively minor biotic events, but are at odds with recent understanding of the ichthyosaur fossil record. Here, we show that ichthyosaurs maintained high but diminishing richness and disparity throughout the Early Cretaceous. The last ichthyosaurs are characterized by reduced rates of origination and phenotypic evolution and their elevated extinction rates correlate with increased environmental volatility. In addition, we find that ichthyosaurs suffered from a profound Early Cenomanian extinction that reduced their ecological diversity, likely contributing to their final extinction at the end of the Cenomanian. Our results support a growing body of evidence revealing that global environmental change resulted in a major, temporally staggered turnover event that profoundly reorganized marine ecosystems during the Cenomanian.

¹ Department of Earth Sciences, University of Oxford, South Parks Road, OX1 3AN Oxford, UK. ² Department of Geology, University of Liège, 14 Allée du 6 Août, 4000 Liège, Belgium. ³ Département Histoire de la Terre, Muséum National d'Histoire Naturelle, Sorbonne Universités, CR2P CNRS-MNHN-UPMC Paris 6, CP 38, 8 rue Buffon, 75005 Paris, France. ⁴ Faculty of Ecology, Saratov State Technical University, Politekhnicheskaya St 77, 410054 Saratov, Russia. ⁵ Faculty of Ecology, Saratov State University, Astrakhanskaya St 83, 410012 Saratov, Russia. Correspondence and requests for materials should be addressed to V.F. (email: v.fischer@ulg.ac.be).

arine predators can be regarded as an epiphenomenon related to the health of open ocean biotas; the waning and waxing of their biodiversity can thus deliver useful insights on the past fluctuations of marine ecosystems¹. Mesozoic marine ecosystems were peculiar in hosting a diverse set of reptile clades occupying their highest trophic levels²; Ichthyosauria is one such emblematic clade. An increasingly well-resolved fossil record places the initial radiation of ichthyosaurs during the Olenekian stage of the Early Triassic³. By contrast, speculation has clouded the severity and timing of their extinction, which was first assumed to occur at the end of the Cretaceous (for example, see refs 4,5). Subsequent analysis placed this extinction at the end of the Cenomanian⁶; ichthyosaurs thus disappeared after a 157-million-year reign, 28 million years before the end-Cretaceous extinction events that marked the demise of other numerous marine taxa of both vertebrates and invertebrates⁷. Previous analyses considered the richness of ichthyosaurs to be low in the Cretaceous and already declining since the Jurassic^{8,9}. In parallel to low taxonomic richness, the ecological variety of Cretaceous ichthyosaurs has also been regarded as narrow^{8,10,11}. As a result, the extinction of ichthyosaurs at the end of the Cenomanian was considered an isolated event associated with minor biotic changes: increased competition with other marine reptiles^{12,13} or teleosts⁹, or a diversity drop in their assumed principal food resource, belemnites⁶.

However, recent data challenge this view of ichthyosaur history, indicating that Early Cretaceous ichthyosaurs were taxonomically^{14–17}, phylogenetically^{18,19} and—possibly ecologically^{13,20} (but see ref. 11) diverse, even a few million years before their extinction²⁰. These data demand re-examination of the factors associated with the waning and waxing of ichthyosaur diversity (including biases), addressing whether their extinction can be explained with existing, ichthyosaur-specific hypotheses, or was instead related to wider environmental changes in marine ecosystems of the early Late Cretaceous. We show that ichthyosaurs were diverse and disparate during the Cretaceous and faced an abrupt two-phase extinction that is associated with reduced evolutionary rates and global environmental volatility.

Results

Parvipelvian phylogenetic relationships. We analysed the evolution of derived ichthyosaurs (Parvipelvia, Late Triassic to early Late Cretaceous) using novel data sets (Supplementary Methods, Supplementary Data 1-4). All analyses yielded topologies congruent with previous results from smaller data sets^{19,21}, most notably the Jurassic origin of Cretaceous ichthyosaur lineages, the rapid divergence of Ophthalmosauridae into two distinct clades (Ophthalmosaurinae and Platypterygiinae) after the divergence of more basal lineages (Arthropterygius chrisorum), and the polyphyletic status of Ophthalmosaurus and Platypterygius (Fig. 1 and Supplementary Figs 1-11). For several decades, all or nearly all ichthyosaur remains from the Cretaceous have been referred to as *Platypterygius*^{20,22}. The status of this taxon has been controversial²³ as no phylogenetic study incorporated the type species of the genus Platypterygius platydactylus. Our equally weighted maximum parsimony analysis finds this species to be phylogenetically isolated from other species currently referred to as Platypterygius (Fig. 1 and Supplementary Figs 1 and 2). Implied weighting analysis places P. platydactylus as the sister taxon of a small clade of Albian-Cenomanian platypterygiines but all other species currently referred to as *Platypterygius* belong to another clade of Cretaceous platypterygiines (Supplementary Fig. 5). It is still premature to make a taxonomic decision on Platypterygius. However, the practise of assigning Cretaceous ichthyosaur remains to Platypterygius by default should be strictly avoided. The diversity dynamics of derived ichthyosaurs should

be analysed at the species level rather than at genus level or above to circumvent these issues (see below).

Nodal support values within Ophthalmosauridae are smaller than those found by other analyses using smaller data sets^{18,19}; this probably results from incorporation of numerous ophthalmosaurid taxa, many of which are based on substantially incomplete remains. However, because both phylogenetic accuracy and macroevolutionary inferences are positively impacted by increased taxon sampling^{24,25}, and because of strong agreement on the parvipelvian tree topology between previous and present maximum parsimony analyses and Bayesian analyses, both in terms of topology and the timing of cladogenesis (see Supplementary Figs 1–12), we are confident in the adequacy of our new detailed data set and results to answer the macroevolutionary questions.

Cretaceous ichthyosaur diversity and disparity. A face-value count of observed species shows a general trend of increasing taxic richness throughout the Early Cretaceous, attaining a peak during the Late Albian (Fig. 2 and Supplementary Tables 1 and 2). Richness in the Late Albian is similar to that of well-sampled Jurassic stages²⁰, but then declines abruptly during the Cenomanian. High diversity is apparent throughout the entire Early Cretaceous, with a marked diversity peak in between the Valanginian and Barremian interval, followed by an apparent extinction. Contrary to observed richness, the phylogenetically adjusted diversity estimates (which include counts of phylogenetic ghost lineages) suggest that ichthyosaur diversity remained high, declining only slightly through the Early Cretaceous (Fig. 2 and Supplementary Tables 3 and 4). This indicates that the apparent post-Barremian diversity loss observed in face-value species counts is an artefact of poor fossil-record sampling.

Disparity metrics calculated from phylogenetic character distributions (weighted mean pairwise dissimilarity and sum of variances including 'ancestors') are congruent and have trajectories broadly matching that for phylogenetic diversity estimates (Fig. 2, Supplementary Tables 5 and 6 and Supplementary Data 4-6). Diversity and disparity metrics record high values during the Valanginian-Barremian interval, reflecting the co-occurrence of diverse platypterygiine lineages, ophthalmosaurines (Acamptonectes densus and Leninia stellans) and the archaic early parvipelvian Malawania anachronus. Although phylogenetic characters contain a strong signal related to phylogenetic distance²⁶, we note that these taxa also show divergent skeletal architecture (Supplementary Figs 13-15), consistent with the observation of high disparity. Surprisingly, the Valanginian-Barremian interval records the highest disparity values for the entire history of Parvipelvia, with much higher values than the average for the entire Jurassic-Early Cretaceous interval (Fig. 2). Early Jurassic parvipelvians are not sampled at the species level, but all genera are represented in the data set (Supplementary Tables 1 and 2; Supplementary Methods); we do not anticipate that the inclusion of additional Early Jurassic species would substantially alter these results.

Disparity is decoupled from taxic/phylogenetic diversity from the Aptian onwards, declining steadily to values well below the Jurassic–Early Cretaceous average (Fig. 2). Nevertheless, it is possible that late Aptian–Albian disparity was higher than estimated here, because no ophthalmosaurine (youngest record at the Albian–Cenomanian boundary¹⁸) from that interval could be coded into the phylogenetic data set; disparity values for those bins thus only rely on platypterygiines. This disparity decrease may therefore have occurred later and more abruptly than suggested by our estimates (Fig. 2). After the earliest



Figure 1 | Phylogeny and ecological diversity of parvipelvian ichthyosaurs. (a) Time scaled strict consensus tree arising from equal weight maximum parsimony analysis. Numbers denote >1 Bremer decay indices. Grey bars denote range extensions by specimens identified at the generic level. Colour coding of taxa refers to the results of **b**. (**b**) Cluster dendrogram based on the ecological data set, with gut-content data and the general features of each guild. (**c**) Teeth representative of each guild across the Late Albian-Cenomanian interval, illustrating the ecological extinction at the beginning of the Cenomanian. *'Platypterygius campylodon'* and *'Platypterygius'* sp. from the US are early Cenomanian in age⁶⁹, *Pervushovisaurus bannovkensis* is Middle Cenomanian in age¹⁶ and *'Platypterygius'* sp. from Germany is Late Cenomanian in age⁷⁰. *denotes taxa from the Stoilensky/Kursk fauna. Scale bar, 50 mm.

Cenomanian, ichthyosaurs were clearly reduced to a very limited range of morphologies with low disparity (Supplementary Figs 13–15).

Evolutionary and extinction rates. Most of the phylogenetic diversity of parvipelvians evolved during the Late Triassic–Middle Jurassic interval (Fig. 3) and not during the Cretaceous, consistent



Figure 2 | Ichthyosaur diversity through the Cretaceous. (a) Taxonomic/lineage richness. The orange thick line is the mean value per bin, while the light orange outline represents the range of values, encompassing all most-parsimonious trees, under both the 'basic' and 'equal' methods of branch length reconstruction (PADE, phylogeny-adjusted diversity estimate). The long-term sea-level is taken from Haq⁶². (b) Weighted mean observed pairwise dissimilarity compared with the Jurassic-Early Cretaceous average value. Light grey outline represents the 95% confidence interval. Bins are: Berriasian-Valanginian, Hauterivian-Barremian, Aptian, Albian, Cenomanian and Turonian. Important events and factors explaining the shape of the curve are indicated. Note the all-time disparity peak for Parvipelvia during the Hauterivian-Barremian. The average value for the Jurassic only is 0.24. (c) Sum of variances from the phylogenetically reconstructed data set, compared with the Jurassic-Early Cretaceous average and light grey outline represent the 95% confidence intervals. Again, an all-time disparity peak for Parvipelvia is recorded during the early Early Cretaceous. The average values for the Jurassic only are 7.53 (basic) and 9.38 (equal). (d) Ecological niches occupied per bin. *denotes data obtained from the Stoilensky/Kursk fauna.

with the results of other recent studies^{19,27}. Peaks of cladogenesis are recorded during the Late Triassic, giving rise to the 'Neoichthyosaurian Radiation'¹⁹ (Figs 1 and 3 and Supplementary Tables 7–9). The 'Ophthalmosaurid Radiation' occurs as a series of peaks spanning the Early–Middle Jurassic. We also recover a platypterygiine radiation during the Berriasian–Hauterivian stages of the Early Cretaceous. This radiation is a modest relative to those of the Triassic and Jurassic; it nevertheless, gave rise to the taxa that dominated the ichthyosaur faunas of the mid-Cretaceous and up to their final extinction in the early Late Cretaceous. Rapid rates of morphological evolution based on phenotypic characters are concentrated along the lineages connecting early ichthyosaurs to Platypterygiinae, but zero branches have rapid rates of phenotypic evolution within either Ophthalmosaurinae or Platypterygiinae (Fig. 3 and Supplementary Table 9), indicating that Cretaceous ichthyosaurs had slow rates of phenotypic evolution. Furthermore, mean rates of phenotypic evolution decelerated earlier than rates of cladogenesis, becoming low from the Early Jurassic onwards (Fig. 3). Therefore, low rates of morphological evolution coincided with low-to-null rates of cladogenesis during the Cretaceous, in a combination not seen in earlier intervals.

ARTICLE



Figure 3 | Evolution and extinction rates for parvipelvian ichthyosaurs. (a) Median rate of morphological evolution (morphological clock) arising from the constrained Bayesian inference. **(b)** Median rate of morphological evolution (morphological clock) arising from the unconstrained Bayesian inference. Both analyses indicate high rates in the early evolution of Parvipelvia, confined in the Triassic (c). **(d)** Cladogenesis rate using the time scaled trees arising from the constrained Bayesian inference. **(e)** Cladogenesis rate using the time scaled trees arising from the maximum parsimony analysis and extinction rate. The light grey outline represents the range of values, encompassing all most-parsimonious trees. **(f)** Number of marine reptile-bearing and ichthyosaur-bearing formations throughout the Cretaceous. **(g)** Proportion of marine reptile-bearing formations containing ichthyosaurs throughout the Cretaceous, with calculation of a 95% confidence interval. **(f,g)** Indicate ichthyosaurs disappeared in a two-phase extinction during the Cenomanian, and that this extinction is not biased by the fossil record: ichthyosaurs rarefy and disappear during a time of excellent recovery potential.

Absolute extinction rates are elevated during the Cretaceous but the estimated per-lineage extinction rates of the Early Cretaceous are generally lower than those of the Triassic and the Jurassic. Per-lineage extinction rates are elevated at the beginning and throughout the Cenomanian (Fig. 4 and Supplementary Tables 10 and 11).

Ecological diversity of ophthalmosaurids. Cluster analysis of ecological data (Supplementary Table 12, Supplementary

Methods and Supplementary Data 7) recovers three main ecomorphological groups, further divided into a range of subgroups, and supported by significant approximated unbiased P values (Fig. 2). The first group is characterized by minute recurved teeth with a smooth and slender crown and no detectable wear. Two of them are ophthalmosaurines, with a large sclerotic aperture, and preserved gut content in one of them (*Ophthalmosaurus natans*) consists of only soft, unshelled coleoid remains²⁸. We propose that these ichthyosaurs had a restricted diet of small, soft-prey

ARTICLE



Figure 4 | A two-phase extinction for ichthyosaurs. (a) Biostratigraphic ranges of the last ichthyosaur taxa. Questions marks indicate uncertainty of the stratigraphic range of the material from Stoilensky quarry (western Russia). Thin lines indicate uncertain but probable occurrence of taxa, based on the presence of compatible remains. See Supplementary Note 1 for the details and discussion on the specimens considered in the bracketed numbers. (b) Evolution of worldwide ichthyosaur diversity (at the species level in black and at the lineage level in orange) for each bin considered (Late Albian, earliest Cenomanian, Early Cenomanian, Mid-Cenomanian, Late Cenomanian, Turonian. The lighter colour indicates how the curve would look in *Platypterygius campylodon* is not regarded as a valid entity. (c) Evolution of the number of feedings guilds colonized, based on the results from the cluster analysis of ecological data. Note the sharp reduction after the earliest Cenomanian. (d) Extinction rate at the boundaries of each bin. Per-lineage extinction rates $\geq 40\%$ are recorded in the two phases of ichthyosaur extinction.

items and were unlikely to process large prey items into smaller pieces; we term this group soft-prey specialists (which probably also incorporate the 'specialized ram feeders' of ref. 11). The second group is the most speciose, contains only platypterygiine ichthyosaurs, and is characterized by large and robust teeth. heavy apical wear and quite often a robust (dorsoventrally deep, which better resists torsional stresses²⁹) rostrum and possibly a relatively shorter symphysis. One member, 'Platypterygius australis'13, has been found with remains of birds, turtles and fishes in its gut. We propose this group fed on a wide range of prey, including other vertebrates; we term this group apex predators. All species currently referred to as Platypterygius except 'Platypterygius sachicarum' unite in this cluster. This grouping could indicate that these species superficially resemble each other because of ecology rather than shared ancestry. The third group contains medium-sized ichthyosaurs with a slender rostrum, bearing small teeth with a robust crown and slight wear; we propose this group preved on a wide range of small animals. Because they share features with the two other groups, we term this group generalists. Subgroups of the cluster are supported by significant P values as well, but do not appear to be supported by radically distinct features. If anything, these groupings probably reflect subtle differences that could allow niche partitioning between coeval taxa. The stratigraphic distributions and counts of feeding guilds through time should be a reliable measure of ecological disparity regardless of the accuracy of our interpretations of their specific diets.

The stratigraphic distributions of our feeding guilds suffer from the same biases as observed diversity and both are broadly correlated. For example, the absence of multiple co-occurring guilds in the Berriasian-Hauterivian and Aptian-Lower Albian intervals likely reflects the poor fossil records of these intervals. Mitigating bias is difficult here, as reconstruction of ancestral ecological niches defies the principle of ecological convergence, which was widespread in marine tetrapods^{10,30}. It is, however, possible to infer the presence of a guild by using the features that appear relevant to identify the different clusters. This approach leads us to propose that the Albian-Cenomanian boundary fauna we investigated in Stoilensky quarry, western Russia (Supplementary Figs 16-19; Supplementary Table 13 and Supplementary Methods) contains taxa occupying three distinct ecological niches. The ecological diversity of Cretaceous ichthyosaurs was high, as is especially apparently at times of better sampling. This ecological diversity declined abruptly during the early Cenomanian, despite the continued sampling of ichthyosaur specimens from all major geographic regions sampled in the late Albian and the increased preservation potential (Figs 3 and 4 and Supplementary Table 14).

Effect of sampling and environmental changes. We used generalized least squares regression with a first-order autoregressive model and pairwise correlations to test the relationship between various biodiversity dynamics metrics, and environmental and sampling proxies (Supplementary Tables 15 and 16). All tests found poor correlations between sampling metrics and diversity variables (Supplementary Tables 17-19 and Supplementary Data 8 and 9). Akaike weights systematically place most sampling metrics among the variables with the lowest explanatory power for most diversity variables. This result suggests that the use of phylogeny-informed diversity metrics yield a signal that at least partially redresses sampling biases (but see ref. 31, as phylogenetic diversity estimates can fill ranges backwards but not forwards and are therefore prone to edge effects). The general absence of correlation between rates (cladogenesis, evolutionary and turnover), except extinction and

sampling metrics is also interesting, especially in the light of recent analyses finding strong correlations between standing diversity and sampling metrics (for example, see ref. 32); this suggests that future analyses should focus on the dynamics of diversity rather than on raw values.

Broadly, bin-averaged environmental data, which represent interval-specific mean environmental conditions, do not appear to explain the diversity metrics for Cretaceous ichthyosaurs and no robust signal common to all four analyses could be recovered (Supplementary Tables 17–19). On the contrary, climate volatility variables ($\partial^{18}0$ and $\partial^{13}C$ variances) are the best or among the best models for predicting the extinction rates and the per-lineage extinction rates in both data sets. A strong correlation is also found in the pairwise tests between the per-lineage extinction rates and the variances of both the $\partial^{18}O$ and the short-term eustasy in the full data set. It is crucial to stress the importance of the extinction of ichthyosaurs in polarizing these correlations. Indeed, analyses of the full data set yielded a much larger number of significant/non-negligible correlations, especially with climate instability variables.

Confidence in the timing and tempo of extinction. Counts of marine reptile fossil bearing formations across the Middle Cretaceous (Albian-Turonian) are among the highest of the Cretaceous, so the Cenomanian last occurrences of ichthyosaurs and their main Cretaceous ecomorphs occur during a wellsampled interval (Fig. 3). During this span, the proportion of marine reptile-bearing formations yielding ichthyosaurs decreased from 84% in the Albian to 19% in the Cenomanian and to 0% in the Turonian. Given the presence of n = 26 marine reptile-bearing formations in the Turonian, the probability of observing zero Turonian ichthyosaur fossils given an occurrence frequency of 0.19 per formation is $(1-0.19)^{N}$, or 0.004. Furthermore, given the observation of zero ichthyosaurs in 26 Turonian marine reptile-bearing formations, the occurrence frequency of Turonian ichthyosaurs would have to be 0.109 (that is, <10.9%) or less to give a probability of at least 0.05 of finding zero Turonian ichthyosaur fossils. To obtain a high probability (0.5) of observing no ichthyosaurs in this many sampling opportunities, the occurrence frequency would need to be no more than 0.026 (that is, <2.6%). Thus, if not actually extinct, to remain undiscovered, Turonian ichthyosaurs would need to be rare to the degree that they were ecologically insignificant. On the basis of these observations, it is likely that our estimate of the timing of ichthyosaur extinction is adequate at the timescale of our study.

Discussion

Two deterministic hypotheses have previously been formulated to explain the latest Cenomanian extinction of ichthyosaurs: (i) a competition hypothesis, in which ichthyosaurs were outcompeted and driven to extinction by other marine reptiles^{12,13} or fishes⁹ and (ii) a resource hypothesis, in which ichthyosaurs vanished because of an extinction event in what was thought to constitute their main diet, soft cephalopods⁶. These scenarios invoke a single, relatively minor biotic cause for the extinction of ichthyosaurs. One major issue of the competition hypotheses are their geographical and temporal discrepancies. The earliest large-bodied mosasauroids, which are the only marine squamates that could have reasonably competed with ichthyosaurs in terms of prey type, prey size and prey location, are Middle Turonian in age^{12,33}, thus appearing about 3 million years after the last appearance of ichthyosaurs (and likely radiating to fill at least some of their niches). Ichthyosaurs and polycotylid plesiosaurs cohabited in Australian basins and the WIS since the Early Albian

ARTICLE

at least^{34,35}, and therefore for 19 million years before the final extinction of ichthyosaurs. In the Canadian Western Interior Seaway^{14,17} and in Stoilensky quarry, abundant polycotylids co-occur with a diverse assemblage of ichthyosaurs. Lingham-Soliar⁹ argued that ichthyosaurs steadily declined in diversity from the Middle Jurassic onwards, based on knowledge of the ichthyosaur fossil record that was highly incomplete compared with our present understanding. In fact, many authors have previously suggested that Cretaceous ichthyosaurs were depauperate in taxonomic and/or ecological diversity^{11,32,36}. Lingham-Soliar⁹ linked this decline with the radiation of teleosts and chondrichthyans, which would have slowly outcompeted ichthyosaurs in their niche of fast thunniform swimmers. However, our data demonstrate that Cretaceous ichthyosaurs were actually about as diverse (taxonomically and ecologically) as they were during the Middle-Late Jurassic, and apparently were at their most disparate phase since the Triassic. The scenario of slow but steady replacement⁹ is therefore not substantiated by the data.

The resource hypothesis alone cannot explain the trajectories of ichthyosaur diversity and disparity through time, nor the profound, but non-terminal, extinction suffered by ichthyosaurs at the beginning of the Cenomanian. However, it remains compatible with our results, because the ecological diversity of ichthyosaurs was strongly reduced after the earliest Cenomanian. Nevertheless, the last ichthyosaurs closely resemble taxa belonging to the apex predator guild, which probably relied on diverse food resources¹³, rather than focussing almost exclusively on belemnites as previously thought¹⁰. In sum, both the long-term competition with selected marine predator clades and the diversity drop in belemnites cannot satisfactorily explain the breadth and tempo of the extinction of ichthyosaurs, even if these factors may have had a local importance.

Our data depict a congruent picture of Cretaceous ichthyosaurs as being highly diverse but slowly evolving. Their slow rates of origination and phenotypic evolution combined with climatic volatility-forced extinction rates to erode their high Early Cretaceous diversity, as indicated by both observed and phylogeny-adjusted taxon counts (Figs 2 and 4), and despite continued sampling of the continental regions yielding Early Cretaceous ichthyosaur fossils (Fig. 3). An apparent reduction of ichthyosaur disparity during the Aptian might be the result of poor fossil-record sampling, and could be an artefact of the absence of ophthalmosaurine specimens complete enough to be included in our data set (Fig. 2, see the 'Results' section). By contrast, inclusion of Cenomanian taxa is more representative because all the major clades that were present can be coded in the phylogeny. A major extinction event took place during the earliest Cenomanian, when a substantial part of ichthyosaur diversity vanished, eliminating Ophthalmosaurinae and most of the ecological diversity that was present in the late Early Cretaceous. Following this event, ichthyosaurs had low diversity (Figs 2 and 4), low abundance (Fig. 3) and an extremely restricted morphospace occupation (Supplementary Fig. 15), representing only a single ecological guild (apex predators), despite the presence of several ichthyosaur specimens and, more generally, good sampling indicators (Figs 1 and 3). This previously unrecognized event presumably contributed to their extinction risk and ultimate extinction during the latest Cenomanian. Adding the Cenomanian-Turonian bins has a strong effect on the results of the correlation tests. This effect suggests that Cenomanian diversity losses cannot be explained under the same paradigm as more typical 'background' diversity fluctuations. Interestingly, climate volatility, characterized by ∂^{18} O variance, is regarded as the best explanation for the per-lineage extinction rate of Cretaceous ichthyosaurs when the full data set is

considered (Supplementary Tables 17–19). This finding highlights the potential of using the variances of environmental parameters, instead of bin-averaged mean values, in understanding diversity dynamics.

The extinction of ichthyosaurs did not happen in an ecological vacuum. It has long been recognized that the Cenomanian and the Cenomanian-Turonian boundary represents a peculiar period representing the apex of numerous climatic and oceanic perturbations, with no polar ice, extremely high sea levels, unique sedimentation, strong anoxia and very high temperature and pCO₂ (for example, see refs 37-40). There is evidence for profound global environmental volatility within the Cenomanian, the most notable being the 'mid-Cenomanian events', involving sea level fall and perturbations of geochemical cycles (for example, see refs 41,42). As a parallel to these profound environmental events, myriad biotic turnover events occurred at the beginning, within and at the end of the Cenomanian. Most trophic levels in marine ecosystems underwent profound changes before the Cenomanian-Turonian boundary extinction; step-like declines spread over the Cenomanian are not unique to ichthyosaurs and are actually recorded in microplankton^{43,44}, ammonites⁴⁵⁻⁴⁷, belemnites⁴⁸ and reef builders^{49,50}. Simultaneously, a number of marine clades underwent explosive radiations and rose to ecological dominance during the Cenomanian, including hippuritoid bivalves^{49,50}, euteleost fishes^{51,52}, elasmobranch chondrichthyans⁵³ and marine squamates, including early mosasauroids³³. As such, the abrupt yet staggered extinction of ichthyosaurs thus appears as just a facet of a much broader series of biotic events that are clustered in the Cenomanian stage and ending with Cenomanian-Turonian boundary extinction. Evidence from ichthyosaurs supports a growing body of evidence 33,47,52 revealing that a major, global change-driven turnover profoundly reorganized marine ecosystems during the Cenomanian to give rise to the highly peculiar and geologically brief Late Cretaceous marine world.

Methods

Material examined. Analyses are based upon a survey of literature and museum collections, including a reassessment of Cenomanian material from UK (Grey Chalk Subgroup) and description of novel remains from the Albian–Cenomanian of Russia (see Supplementary Methods and Supplementary Figs 16–18). An updated systematic framework for Cretaceous ichthyosaurs and a review of Cenomanian ichthyosaur occurrences are proposed (see Supplementary Methods). We use this updated taxonomic scheme to investigate the phylogeny and diversity of ichthyosaurs through the Late Triassic–early Late Cretaceous.

Because of the wide scope of our analysis, a large number of data, results and references of primary importance for specialists is placed in the Supplementary Methods because of space constrains. We consider these data crucial for building our conclusions and we will take all possible ways to ensure the widest possible dissemination of these data.

Phylogenetic data and analyses. We assembled a novel phylogenetic data set for parvipelvian ichthyosaurs (see Supplementary Methods); it contains 88 characters and 36 taxa and samples Ophthalmosauridae extensively at the species level (69–76% of all valid species, depending on taxonomic opinion on Late Jurassic material from Russia; 75% of all valid Cretaceous ichthyosaur taxa are incorporated in the phylogenetic data set). Character state illustrations are given in the Supplementary Methods. We first analysed this data set using maximum parsimony, using equal and implied weighting. We also submitted this data set to Bayesian inference. Characters 33, 34 and 78 were treated as ordered, as in previous analyses. The OTU list, character list and detailed analytical settings can be found in Supplementary Methods.

Taxic and phylogenetic diversity. Mesozoic stages greatly differ in duration, which can potentially bias our analyses, especially across the Early–Late Cretaceous boundary. We divided the largest stages (Aptian and Albian) into their widely accepted substages (lower and upper Aptian; lower, middle and upper Albian), based on ammonite biostratigraphy (see Supplementary Methods). By doing so, Cretaceous bins have a mean duration 5.02 My and a standard deviation of 1.56 My (not encompassing the error margin for stage boundaries). The observed diversity is a count of the parvipelvian-specific richness for each bin, from the

Norian to the Turonian, following the results of our taxonomic revision (we have updated the Paleobiology Database record accordingly, up to the specimen level for many Cretaceous stages). This diversity count should be appraised cautiously, as it embodies a mixed signal combining underlying diversity patterns with geological preservation biases and anthropogenic sampling biases. Unfortunately, the scarcity of ichthyosaur occurrences for many stages prohibits the use of subsampling methods such as rarefaction to analyse ichthyosaur diversity. Phylogenetic analyses imply the presence of unsampled ghost lineages, and are therefore useful in predicting the diversity of a group during poorly sampled intervals⁵¹, providing a partial correction of diversity patterns that can be interpreted cautiously as it retains some elements of bias, and introduces edge effects³¹. These methods are still rarely used, even though ichthyosaurs and many Mesozoic vertebrate clades in general have mature and robust taxonomic and phylogenetic frameworks that permit confident phylogeny-informed inference of their diversity³². Because methods of branch length reconstruction can drastically impact the shape of a diversity curve, we used three methods to assess the length of branches: (i) simple timescaling of each most-parsimonious tree, which implies the minimum number of ghost lineages and, thus, the minimum phylogenetic diversity ('basic' method of Norell⁵⁴); (ii) equal sharing of the branch lengths between stem and ghost ranges ('equal' method of Brusatte et al.55); (iii) morphological clock using Bayesian methods. We applied the basic and equal methods to all mostparsimonious trees and extracted the median phylogenetic diversity estimate as well as 95% confidence intervals using R (paleotree, ape and strap packages; see Supplementary Methods). Then, we added the stratigraphic ranges of each taxon in the phylogeny, as well as those of the valid taxa not included in the phylogeny to obtain a phylogenetic diversity estimate at the species level for Parvipelvia across its entire history (Late Triassic-early Late Cretaceous).

We also estimated branch lengths using Bayesian inference in MrBayes v3.2.4 (ref. 56). In addition to the analysis described above, we estimates branch lengths using a semi-fixed tree topology (hereafter named 'constrained'), fixing all resolved nodes of the consensus tree of the maximum parsimony analysis, thus letting the program infer both branch durations and the ambiguous parts of the maximum parsimony analysis. The parameters for the latter analysis were similar to the Bayesian inference described above (see Supplementary Methods for analytical details). Morphological clock results suggest low rates of morphological evolution and thus long branches for parvipelvian ichthyosaurs. This implies, for example, the presence of multiple ophthalmosaurid lineages by the latest Triassic. While not impossible, this is currently at odds with the fossil record and the biostratigraphy of the successive outgroups of ophthalmosaurids. Bayesian estimates could thus be considered as at the 'old' end of the spectrum of possible branch lengths. At any rate, all results are congruent in implying reduced evolutionary rates for ichthyosaurs during the Cretaceous, especially after the Hauterivian. The results of all branch length reconstruction methods can be found in the Supplementary Methods and Supplementary Fig. 1 and 2 and 7-11.

We assessed the disparity of parvipelvian ichthyosaur through time using two methods: a weighted mean and median pairwise dissimilarity using our raw phylogenetic data set and stratigraphic ranges of taxa⁵⁷ and a sum of the variances of PCO scores from a phylogeny-informed data set, incorporating the OTUs and all hypothetical ancestors⁵⁸. For the former method (dissimilarity), missing/scarcity of the data prevent computation of the dissimilarity and/or confidence intervals for some stages and substages. Thus, as in ref. 57, we used coarser bins here than in our other analyses, grouping stages in pairs, except the Aalenian-Bajocian-Bathonian, which are grouped together, and the Norian, Aptian and Albian, which are each considered in isolation of their long durations. We implemented a mean that is weighted relative to the number of comparable characters⁵⁹. For the latter method (sum of variances), we followed recent attempts at mitigating the impact of missing values (for example, see ref. 58) by reconstructing this data phylogenetically and using only unambiguous ancestral character reconstructions, in Mesquite v3.01 (ref. 60). We used the most-parsimonious tree with the best stratigraphic fit (best GER and RCI indexes, see above and Supplementary Methods, Supplementary Fig. 3), thus minimizing the number of implied unsampled lineages. These methods reduced the amount of missing data from 45.3 to 5.1%. We ran principal coordinate analyses on that reconstructed data set. The sum of variances was calculated for each stage or substage and under both the 'basic' and 'equal' methods of branch length reconstruction. We used the first 45 axes, accounting for 95% of the variance. We then bootstrapped the data 10,000 times to get 95% confidence intervals. All calculations were performed in R.

Ecological diversity. We built a second, independent data set using selected ophthalmosaurid taxa and a set of seven continuous characters based on nine measurements that were selected for their ecological relevance: absolute tooth size, crown shape, crown size relative to gullet diameter, relative symphysial length, snout depth, absolute sclerotic aperture (determining the size of the cornea) and tooth wear. Most studies of the palaeoecology of marine reptiles have only looked at tooth wear only qualitatively^{10,61}. Whereas intrinsic properties of teeth (size, shape) give an idea of the optimal type/range of prey types that could be processed, wear gives indications on the actual use of teeth, although only by a single individual. We used articulated rostra to quantify the amount wear (see Supplementary Methods for the metrics used and their rationale). We submitted this data set to a cluster analysis in R using the Ward method.

Data were scaled to have equal variances and transformed to a Euclidean distance matrix before clustering; see Supplementary Methods and Supplementary Data 7 for data and analytical details. We then mapped fossilized gut-content data^{13,28} on the cluster dendrogram to test the congruence of our results.

Rates. To avoid the spurious correlation of time series and capture the diversity dynamics of ichthyosaurs, we estimated rates of cladogenesis, extinction and discrete-character evolution for parvipelvian ichthyosaurs through time using our data sets. Both the cladogenesis and the evolutionary (morphological clock) rates ultimately rely on morphology (via phylogenetic relationships) and first-occurrence datums. They are thus affected by incomplete information, taxonomic sampling, uncertainties in phylogenetic relationships and fossil dating, and the fluctuations of the quality of the fossil record. Extinction rates only rely on the last-occurrence datum and are thus biased by fluctuations of the quality of the fossil record. Some of these biases can only be addressed qualitatively, by cautious interpretation of resulting patterns. Nevertheless, others can be addressed quantitatively by the following measures. Uncertainties of the dating and of relationships are encompassed using all the most-parsimonious trees, and 3,000 sampled trees from the posterior distributions of our Bayesian analyses. Detailed comparisons between these rates and proxies for fossil-record biases (see below) have also been conducted; we found no significant relationships between these rates and our sampling proxies. Rates of cladogenesis were computed for both the maximum parsimony and the Bayesian inference analyses, by counting the number of cladogenesis events implied by the phylogeny in each time bin. For the maximum parsimony data set, all most-parsimonious trees and under both the 'basic' and equal' methods of branch length reconstruction were used. For the Bayesian data sets, we sampled 1,000 trees per run, resulting in 3,000 sampled trees per data set. Extinction rates were calculated as the number of taxa (with their Lazarus ranges, if any) going extinct before or at the upper boundary of each stage or substage. Per-lineage ('relative') extinction rates are the percentage of lineages going extinct during a bin. Turnover rates are the sum of the cladogenesis and extinction rates.

Biases and sampling metrics. A large body of literature demonstrates strong links and potentially causal relationships between the rock and fossil records, notably of marine reptiles³². We compare several variables of ichthyosaur diversity (observed diversity, phylogenetic diversity estimates, cladogenesis rates, evolutionary rates, extinction rates and turnover rates) with a number of a rock record proxies, for each bin: mean sea level⁶² and the number of occurrences, collections and formations of all metazoan fossils in a marine setting, all vertebrates in a marine setting, and all aquatic tetrapods in all depositional settings, downloaded from the Paleobiology Database (paleobiodb.org) before updating the Cretaceous ichthyosaur record at the specimen level in that database, in order to avoid a bias in our correlations. As these data are often not resolved at the substage level, we assigned a fraction of the Aptian and Albian data sets to each of their substages, based on their relative durations, as in ref. 58. We refrained from analysing rock area/volume because of issues of redundancy and common cause which could be difficult to identify using a data set on ichthyosaurs alone. Instead, we have also analysed the extinction of ichthyosaurs statistically, by (i) comparing a potential recovery metric (the number of marine reptile-bearing formations) with the number of ichthyosaur-bearing formations and (ii) computing confidence intervals for the extinction of ichthyosaurs as a whole. For this test, we used the simple method of Strauss and Sadler⁶³, which implies constant recovery potential. The mean ichthyosaur recovery potential along their entire history is 0.76 formations per My (120 ichthyosaur-bearing formations over 157.3 My, as downloaded from the Paleobiology Database on 13 October 2015). This translates into a mean 5.34 and 3.13 formations for the Cenomanian and the Turonian, respectively, while these stages record a much higher value of 36 and 26 marine reptile-bearing formations. Integrating this higher recovery potential in the confidence interval calculation would result in smaller range extension; the Strauss and Sadler⁶³ test is thus more generous towards a younger extinction for ichthyosaurs. This test gives a 95% confidence range extension of 0.99 My and of 1.52 My with a confidence of 97.5%, thus firmly placing the extinction of Ichthyosauria as a whole in the earliest Turonian at the latest.

Environmental drivers. We investigated potential drivers of ichthyosaur diversity during the Cretaceous by running correlation tests between our diversity variables and environmental proxies. We used the mean and variance (both at short and long term, using data from Haq⁶²), two measures of sea-surface temperatures and/or ∂^{18} O (refs 64,65) per bin.

Correlation tests. We performed pairwise correlation tests after applying generalized differencing⁶⁶ to the relevant data series. We also fitted generalized least square linear models including a first-order serial correlation coefficient⁶⁷ and estimated their explanatory power using the modified Akaike information criterion for finite sample sizes (AICc⁶⁸). The performance of an intercept-only model, in which a serial correlation parameter describes a spectrum of possibilities between stationary values drawn from a normal distribution and a non-stationary random walk with step sizes drawn from a normal distribution, was also tested. We ran these analyses on the entire data set (Berriasian–Cenomanian) and on an Early

ARTICLE

Cretaceous data set excluding the Cenomanian (Berriasian–Albian) to investigate the influence of the final extinction of ichthyosaurs on factors explaining their waning and waxing of their diversity and the potential uniqueness of that event compared with their previous history.

References

- Kelley, N. P. & Pyenson, N. D. Evolutionary innovation and ecology in marine tetrapods from the Triassic to the Anthropocene. *Science* 348, aaa3716 (2015).
- 2. Motani, R. The evolution of marine reptiles. *Evol. Educ. Outreach* **2**, 224–235 (2009).
- 3. Motani, R. *et al.* A basal ichthyosauriform with a short snout from the Lower Triassic of China. *Nature* **517**, 485–488 (2015).
- McGowan, C. An isolated coracoid from the Maastrichtian of New Jersey. Can. J. Earth Sci. 15, 169–171 (1978).
- Russell, D. A. in *The Cretaceous System in the Western Interior of North America* (ed. Caldwell, W. G. E.) 119–136 (Geological Association of Canada, 1975).
- Bardet, N. Stratigraphic evidence for the extinction of the ichthyosaurs. *Terra* Nova 4, 649–656 (1992).
- 7. Bardet, N. Extinction events among Mesozoic marine reptiles. *Hist. Biol.* 7, 313–324 (1994).
- Bakker, R. T. in Evolution of the Western Interior Basin: Geological Association of Canada, Special Paper (eds Caldwell, W. G. E. & Kauffman, E. G.) Vol 39, 641–664 (1993).
- Lingham-Soliar, T. Extinction of ichthyosaurs: a catastrophic or evolutionary paradigm? *Neues Jahrb. für Geol. und Paläontologie, Abhandlungen* 228, 421–452 (2003).
- 10. Massare, J. A. Tooth morphology and prey preference of Mesozoic marine reptiles. J. Vertebr. Paleontol. 7, 121-137 (1987).
- Dick, D. G. & Maxwell, E. E. The evolution and extinction of the ichthyosaurs from the perspective of quantitative ecospace modelling. *Biol. Lett.* 11, 20150339 (2015).
- 12. Schumacher, B. A. A 'woollgari-zone mosasaur' (Squamata; Mosasauridae) from the Carlile Shale (Lower Middle Turonian) of central Kansas and the stratigraphic overlap of early mosasaurs and pliosaurid plesiosaurs. *Trans. Kansas Acad. Sci.* **114**, 1–14 (2011).
- Kear, B. P., Boles, W. E. & Smith, E. T. Unusual gut contents in a Cretaceous ichthyosaur. Proc. R. Soc. London B Biol. Sci. 270, S206–S208 (2003).
- Druckenmiller, P. S. & Maxwell, E. E. A new Lower Cretaceous (lower Albian) ichthyosaur genus from the Clearwater Formation, Alberta, Canada. *Can. J. Earth Sci.* 47, 1037–1053 (2010).
- Fischer, V., Masure, E., Arkhangelsky, M. S. & Godefroit, P. A new Barremian (Early Cretaceous) ichthyosaur from western Russia. J. Vertebr. Paleontol. 31, 1010–1025 (2011).
- Fischer, V. et al. Simbirskiasaurus and Pervushovisaurus reassessed: implications for the taxonomy and cranial osteology of Cretaceous platypterygiine ichthyosaurs. Zool. J. Linn. Soc. 171, 822–841 (2014).
- Maxwell, E. E. & Caldwell, M. W. A new genus of ichthyosaur from the Lower Cretaceous of Western Canada. *Palaeontology* 49, 1043–1052 (2006).
- Fischer, V. *et al.* New ophthalmosaurid ichthyosaurs from the European Lower Cretaceous demonstrate extensive ichthyosaur survival across the Jurassic-Cretaceous boundary. *PLoS ONE* 7, e29234 (2012).
- Fischer, V. *et al.* A basal thunnosaurian from Iraq reveals disparate phylogenetic origins for Cretaceous ichthyosaurs. *Biol. Lett.* 9, 1–6 (2013).
- Fischer, V., Bardet, N., Guiomar, M. & Godefroit, P. High diversity in Cretaceous ichthyosaurs from Europe prior to their extinction. *PLoS ONE* 9, e84709 (2014).
- 21. Arkhangelsky, M. S. & Zverkov, N. G. On a new ichthyosaur of the genus Undorosaurus. Proc. Zool. Inst. RAS **318**, 187–196 (2014).
- McGowan, C. The systematics of Cretaceous ichthyosaurs with particuliar reference to the material from North America. *Contrib. Geol* 11, 9–29 (1972).
- Fischer, V. New data on the ichthyosaur *Platypterygius hercynicus* and its implications for the validity of the genus. *Acta Palaeontol. Pol.* 57, 123–134 (2012).
- 24. Heath, T. Taxon sampling and the accuracy of phylogenetic analyses. J. Syst.s Evol. 46, 239–257 (2008).
- Heath, T. A., Zwickl, D. J., Kim, J. & Hillis, D. M. Taxon sampling affects inferences of macroevolutionary processes from phylogenetic trees. *Syst. Biol.* 57, 160–166 (2008).
- Anderson, P. S. L. & Friedman, M. Using cladistic characters to predict functional variety: experiments using early gnathostomes. J. Vertebr. Paleontol. 32, 1254–1270 (2012).
- Druckenmiller, P. S. & Maxwell, E. E. A Middle Jurassic (Bajocian) ophthalmosaurid (Reptilia, Ichthyosauria) from the Tuxedni Formation, Alaska and the early diversification of the clade. *Geol. Mag.* 151, 41–48 (2014).
- Massare, J. A. & Young, H. A. Gastric contents of an ichthyosaur from the Sundance formation (Jurassic) of central Wyoming. *Paludicola* 5, 20–27 (2005).
- 29. Walmsley, C. W. *et al.* Why the long face? The mechanics of mandibular symphysis proportions in crocodiles. *PLoS ONE* **8**, e53873 (2013).

- 30. Kelley, N. P. & Motani, R. Trophic convergence drives morphological convergence in marine tetrapods. *Biol. Lett.* **11**, 1–5 (2015).
- Wagner, P. J. The quality of the fossil record and the accuracy of phylogenetic inferences about sampling and diversity. Syst. Biol. 49, 65–86 (2000).
- 32. Benson, R. B. J., Butler, R. J., Lindgren, J. & Smith, A. S. Mesozoic marine tetrapod diversity: mass extinctions and temporal heterogeneity in geological megabiases affecting the vertebrates. *Proc. R. Soc. B Biol. Sci.* 277, 829–834 (2010).
- Bardet, N., Houssaye, A., Rage, J.-C. & Suberbiola, X. P. The Cenomanian-Turonian (late Cretaceous) radiation of marine squamates (Reptilia): the role of the Mediterranean Tethys. *Bull. la Société géologique Fr* 179, 605–622 (2008).
- Kear, B. P. Cretaceous marine reptiles of Australia: a review of taxonomy and distribution. Cretac. Res. 24, 277–303 (2003).
- Druckenmiller, P. S. & Russell, A. P. Earliest North American occurrence of Polycotylidae (Sauropterygia: Plesiosauria) from the Lower Cretaceous (Albian) Clearwater formation, Alberta, Canada. J. Paleontol. 83, 981–989 (2009).
- Thorne, P. M., Ruta, M. & Benton, M. J. Resetting the evolution of marine reptiles at the Triassic-Jurassic boundary. *Proc. Natl Acad. Sci. USA* 108, 8339–8344 (2011).
- Bellier, J.-P. in Les événements de la partie moyenne du Crétacé (Aptien à Turonien) (ed. Cotillon, P.) Vol 11, 295–301 (Geobios, mémoire spécial, 1989).
- Linnert, C. *et al.* Evidence for global cooling in the Late Cretaceous. *Nat. Commun.* 5, 1–7 (2014).
- 39. Hay, W. W. Can humans force a return to a 'Cretaceous' climate? *Sediment. Geol.* 235, 5–26 (2011).
- 40. Herrle, J. O. et al. Mid-Cretaceous High Arctic stratigraphy, climate, and Oceanic Anoxic Events. Geology 43, 403–406 (2015).
- Coccioni, R. & Galeotti, S. The mid-Cenomanian Event: prelude to OAE 2. Palaeogeogr. Palaeoclimatol. Palaeoecol. 190, 427–440 (2003).
- Gale, A. S., Voigt, S., Sageman, B. & Kennedy, W. J. Eustatic sea-level record for the Cenomanian (Late Cretaceous)—Extension to the Western Interior Basin, USA. *Geology* 11, 859–862 (2008).
- 43. Leckie, R. M., Bralower, T. J. & Cashman, R. Oceanic anoxic events and plankton evolution: biotic response to tectonic forcing during the mid-Cretaceous. *Paleoceanography* **17**, 1–28 (2002).
- Bilotte, M. in Les événements de la partie moyenne du Crétacé (Aptien à Turonien) (ed. Cotillon, P.) Vol 11, 255–266 (Geobios, mémoire spécial, 1989).
- 45. Monnet, C. The Cenomanian-Turonian boundary mass extinction (Late Cretaceous): new insights from ammonoid biodiversity patterns of Europe, Tunisia and the Western Interior (North America). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **282**, 88–104 (2009).
- Jagt-Yasykova, E. A. Ammonite faunal dynamics across bio events during the mid – and Late Cretaceous along the Russian Pacific coast. *Acta Palaeontol. Pol.* 57, 737–748 (2012).
- Monnet, C. & Bucher, H. European ammonoid diversity questions the spreading of anoxia as primary cause for the Cenomanian/Turonian (Late Cretaceous) mass extinction. Swiss J. Geosci. 100, 137–144 (2007).
- Iba, Y. et al. Belemnite extinction and the origin of modern cephalopods 35 m.y. prior to the Cretaceous-Paleogene event. Geology 39, 483–486 (2011).
- Pandolfi, J. M. & Kiessling, W. Gaining insights from past reefs to inform understanding of coral reef response to global climate change. *Curr. Opin. Environ. Sustain.* 7, 52–58 (2014).
- Skelton, P. W. in North African Cretaceous Carbonate Platform Systems: Proceedings of the NATO Advanced Research Workshop, Tunis, Tunisia 13-18 May 2002 (eds Gili, E., Negra, M. E. H. & Skelton, P. W.) Vol 28, 215–227 (Kluwer Academic Publishers (2003).
- Cavin, L. & Forey, P. L. Using ghost lineages to identify diversification events in the fossil record. *Biol. Lett.* 3, 201–204 (2007).
- Cavin, L., Forey, P. L. & Lécuyer, C. Correlation between environment and Late Mesozoic ray-finned fish evolution. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 245, 353–367 (2007).
- Guinot, G. & Cavin, L. 'Fish' (Actinopterygii and Elasmobranchii) diversification patterns through deep time. *Biol. Rev. Camb. Philos. Soc.* 25, 2314–2318 (2015).
- Norell, M. A. in *Extinction and Phylogeny* (eds Novacek, M. J. & Wheeler, Q. D.) 89–118 (Columbia University Press, 1992).
- Brusatte, S. L., Benton, M. J., Ruta, M. & Lloyd, G. T. Superiority, competition, and opportunism in the evolutionary radiation of dinosaurs. *Science* 321, 1485–1488 (2008).
- Ronquist, F. & Huelsenbeck, J. P. MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19, 1572–1574 (2003).
- 57. Benson, R. B. J. & Druckenmiller, P. S. Faunal turnover of marine tetrapods during the Jurassic-Cretaceous transition. *Biol. Rev.* 89, 1-23 (2014).
- Marx, F. G. & Fordyce, R. E. Baleen boom and bust: a synthesis of mysticete phylogeny, diversity and disparity. *R. Soc. Open Sci.* 2, 140434 (2015).
- Close, R. A., Friedman, M., Lloyd, G. T. & Benson, R. B. J. Evidence for a Mid-Jurassic adaptive radiation in mammals. *Curr. Biol.* 25, 1–6 (2015).
- 60. Maddison, W. P. & Maddison, D. R. Mesquite: A modular sytem for evolutionary analysis (2011).

- 61. Young, M. T. et al. The cranial osteology and feeding ecology of the metriorhynchid crocodylomorph genera Dakosaurus and Plesiosuchus from the Late Jurassic of Europe. PLoS ONE 7, e44985 (2012).
- 62. Haq, B. U. Cretaceous eustasy revisited. Glob. Planet. Change 113, 44-58 (2014).
- 63. Strauss, D. & Sadler, P. M. Classical confidence intervals and Bayesian probability estimates for ends of local taxon ranges. Math. Geol. 21, 411-427 (1989).
- 64. Prokoph, A., Shields, G. A. & Veizer, J. Compilation and time-series analysis of a marine carbonate 818O, 813C, 87Sr/86Sr and 834S database through Earth history. Earth Sci. Rev. 87, 113-133 (2008).
- 65. Martin, J. E., Amiot, R., Lécuyer, C. & Benton, M. J. Sea surface temperature contributes to marine crocodylomorph evolution. Nat Commun. 5, 1-7 (2014).
- 66. Lloyd, G. T. Generalized differencing of time series (2008; Available at: http:// www.graemetlloyd.com/methgd.html. Accessed 19 October 2015.
- 67. Chatfield, C. The Analysis of Time Series: An Introduction Sixth edn, 19 (CRC Press, 2013).
- 68. Burnham, K. P. & Anderson, D. Model Selection and Multi-Model Inference: A Practical Information- Theoretic Approach (Springer, 2001).
- 69. Adams, T. L. & Fiorillo, A. Platypterygius Huene, 1922 (Ichthyosauria, Ophthalmosauridae) from the Late Cretaceous of Texas, USA. Palaeontol. Electron 14, 19A (2011).
- 70. Bardet, N., Wellnhofer, P. & Herm, D. Discovery of ichthyosaur remains (Reptilia) in the upper Cenomanian of Bavaria. Mitteilungen der Bayer. Staatssammlung für Paläontologie und Hist. Geol. 34, 213–220 (1994).

Acknowledgements

V.F. warmly thanks, in no particular order, P. Godefroit, E. Poty, P. Vincent, G. Guinot, M.S. Fernández, M. Talevi, A.J. Roberts, N. Pyenson and M. Trotta for their care, logistic help and fruitful discussions. V.F.'s research was supported by a Newton International Fellowship (NF140022) from the Royal Society (UK), a Chargé de Recherches fellowship from the F.R.S.-FNRS (Belgium) and a grant from the Vocatio foundation (Belgium). This is Paleobiology Database publication number 254.

Author contributions

V.F., N.B., M.F., and R.B.J.B. designed the project. V.F., M.S.A. and R.B.J.B. analysed the material and ran the analyses. V.F. wrote the paper and designed the illustrations. All authors discussed the results and revised the manuscript.

Additional information

Supplementary Information accompanies this paper at http://www.nature.com/ naturecommunications

Competing financial interests: The authors declare no competing financial interests.

Reprints and permission information is available online at http://npg.nature.com/ reprintsandpermissions

How to cite this article: Fischer, V. et al. Extinction of fish-shaped marine reptiles associated with reduced evolutionary rates and global environmental volatility. Nat. Commun. 7:10825 doi: 10.1038/ncomms10825 (2016).



This work is licensed under a Creative Commons Attribution 4.0 (\mathbf{i}) International License. The images or other third party material in this article are included in the article's Creative Commons license, unless indicated otherwise in the credit line; if the material is not included under the Creative Commons license, users will need to obtain permission from the license holder to reproduce the material. To view a copy of this license, visit http://creativecommons.org/licenses/by/4.0/





Supplementary Figure 1 | Most parsimonious tree with the best stratigraphic fit. The The tree presented is the one with the best GER (Gap Excess Ratio¹) and SCI (Stratigraphic Congruence Index²) scores, in 'basic' reconstruction of branch lengths, arising from the equal weight maximum parsimony analysis. This analysis recovered twelve most parsimonious trees with a length of 209 steps. The strict consensus typology strongly matches those of previous attempts³⁻⁶ and only a few differences are present. Notably, Athabascasaurus bitumineus is recovered as a platypterygiine slightly more derived than Aegirosaurus leptospondylus and Sveltonectes insolitus, unlike in ⁵. The increase coverage of Cretaceous taxa did not destabilise the structure of the tree. These additional Cretaceous taxa are recovered as platypterygine ophthalmosaurids, occupying various positions within this clade. The type species of *Platypterygius*, *Platypterygius platydactylus* is recovered outside the clade containing most species currently referred to as *Platypterygius*. Sisteronia seelevi appears closely related to 'Platypterygius' hercynicus, forming a clade that is the sister clade of platypterygines with a divided naris ('Platypterygius' australis + 'Platypterygius' birjukovi + Pervushovisaurus bannovkensis) sachicarum +Simbirskiasaurus 'Platypterygius' americanus.



Supplementary Figure 2 | **Most parsimonious tree with the best stratigraphic fit.** The The tree presented is the one with the best GER and SCI scores, in 'equal' reconstruction of

branch lengths, arising from the equal weight maximum parsimony analysis. See Supplementary Figure 1 caption for details of the results.



Supplementary Figure 3 | **Stratigraphic congruence.** Distribution of GER scores from most parsimonious trees compared to a sample of 1000 randomly generated trees using strap⁷, showing the excellent stratigraphic congruence of the most parsimonious trees.



Supplementary Figure 4 | **Stratigraphic congruence.** Distribution of SCI scores from most parsimonious trees compared to a sample of 1000 randomly generated trees using strap⁷, showing the excellent stratigraphic congruence of the most parsimonious trees.



Supplementary Figure 5 | **Most parsimonious tree from the implied weighting analysis**. Length = 20.87381. This analysis recovered a single tree (length=20.87381). Although strongly similar, slight differences with the consensus tree from the equal weight analysis are recovered. *Temnodontosaurus* spp. is recovered as the sister taxon to *Suevoleviathan disinteger* + Thunnosauria instead of forming a clade with Leptonectidae. *Aegirosaurus leptospondylus, Sveltonectes insolitus, Athabascasaurus bitumineus* and *Brachypterygius extremus* are successive outgroups of more derived platypterygines, which belong to two clades: (*Caypullisaurus bonapartei* + Platypterygines with a paired narial aperture) on one side and (*Platypterygius platydactylus* + (*Sisteronia seeleyi* + '*Platypterygius' americanus* + '*Platypterygius' hercynicus*)) on the other side. This analysis supports a clade of Cretaceous ophthalmosaurines (*Acamptonectes densus* + *Leninia stellans*), as do a number of most parsimonious trees arising from the analysis with equal weights.



Supplementary Figure 6 | **95% confidence age intervals of clades.** Computed for each node of the Bayesian inference of phylogeny, with the constrained typology. The topology of the majority rule consensus match that of the maximum parsimony tree with the best RCI and GER scores. Ages are expressed in millions years before present. It recognizes Leptonectidae with *Temnodontosaurus* as its sister group; a clade of younger leptonectids (*Excalibosaurus costini* + *Eurhinosaurus longirostris*); a clade of Cretaceous ophthalmosaurines (*Acamptonectes densus* + *Leninia stellans*); the two youngest taxa within the platypterygiine clade with a peculiar narial aperture, '*Platypterygius*' *australis* and *Pervushovisaurus bannovkensis* also form a clade.



Supplementary Figure 7 | **Posterior probabilities of each node**. Computed on the Bayesian inference of phylogeny, with the constrained typology.



Supplementary Figure 8 | **Evolutionary rates.** Computed on the Bayesian inference of phylogeny, with the constrained typology. Exceptionally high rates are written in orange and are restricted to the early evolution of Parvipelvia, here entirely dragged into the Triassic.



Supplementary Figure 9 | 95% confidence age intervals of clades. Computed for each node of the Bayesian inference of phylogeny, (unconstrained analysis). Ages are expressed in millions years before present. The majority rule consensus is less well resolved but congruent with the results from the maximum parsimony analyses, with two exceptions: the Aalenian-Bajocian baracromians Stenopterygius aalensis and Stenopterygius/Chacaicosaurus cayi form a clade rather than a grade that is the sister group of Ophthalmosauridae and the Albian platypterygiine Athabascasaurus bitumineus is recovered as more derived than Brachypterygius extremus, Aegirosaurus leptospondylus and Sveltonectes insolitus, which form a polytomy at the base of Platypterygiinae. Particularly, the Bayesian inference supports the existence and further resolves the (Temnodontosaurus spp. + Leptonectidae) clade, the (Ophthalmosaurus icenicus + Ophthalmosaurus natans + Cretaceous ophthalmosaurines) clade and the base of the platypterygiine clade. Most importantly, despite its lower resolution, the Bayesian inference support the general shape of the parvipelvian tree that has emerged some years ago, with (i) the presence of three distinct clades of Cretaceous ichthyosaurs (early parvipelvians, ophthalmosaurines and platypterygiines), which (ii) diverged and rapidly evolved between the Late Triassic and the Middle Jurassic, (iii) relatively minor extinction events during or at the end of the Jurassic.



Supplementary Figure 10 | **Posterior probabilities of each node**. Computed on the Bayesian inference of phylogeny (**unconstrained analysis**).



Supplementary Figure 11 | **Evolutionary rates.** Computed on the Bayesian inference of phylogeny (unconstrained analysis). Exceptionally high rates are written in orange and are restricted to the early evolution of Parvipelvia, here entirely dragged into the Triassic.



Supplementary Figure 12 | **Congruence between the mean cladogenesis results.** This graph shows that both the constrained and unconstrained analyses yield the same picture of parvipelvian evolutionary dynamics, even if the consensus tree arising from the unconstrained Bayesian analysis is less well-resolved than in the maximum parsimony analysis. Note the low values for the Cretaceous.



Supplementary Figure 13 | **PCOA results.** It shows the position of each taxon and each internal node relative to the first and second axes.



Supplementary Figure 14 | **PCOA results.** Note the clear morphological distinction between the three main clades of parvipelvian ichthyosaurs (Early Parvipelvians, Ophthalmosaurinae, Platypterygiinae). The left corner of the Ophthalmosauridae polygon is *Arthropterygius chrisorum*.



Supplementary Figure 15 | Morphospace occupation during the evolution of Parvipelvia. Note the extremely narrow areas for the Late Triassic and the post earliest Cenomanian, and the fact that the largest area is occupied during the Early Cretaceous.



Supplementary Figure 16 | **Localisation of the Stoilensky quarry.** It is located northeastern to the town of Stary Oskol, in the Belgorod region, western-most Russia. The quarry was established in 1961 and exploits iron ore deposit of the 'Kursk Magnetic Anomaly'.



Supplementary Figure 17 | Stratigraphic log of the Stoilensky quarry. Data from Gabdullin⁸. "Greensand" refers to a 'greensand-like' phosphatic and glauconitic sandstone. This quarry section was described by Gabdullin⁸; a summary of the section is provided here. Lenticular intercalation of sands and sandstones forms the basal part of the section (1 m). The top of these sand/sandstone contains the late Albian ammonite Mortoniceras inflatum. Above, a lenticular, phosphatic, glauconitic, and fossiliferous sandstone (0–2.5 m) and its overlying two meters of clayey sandstone mark the Albian-Cenomanian boundary. Above, a thick layer of ferruginous sandstone (8 m) contains the following macrofauna according to Gabdullin⁸: chimaeriform (Ischyodus 'bifurcatus' and shark teeth ('Protosquales' sp.), bivalves (Neithea sp.), and belemnites (Praeactinocamax primus, which ranges in the Russian platform from the Mantelliceras mantelli Zone (base of the Cenomanian) to the Acanthoceras rhotomagense Zone (early middle Cenomanian)^{9,10}. The microfauna consists of late Cretaceous calcareous nannoplankton (Broisonia matalosa, Cenomanian-Turonian; Manivitella redimiculata and *Prediscosphaera cretacea*, Cenomanian–Maastrichtian⁸). The greensand-like rock thus deposited between the late Albian Mortoniceras inflatum Zone and the early-middle Cenomanian; it probably contains the Early-Late Cretaceous boundary and likely represents the onset of the early Cenomanian transgression. However, the precise position of the boundary is impossible to place. The Stoilensky fauna is thus considered here to occur at the Early-Late Cretaceous boundary, as hypothesized by Rozhdestvenskiy¹¹. The 'greensandlike' layer and its fossils are therefore roughly contemporaneous with other similar deposits in France ('Gaize' formation)¹² and England (the Upper Greensand Formation and Cambridge Greensand Member)^{13–15}.



Supplementary Figure 18 | Marine reptile assemblage of the Stoilensky quarry. Based on the teeth housed at the Saratov State University (SSU). Plesiosaurs are coloured in grey, ichthyosaurs in orange (platypterygiine ichthyosaurs in dark orange; other ichthyosaurs in light orange). Ichthyosaurs dominate the assemblage, but a peculiarity of this ecosystem is the abundance of a yet indeterminate ichthyosaur and of polycotylid plesiosaurs¹⁶. As these abundance data rely on teeth, the relative proportions of these taxa should be taken with extreme caution because their tooth shedding frequencies is unknown, and likely pollute the signal.



Supplementary Figure 19 | **Selected plesiosaur teeth from the Stoilensky quarry.** Specimens (GPV 2/ partim) illustrating the two feeding guilds colonised by plesiosaurs in this ecosystem.

SUPPLEMENTARY TABLES

Supplementary Table 1 | Names and ages of OTUs.

#	taxon_names	FAD LAD FAD		FAD Cret	LAD Cret	Strati/info	Range/Un
		Timescale	Timescale	CSDB3	CSDB3		certainty
		2014	2014				
1	Mikadocephalus_	247.2	242	247.2	242	Topmost Anisian	U
	gracilirostris						
2	Hudsonelpidia_br	227	216.4	227	216.4	Lower Norian (Norian substages ages from Husing et	U
	evirostris					al. ¹⁷)	
3	Macgowania_jani	216.4	211.4	216.4	211.4	Middle Norian (Norian top from Wotzlaw et al ¹⁸)	U
	ceps						
4	Leptonectes_tenu	201.3	182.7	201.3	182.7	Lower Hettangian-Lower Pliensbachian	R
	irostris						
5	Excalibosaurus_c	199.3	190.8	199.3	190.8	Sinemurian	U
	ostini						
6	Eurhinosaurus_lo	182.7	174.1	182.7	174.1	Lower Toarcian	R
	ngirostris						
7	Suevoleviathan_d	182.7	174.1	182.7	174.1	Lower Toarcian	U
	isinteger						
8	Temnodontosaur	201.3	174.1	201.3	174.1	Upper Hettangian-Upper Toarcian	R
	us_spp.						
9	Hauffiopteryx_ty	182.7	174.1	182.7	174.1	Lower Toarcian	R
	picus						
1	Malawania_anac	132.9	125	132.13	124.55	upper Hauterivian-Barremian	U
0	hronus						
1	Ichthyosaurus_co	201.3	182.7	201.3	182.7	Hettangian-lower Pliensbachian	R
1	mmunis						
1	Stenopterygius_q	182.7	174.1	182.7	174.1	Lower Toarcian	R
2	uadriscissus						
1	Chacaicosaurus_c	170.3	168.3	170.3	168.3	Lower Bajocian	U
3	ayi						
1	Stenopterygius_a	174.1	170.3	174.1	170.3	Lower Aalenian	U
4	alensis						
1	Ophthalmosaurus	166.1	139.8	166.1	141.6	Middle Callovian-Lower Tithonian + cf.	R
5	_icenicus					Ophthalmosaurus from Berriasian Nettleton (Primitivus	
	0.1.1.1	1661	157.0	1661	157.0		D
	ophthalmosaurus	100.1	157.3	100.1	157.3	upper Callovian–middle Oxfordian	к
0	_natans	170.2	169.2	170.2	169.2	Lawar Daisaian	TI
7	alue	170.5	108.5	170.5	108.5	Lower Dajocian	U
1	dius	122.0	120.4	126.44	120.2	Houtorivian	D
1	Acampionectes_d	132.9	129.4	130.44	150.2	riauci i viäli	л
1	Leninia stallans	125	121	123 75	123 61	Lower Antian: Deshavesites volgensis - D. forhesi Zona	II
9	Lemma_stemans	125	121	123.13	125.01	in Europe	0
2	Brachynterygius	157.3	145	157 3	144 07	Middle Kimmeridgian-lower Tithonian	R
0	extremus	107.0	110	101.0	111.07	Andre Kinniendemi jower Finloniun	
2	Arthroptervoius	163.5	145	163.5	144.07	Oxfordian–Tithonian	R
1	chrisorum						
2	Caypullisaurus b	152.1	139.8	152.1	141.06	Lower Tithonian–Lower Berriasian	R
2	onapartei						
2	Aegirosaurus lep	152.1	132.9	152.1	136.44	Lowermost Tithonian + lazarrus range from Fischer et	R
3	tospondylus					al ¹⁹ CR: up to Upper Valanginian	
2	Athabascasaurus	113	107.8	113.07	107.65	Lowermost Albian: Wabiskaw Member	U
4	bitumineus						

2	Sveltonectes_inso	129.4	125	126.82	124.55	Upper Barremian	U
5	litus						
2	Simbirskiasaurus	129.4	125	130.2	126.82	Lower Barremian	U
6	_birjukovi						
2	Platypterygius_au	107.8	100.5	107.65	97.13	Middle-Upper Albian	R
7	stralis						
2	Pervushovisaurus	100.5	93.9	96	94.8	Middle Cenomanian (see ²⁰)	U
8	_bannovkensis						
2	Platypterygius_he	121	100.5	121.25	98.14	Uppermost Aptian–Upper Albian (Mortoniceras inflatum	R
9	rcynicus					Zone)	
3	Platypterygius_a	105.5	93.9	101.83	95.05	Upper Albian- lower Cenomanian	R
0	mericanus						
3	Platypterygius_pl	125	121	123.61	122.93	Lower Aptian: Deshayesites deshayesi	U
1	atydactylus						
3	Platypterygius_sa	125	121	124.55	121.25	Lower Aptian (Hampe ²¹)	U
2	chicarum						
3	Palvennia_hoyber	152.1	145	152.1	144.07	Tithonian	U
3	geti						
3	Cryopterygius_kr	152.1	145	152.1	144.07	Tithonian	U
4	istiansenae						
3	Janusaurus_lundi	152.1	145	152.1	144.07	Tithonian	U
5							
3	Sisteronia_seeley	107.8	93.9	107.65	95.05	Mid Albian (Marnes bleues Fm)-Lower Cenomanian	R
6	i					(basal mantelli Zone: Glauconitic Marl Member)	

Supplementary Table 2 | Names and ages of additional taxa.

Maiaspondylus_lindoei	113	107.8	113.07	107.6	Lower Albian	U
				5		
Cetharthrosaurus_walkeri	105.5	100.5	101.83	97.13	Uppermost Albian	U
Platypterygius_hauthali	129.4	125	130.2	124.5	Barremian	U
				5		
Platypterygius_ochevi	105.5	93.9	101.83	95.05	Upper Albian-lower Cenomanian	U
Nannopterygius_enthekiodon	157.3	145	157.3	144.0	Middle Kimmeridgian-lower Tithonian	U
				7		
Undorosaurus_gorodischensis	152.1	145	152.1	144.0	Tithonian	U
				7		
Undorosaurus_trautscholdi	152.1	145	152.1	144.0	Tithonian	U
				7		
Platypterygius_campylodon&s	100.5	93.9	113.07	93	Cenomanian	R
р						
Ophthalmosaurinae_indet2+gh	121	100.5		97.13	Upper Albian (ghost is: Upper Aptian-Middle Albian)	U
ost						
Ophthalmosaurinae_indet1	170.3	168.3	170.3	168.3	Bajocian Druckenmiller & Maxwell ²²	U

Supplementary Table 3 | Phylogeny-adjusted diversity estimates.

n p<		S	М	М	М	М	М	М	М	М	М	М	М	М	М	М	М	М	М	М	М	М	М	М	М	М
a T<		u	Р	Р	Р	Р	Р	Р	Р	Р	Р	Р	Р	Р	Р	Р	Р	Р	Р	Р	Р	Р	Р	Р	Р	Р
<t tr=""></t>		р	Т	Т	Т	Т	Т	Т	Т	Т	Т	Т	Т	Т	Т	Т	Т	Т	Т	Т	Т	Т	Т	Т	Т	Т
		р	1_	1_	2_	2_	3_	3_	4_	4_	5_	5_	6_	6_	7_	7_	8_	8_	9_	9_	10	10	11	11	12	12
i i		_	ba	eq	_b	_e	_b	_e	_b	_e																
a c b c c c c <		t	si		as	q	as	q	as	q																
x x x x x <		a	с		с		с		с		с		с		с		с		с		ic		ic		ic	
n n		x																								
TH 0		a																								
Cen 2 5	Tur	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1 1<	Cen	2	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5
Ath I <thi< th=""> I I I</thi<>	U_	3	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8
M. I S	Alb																									
Ath I <thi< th=""> I I I</thi<>	M_	1	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6
I.A. 2 8	Alb																									
Ib I	L_A	2	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8	8
Ca 1 <th1< th=""> 1 1 1</th1<>	lb	1	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7
repr r <	O_ Apt	1	/	'	'	/	/	'	'	'	'	'	/	/	'	'	'	,	'	'	'	'	'	/	'	/
Lase N	ТЛ	0	8	0	8	0	8	0	8	0	8	0	8	0	8	0	8	0	8	0	8	0	8	0	8	0
pr pr< p	nt	0	0		0		0		0		0		0		0		0		0		0		0		0	
Hat 0 7 13 10 13 10 13 10 13 10 13 10 13 10 13 10 13 10 13 10 13 10 13 </td <td>Bar</td> <td>1</td> <td>12</td> <td>13</td>	Bar	1	12	13	12	13	12	13	12	13	12	13	12	13	12	13	12	13	12	13	12	13	12	13	12	13
Name O 7 14 <	Hau	0	7	13	7	13	7	13	7	13	7	13	7	13	7	13	7	13	7	13	7	13	7	13	7	13
Her 0 9 13 9 13 9 13 9 13 9 13 9 13 10 13	Val	0	7	14	7	14	7	14	7	14	7	14	7	14	7	14	8	14	7	14	8	14	8	14	8	14
Tit 3 17 19 17 19 17 19 17 19 17 19 17 19 17 19 17 19 17 19 17 19 17 19 17 19 18 19 13 7 13 7 13 7 13 7 13 7 13 7 13 7 13 7 13 7 13 7	Ber	0	9	13	9	13	9	13	9	13	9	13	9	13	9	13	10	13	9	13	10	13	10	13	10	13
Kim 1 10 15 11 15 1 15 1 15 <td>Tit</td> <td>3</td> <td>17</td> <td>19</td> <td>18</td> <td>19</td> <td>17</td> <td>19</td> <td>18</td> <td>19</td> <td>18</td> <td>19</td> <td>18</td> <td>19</td>	Tit	3	17	19	17	19	17	19	17	19	17	19	17	19	17	19	18	19	17	19	18	19	18	19	18	19
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	Kim	1	10	15	11	15	10	15	11	15	11	15	10	15	11	15	11	16	10	15	10	16	11	16	10	16
Cal 0 7 9 7	Oxf	0	7	12	7	12	7	12	7	12	7	13	7	13	7	13	7	13	7	13	7	13	7	13	7	13
Bat 0 4 8 7 8 7 8 7 8 7 8 7 8 7 8 7 8 7 8 7 8 7 8 7 8 7 8 7 8 7 8 7 8 7 8 7 8 7 8 7 9 7 9 7 9 7 9 7 9 7 9 7 9 7 9 7 9 7 9 7 9 7 9 7 9 7 9 7 9 7 9 7	Cal	0	7	9	7	9	7	9	7	9	7	9	7	9	7	9	7	9	7	9	7	9	7	9	7	9
Baj 1 7 8 7 9 7	Bat	0	4	8	4	8	4	8	4	8	4	8	4	8	4	8	4	8	4	8	4	8	4	8	4	8
Aal 0 4 7 4	Baj	1	7	8	7	8	7	8	7	8	7	8	7	8	7	8	7	8	7	8	7	8	7	8	7	8
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	Aal	0	4	7	4	7	4	7	4	7	4	7	4	7	4	7	4	7	4	7	4	7	4	7	4	7
Pli 0 7 9 7	Тоа	0	7	9	7	9	7	9	7	9	7	9	7	9	7	9	7	9	7	9	7	9	7	9	7	9
Sin 0 8 9 8 8 8 8 8 8 8 8 8 1 8 1 8 1 8 1 8 1 8	Pli	0	7	9	7	9	7	9	7	9	7	9	7	9	7	9	7	9	7	9	7	9	7	9	7	9
Het 0 7 8 7 8 8 7 8 8 7 8 8 7 8 8 7 8 8 7 8 8 7 8 8 7 8 8 7 8 8 7 8 8 7 8 8 7 8 8 7 8 8 7 1 7 1 8 1 7 1 8 1 7 1 8 1 7 1 8 1 7 1 8 1 7 1 8 1 7 1 8 1 7 1 8 1 7 1 8 1 7 1 8 1 8 1 8 1 7 1 8 1 7 1 8 1 8 1 7 1 8 1 8 1 8 1 7 1 8 1 8 1 7 1 8 1 8 1	Sin	0	8	9	8	9	8	9	8	9	8	9	8	9	8	9	8	9	8	9	8	9	8	9	8	9
Rhe 0 1 7 1 8 1 8 1 7 1 7 1 8 1 6 1 6 1 6 1 6 1 6 1 6 1 6 1 6 1 6 1 6 1 6 1 6 1 6 1 6 1	Het	0	7	8	7	8	8	8	8	8	7	8	7	8	8	8	7	8	8	8	7	8	8	8	8	8
UNor 0 1 5 1 6 1 6 1 5 1 5 1 6 1 5 1 6 1 5 1 6 1 5 1 6 1 5 1 6 1 5 1 6 1 5 1 6 1 5 1 6 1 5 1 6 1 5 1 6 1 5 1 6 1 5 1 6 1 5 1 6 1 5 1 6 1<	Rhe	0	1	7	1	7	1	8	1	8	1	7	1	7	1	8	1	7	1	8	1	7	1	8	1	8
M_ 0 2 3 2	U_ Nor	0	1	5	1	5	1	6	1	6	1	5	1	5	1	6	1	5	1	6	1	5	1	6	1	6
Nor I	М	0	2	3	2	3	2	3	2	3	2	3	2	3	2	3	2	3	2	3	2	3	2	3	2	3
L_N 0 2 3 2	Nor		_	-	_	-	_	-	_	-	_	-	_	-	_	-	_	-	_	-	_	-	_	-	_	-
or I	L_N	0	2	3	2	3	2	3	2	3	2	3	2	3	2	3	2	3	2	3	2	3	2	3	2	3
Car 0 1 2 1	or																									
Lad 0 1 2 1	Car	0	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2
Ani 0 2 <th2< th=""> <th2< th=""> <th2< th=""></th2<></th2<></th2<>	Lad	0	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2	1	2
Ole 0 2 <th2< th=""> <th2< th=""> <th2< th=""></th2<></th2<></th2<>	Ani	0	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2
	Ole	0	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2

Computed for each most parsimonious trees under both the basic and equal methods of branch length reconstruction. We applied the 'basic' and 'equal' methods to all most parsimonious trees and extracted the median phylogenetic diversity estimate as well as 95% confidence intervals using the R, using the following packages: ape^{23} , $strap^7$, and paleotree v2.3²⁴.

	median	low.95.quantile	high.95.quantile
Tur	0	0	0
Cen	3	3	3
U_Alb	5	5	5
M_Alb	5	5	5
L_Alb	6	6	6
U_Apt	6	6	6
L_Apt	8.5	8	9
Bar	11.5	11	12
Hau	10	7	13
Val	11	7	14
Ber	11.5	9	13
Tit	15.5	14	16
Kim	12	9	15
Oxf	9.5	7	13
Cal	8	7	9
Bat	6	4	8
Baj	6.5	6	7
Aal	5.5	4	7
Тоа	8	7	9
Pli	8	7	9
Sin	8.5	8	9
Het	8	7	8
Rhe	4	1	8
U_Nor	3	1	6
M_Nor	2.5	2	3
L_Nor	2.5	2	3
Car	1.5	1	2
Lad	1.5	1	2
Ani	2	2	2
Ole	2	2	2

Supplementary Table 4 | Phylogeny-adjusted diversity estimates.

Median and 95% confidence interval values.

	basic	basic_05	basic_95	eq	eq_05	eq_95
Tur	0	0	0	0	0	0
Cen	2.922526442	2.433795789	5.759348039	2.922526442	2.433795789	5.759348039
U_Alb	4.972452414	4.174608598	9.690037237	4.972452414	4.174608598	9.690037237
M_Alb	4.972452414	4.170352073	9.672162499	4.972452414	4.170352073	9.672162499
L_Alb	5.787084788	4.918089302	11.43161404	5.787084788	4.918089302	11.43161404
U_Apt	5.787084788	4.928377068	11.41592151	5.787084788	4.928377068	11.41592151
L_Apt	7.372678979	6.604640129	14.64344293	8.423765351	7.487005801	16.62169364
Bar	14.00410551	12.2718051	27.6365967	11.1280948	9.965607926	22.17570461
Hau	9.871812203	8.855907151	19.84021066	12.00662083	10.79103206	24.10466287
Val	5.869844517	5.408472518	12.06602566	15.75275897	14.007219	30.7439694
Ber	7.549072758	6.979618952	15.81268942	13.45295606	12.1474114	27.36095578
Tit	12.8054886	12.01315218	26.82981355	15.06688999	14.07941177	31.46060219
Kim	9.740763644	9.247244808	21.06243851	13.55150102	12.69070022	28.53591377
Oxf	6.631850487	6.439518403	14.49675107	11.60900305	11.0597531	24.64986837
Cal	6.57178483	6.596172187	14.59816062	7.575887334	7.23215267	16.37365647
Bat	4.212808214	4.183454853	9.885335355	8.112146077	7.926033741	18.07485897
Baj	4.962313983	5.020580063	11.74765423	5.519647067	5.543728138	12.77534203
Aal	3.845336481	4.029228215	9.01881203	5.963973371	6.133401575	14.14164499
Тоа	7.471570395	6.916494727	14.97679593	8.367676359	7.961710804	17.13718265
Pli	7.436163378	6.753145153	14.62635706	9.021056128	8.237774735	17.92315547
Sin	7.893493319	7.128897267	15.08777559	9.443632849	8.56708154	18.39679264
Het	11.25769498	10.12574734	21.62564991	8.943907052	8.133285869	17.23591065
Rhe	5.532269856	4.89615084	10.21039276	8.499208471	7.69780416	16.32490838
U_Nor	NA	NA	NA	7.342866032	6.545221173	14.20584084
M_Nor	1.877058022	1.745064101	3.604100587	3.792381198	3.394526035	7.0286689
L_Nor	2.117533846	1.780630902	3.558150711	3.994591868	3.541769735	7.16302078
Car	NA	NA	NA	2.117533846	1.782596749	3.606101802
Lad	NA	NA	NA	3.17009254	2.628764709	5.202015955
Ani	2.186923003	1.831439887	3.654618086	2.186923003	1.831439887	3.654618086
Ole	2.186923003	1.822753028	3.651363229	2.186923003	1.822753028	3.651363229

Supplementary Table 5 | Sum of variances of first 46 axes of pcoa for each bin.

We used both the basic and equal methods of branch length reconstruction. These axes explain 95.03+% of the variance explained. 95% confidence intervals achieved by bootstrapping the data 10000 times.

	weighted_mean	weighted_mean_0.05	weighted_mean_0.95
Cen_Tur	0.157894737	0.066666667	0.217391304
Alb	0.142553191	0.096774194	0.196721311
Apt	0.263888889	0.121212121	0.487179487
Hau_Bar	0.365591398	0.32	0.421052632
Ber_Val	0.261904762	0.261904762	0.261904762
Kim_Tit	0.273709484	0.248979592	0.297802198
Cal_Oxf	0.217391304	0.160839161	0.310344828
Aal_Baj_Bat	0.233333333	0.076923077	0.523809524
Pli_Toa	0.237997957	0.2113127	0.264880952
Het_Sin	0.240896359	0.166153846	0.310606061
L_Tr	0.109090909	0.068965517	0.153846154

Supplementary Table 6 | Weighted mean pairwise phenetic dissimilarity.

95% confidence intervals achieved by bootstrapping the data 10000 times.

	mean media		med.05%	med.95%	mean-stdev	mean+stdev	
Tur	0	0	0	0	0	0	
Cen	0	0	0	0	0	0	
U_Alb	0	0	0	0	0	0	
M_Alb	0	0	0	0	0	0	
L_Alb	0	0	0	0	0	0	
U_Apt	0	0	0	0	0	0	
L_Apt	0.5	0.5	0	1	-0.010753918	1.010753918	
Bar	0	0	0	0	0	0	
Hau	2.5	2.5	0	5	-0.053769592	5.053769592	
Val	1.833333333	2	1	3	0.593885116	3.072781551	
Ber	1	1	0	2	-0.021507837	2.021507837	
Tit	0.833333333	0.5	0	1	-0.083498009	1.750164676	
Kim	3.75	3.5	2.5	4.5	2.490255374	5.009744626	
Oxf	3.4166666667	3	3	3	2.913056511	3.920276822	
Cal	0.6666666667	0.5	0	1	-0.094720321	1.428053654	
Bat	3	3	3	3	3	3	
Baj	0.5	0.5	0	1	-0.010753918	1.010753918	
Aal	3	3	3	3	3	3	
Тоа	2	2	2	2	2	2	
Pli	1.5	1.5	1	2	0.989246082	2.010753918	
Sin	0.5	0.5	0	1	-0.010753918	1.010753918	
Het	0.5	0.5	0	1	-0.010753918	1.010753918	
Rhe	4.25	4	2	6	1.923405175	6.576594825	
U_Nor	1.75	1.5	0	3	-0.073756277	3.573756277	
M_Nor	0.5	0.5	0	1	-0.010753918	1.010753918	
L_Nor	1	1	1	1	1	1	
Car	0.5	0.5	0	1	-0.010753918	1.010753918	
Lad	0.5	0.5	0	1	-0.010753918	1.010753918	
Ani	0	0	0	0	0	0	
Ole	1	1	1	1	1	1	
Ind	0	0	0	0	0	0	

Supplementary Table 7 | Mean and median cladogenesis rates for each bin.

Computed using the results from the maximum parsimony analysis.

	Const_mean	Const_median	Const_5%	Const_95%	Unconst_mea	Unconst_media	Unconst_5%	Unconst_95
					n	n		%
Tur	0	0	0	0	0	0	0	0
Cen	0	0	0	0	0	0	0	0
U_Alb	0	0	0	0	0.000333333	0	0	0
M_Alb	0.0176666667	0	0	0	0.0226666667	0	0	0
L_Alb	0.164333333	0	0	1	0.166333333	0	0	1
U_Apt	0.464	0	0	2	0.476	0	0	2
L_Apt	0.3886666667	0	0	1	0.392333333	0	0	1
Bar	0.674	1	0	2	0.654333333	1	0	2
Hau	0.632666667	0	0	2	0.588	0	0	2
Val	1.256333333	1	0	3	1.218	1	0	3
Ber	0.875333333	1	0	2	0.887	1	0	2
Tit	1.2976666667	1	0	3	1.273	1	0	3
Kim	1.303333333	1	0	3	1.3466666667	1	0	3
Oxf	1.456333333	1	0	3	1.463666667	1	0	3
Cal	0.615	0	0	2	0.570333333	0	0	2
Bat	0.525333333	0	0	2	0.534333333	0	0	2
Baj	0.467333333	0	0	2	0.473	0	0	2
Aal	1.065333333	1	0	3	1.0736666667	1	0	3
Тоа	2.700333333	3	0	5	2.753	3	1	5
Pli	2.456333333	2	0	5	2.483333333	2	0	5
Sin	2.5546666667	2	0	5	2.522	2	0	5
Het	0.639666667	0	0	2	0.645333333	0	0	2
Rhe	1.385	1	0	3	1.381333333	1	0	3
U_Nor	1.921333333	2	0	4	1.891666667	2	0	4
M_Nor	1.596333333	1.5	0	4	1.606333333	1	0	4
L_Nor	3.198333333	3	1	6	3.2	3	1	6
Car	2.885666667	3	1	5	2.915333333	3	1	5
Lad	1.391666667	1	0	3	1.408333333	1	0	3
Ani	1.385333333	1	0	3	1.389	1	0	3
Ole	1.428666667	1	0	3	1.402333333	1	0	3
Ind	0.253333333	0	0	1	0.262333333	0	0	1

Supplementary Table 8 | Mean and median cladogenesis rates.

Using the results (1000 posterior trees randomly sampled in each run, total of 3000 trees for each analysis) from the constrained and unconstrained Bayesian inference of phylogeny.
	Mean_const	Const_05	Const_95	Mean_unconst	Unconst_05	Unconst_95
Tur	NA	NA	NA	NA	NA	NA
Cen	0.682754	4.00E-06	1.528389	0.663055	4.00E-06	1.522824
U_Alb	0.716906	0.1045845	1.4496345	0.753216	0.053324	1.6652415
M_Alb	0.7159955	0.0522965	1.56776675	0.7532165	0.0266625	1.75057925
L_Alb	0.7633372	0.1225176	1.5704762	0.8371392	0.072099	1.8795408
U_Apt	0.729599286	0.087512857	1.621734857	0.815193167	0.060082667	1.8971625
L_Apt	0.725390375	0.0955945	1.6354485	0.791801556	0.040074111	1.876763778
Bar	0.843733917	0.099521417	1.940768583	0.824172	0.060258	1.923865833
Hau	0.886361909	0.108567364	2.001046091	0.825717769	0.055622846	1.921007308
Val	0.92093425	0.099520167	2.174381167	0.825717769	0.055622846	1.921007308
Ber	0.8403883	0.119424	1.9002227	0.825717769	0.055622846	1.921007308
Tit	0.994929333	0.076591867	2.479888667	0.859543722	0.040172389	2.085857889
Kim	1.043872538	0.093116231	2.518166308	0.860652667	0.040163222	2.086034111
Oxf	1.133720308	0.116077308	2.682957462	0.934161389	0.060416222	2.186590889
Cal	1.2733842	0.100600533	3.019271	0.955613	0.0543747	2.25805155
Bat	1.252741818	0.108664091	2.817428909	0.959618053	0.050222053	2.272890895
Baj	1.254887167	0.115080167	2.797144417	0.966413762	0.045439143	2.285317238
Aal	1.208743538	0.112778154	2.680774231	0.965792136	0.043373773	2.3035995
Тоа	1.163058	0.10626355	2.76963225	1.073937889	0.0560715	2.499881444
Pli	1.342159313	0.103623063	3.236045563	1.150050471	0.059369765	2.662828294
Sin	1.364899077	0.127535615	3.351071538	1.295151875	0.063080313	3.089749625
Het	1.588552733	0.1136834	4.2091656	1.250321938	0.072162875	2.940938188
Rhe	2.098113467	0.113683533	5.7586372	1.241133412	0.067918059	2.932373412
U_Nor	1.98252875	0.1099825	5.470389833	1.290443133	0.072925	3.028871933
M_Nor	1.240538583	0.111171417	3.315729333	1.265909688	0.068367313	2.969748875
L_Nor	1.554817077	0.084344769	4.341444692	1.866992474	0.057573632	4.764909789
Car	1.9090909	0.0601348	5.3759116	2.465652385	0.056103	6.759598692
Lad	1.779416	0.0369234	5.3052644	2.3741406	1.60E-06	6.8868954
Ani	1.508123667	0.030769833	5.029193667	2.617428571	1.43E-06	8.506329143
Ole	0.934651	1.00E-06	3.9287715	1.393607	1.00E-06	5.903716
Ind	NA	NA	NA	NA	NA	NA

Supplementary Table 9 | Evolutionary rates.

Mean values and 95% confidence interval. These are the morphological clock rates, for each bin, arising from the constrained and unconstrained Bayesian inference of phylogeny.

	Extinction	Per_lineage_extinction	Turnover_est
Tur	0	NA	0
Cen	5	100.00%	5
U_Alb	4	50.00%	4
M_Alb	0	0.00%	0
L_Alb	2	25.00%	2
U_Apt	0	0.00%	0
L_Apt	3	35.29%	3.5
Bar	4	32.00%	4
Hau	1	10.00%	3.5
Val	1	9.09%	2.833333333
Ber	2	17.39%	3
Tit	8	45.71%	8.833333333
Kim	0	0.00%	3.75
Oxf	1	10.53%	4.416666667
Cal	0	0.00%	0.6666666667
Bat	0	0.00%	3
Baj	3	40.00%	3.5
Aal	1	18.18%	4
Тоа	5	62.50%	7
Pli	2	25.00%	3.5
Sin	1	11.76%	1.5
Het	0	0.00%	0.5
Rhe	0	0.00%	4.25
U_Nor	0	0.00%	1.75
M_Nor	1	40.00%	1.5
L_Nor	1	40.00%	2
Car	0	0.00%	0.5
Lad	0	0.00%	0.5
Ani	1	50.00%	1
Ole	0	0.00%	1

Supplementary Table 10 | Extinction and turnover rates per bin.

Values claculated at the top boundary of each bin. The relative extinction (per lineage extinction) rate is the percentage of the total diversity estimate going extinct during that bin. The estimated turnover rate (turnover_est) is the sum of the mean cladogenesis rate and the extinction rate.

	Late Albian	Basal	Early	Mid	Late
		Cenomanian	Cenomanian	Cenomanian	Cenomanian
Lineages	7	5	3-4	2-3	1
Extinction	3	2	1	2	1
Per lineage extinction	0.42	0.4	0.25	0.6	1

Supplementary Table 11 | Diversity dynamics for the Albian–Cenomanian interval.

	Data sources	Tooth	Crown	Crown	Symphysis	Snout	Sclerotic	Wear
		size	shape	relative size		depth	aperture	
Ophthalmosaurus_icenicus	HM V1129 ²⁵	37.3	1.66	0.16	53.05	0.54	71.1	NA
Ophthalmosaurus_natans	^{26,27} ; CM 603	29	2.35	0.14	NA	0.54	100	NA
Mollesaurus_perialus	28	20	NA	0.08	NA	NA	70.6	NA
Acamptonectes_densus	GLAHM 13285	5 NA	2.66	0.17	NA	0.44*	NA	NA
	(*=SNHM1284-R)							
Brachypterygius_extremus	²⁵ , CAMSMJ68516	53.4	1.54	0.26	NA	0.8	NA	NA
Aegirosaurus_leptospondylus	²⁹ , (*=RGHP LA 1)	26*	1.4*	NA	NA	0.62	32.76	1.5*
Sveltonectes_insolitus	IRSNB R129	19	2.86	0.12	50.6	0.47	34.4	1.2
Simbirskiasaurus_birjukovi	YKM 65119	NA	1.91	0.26	NA	NA	NA	2
Platypterygius_australis	30-32	55	1.65	0.31	40	0.48	31.5	NA
Pervushovisaurus_bannovkensis	SSU 104a/24	60	1.49	NA	NA	NA	NA	NA
Platypterygius_hercynicus	³³ , MNHN2010	50	1.51	0.22	0.51	NA	NA	NA
Platypterygius_americanus	UW 2421 (³⁴ and	i NA	1.63	0.23	50.8	0.43	51	NA
	photographs)							
Platypterygius_sachicarum	DON-19671 (³⁵ and	1 40	1.53	NA	NA	0.49	NA	2.3
	photographs)							
Sisteronia_seeleyi	CAMSM TN1779	33.8	1.75	0.2	NA	NA	NA	1.7
Platypterygius_spEurope	RGHP PR1	55	1.91	NA	NA	NA	NA	2.4

Supplementary Table 12 | Ecological data for selected Ophthalmosauridae.

The values are rounded to the nearest % for visual purposes; the precise values can be found

in "Supplementary data 7 ecodata.txt".

Specimen	Material	Assignation	Locality
NHMUK 33245	4 teeth (Kiprijanoff	'Platypterygius' sp.	Kursk
	collection)		
NHMUK 33245	Tooth (Kiprijanoff	cf. Sisteronia	Kursk
	collection)		
SSU 14/8 137/176	Interclavicle	Ichthyosauria indet.	Stoilensky quarry
SSU 14/8 137/177	Interclavicle	Ichthyosauria indet.	Stoilensky quarry
SSU 14/5 137/174	Centrum	Ichthyosauria indet.	Stoilensky quarry
SSU 14/6 137/152,54	Centra	Ichthyosauria indet.	Stoilensky quarry
SSU GPV 2/xx	9 teeth	'Platypterygius' sp.	Stoilensky quarry
partim			
SSU GPV 2/ partim	5 teeth	Cf. Sisteronia	Stoilensky quarry
SSU GPV 2/ partim	2 teeth	Cf.	Stoilensky quarry
		Ophthalmosaurinae	
SSU GPV 2/ partim	14 teeth	Ichthyosauria indet.	Stoilensky quarry
SSU 14/37	Left humerus	Cf.	Stoilensky quarry
		Ophthalmosaurinae	
SSU 14/37 837/46	Left humerus	Cf.	Late Albian of the
		Ophthalmosaurinae	Krasny Tekstilshik
			locality (Saratov
			region)
SSU 14/44 137/122	Left femur	'Platypterygius' sp.	Cenomanian of the
			Pudovkino locality
			(Saratov region),
			reworked in a
			Turonian deposit

Supplementary Table 13 | Cretaceous ichthyosaur from Russia studied here.

All specimens are from the Early-Late Cretaceous boundary.

Specimen	Material	Assignation	Locality
CAMSM	Tooth	Platypterygiinae indet.	Hunstanton
B20643		(holotype of <i>I. angustidens</i>)	
CAMSM	Tooth	P. campylodon (syntype,	Cambridge area
B20644		Carter's series)	
CAMSM	Tooth	P. campylodon (syntype,	Cambridge area
B20645		Carter's series)	
CAMSM	Tooth	P. campylodon (syntype,	Cambridge area
B20646		Carter's series)	
CAMSM	Tooth	P. campylodon (syntype,	Cambridge area
B20647		Carter's series)	
CAMSM	Tooth	P. campylodon (syntype,	Cambridge area
B20648		Carter's series)	
CAMSM	Tooth	P. campylodon (syntype,	Cambridge area
B20649		Carter's series)	
CAMSM	Tooth	P. campylodon (syntype,	Cambridge area
B20650		Carter's series)	
CAMSM	Tooth	P. campylodon (syntype,	Cambridge area
B20651		Carter's series)	
CAMSM	Tooth	P. campylodon (syntype,	Cambridge area
B20652		Carter's series)	
CAMSM	Tooth	P. campylodon (syntype,	Cambridge area
B20653		Carter's series)	
CAMSM	Tooth	P. campylodon (syntype,	Cambridge area
B20654		Carter's series)	
CAMSM	Tooth	P. campylodon (syntype,	Cambridge area
B20655		Carter's series)	
CAMSM	Tooth	P. campylodon (syntype,	Cambridge area
B20656		Carter's series)	
CAMSM	Tooth	P. campylodon (syntype,	Cambridge area
B20657		Carter's series)	
CAMSM	Tooth	P. campylodon (syntype,	Cambridge area

Supplementary Table 14 | Important ichthyosaurs from the British Cenomanian.

B20658		Carter's series)	
CAMSM	Partial rostrum	P. campylodon (syntype,	Cambridge area
B20659		Carter's series)	
CAMSM	Rostrum	'Platypterygius' sp.	Barrington
B20671			
CAMSM	Atlas-axis	Ichthyosauria indet.	Cambridge area
B75736			
CAMSM	Centrum	Ichthyosauria indet.	Hunstanton
B42257			
CAMSM	Humerus (HM1	'Platypterygius' sp.	Cambridge area
unnumbered	morphotype of Fischer		
	et al. ³⁶		
NHMUK 5648	Teeth	'Platypterygius' sp.	?
NHMUK	Teeth	'Platypterygius' sp.	Isleham,
33294 partim			Cambridgeshire
NHMUK	Anterior tip of rostrum	'Platypterygius' sp.	?
41367			
NHMUK	Anterior tip of rostrum	'Platypterygius' sp.	?
41895			
NHMUK R13	Teeth	'Platypterygius' sp.	?
NHMUK R49	Teeth	'Platypterygius' sp.	Lyden Spout,
			Folkestone
NHMUK	Rostrum	'Platypterygius' sp.	?
R2335			
NHMUK	Fragmentary rostrum	'Platypterygius' sp.	?
R2385			

We surveyed the entire Cenomanian collections of both the CAMSM and the NHMUK, but only listed important specimens; unlisted remains include centra, undeterminable skeletal fragments and isolated teeth. The specimens studied here belong to the 'Lower Chalk', which corresponds to the Grey Chalk Subgroup (Chalk Group), above the Cambridge Greensand Member. We found no compelling evidence for the presence of radically distinct species in this deposit, notably in terms of tooth shape and inferred ecological niche.

	meta.Col	meta.Occ	meta.Fm	vert.Coll	vert.Occ	vert.Fm	aqua.Coll	aqua.Occ	aqua.Fm
	1								
Tur	296	1283	56	20	24	10	8	22	5
Cen	1366	7294	175	140	471	58	129	406	51
U_Alb	616.8	3201.2	82	45.6	167.6	23.6	26.4	106.8	12.4
M_Al	283.728	1472.552	37.72	20.976	77.096	10.856	12.144	49.128	5.704
b									
L_Alb	641.472	3329.248	85.28	47.424	174.304	24.544	27.456	111.072	12.896
U_Apt	626	2878	93.33333333	22.666666667	45.33333333	11.33333333	25.3333333	66	19.33333333
							3		
L_Apt	313	1439	46.66666667	11.33333333	22.666666667	5.666666667	12.6666666	33	9.666666667
							7		
Bar	508	2155	63	10	36	5	23	60	19
Hau	651	2607	57	24	38	15	20	41	14
Val	736	2859	73	10	33	4	34	50	20
Ber	441	1906	60	67	241	31	52	150	29

Supplementary Table 15 | Sampling metrics used in this paper.

Number of collections, number of occurrences and number of formations for (i) all metazoans in marine setting, (ii) all vertebrates in marine settings, (iii) main aquatic vertebrates (Ichthyosauria, Plesiosauria, Actinopterygii, Actinistia, Dipnoi, Chondrichthyes, Chelonioidea, Mosasauroidea, Dolichosauridae, Pholidosauridae, Hesperornithes) in all settings. These were downloaded from the Paleobiology Database on the 24-25/03/15.

	Mean_long	Var_long	Mean_shor	Var_short	Prok_d180	Prok_d180_	Mart_SST	Mart_SST	Prok_d13C	Prok_d13C
			t			var		_var		_var
Tur	245.54565	88.611055	201.90563	478.93468	-	2.17061674	32.2375	19.895625	3.30876712	1.53856455
		77	87	41	3.21045751	9			3	
					6					
Cen	237.49409	54.009339	192.45880	1205.8337	-	4.38208939	26.95	25.272	3.27355932	0.95752294
	01	37	67	66	2.47406779	4			2	4
					7					
U_	212.23961	335.31163	172.90534	1014.1334	-	0.09211026	24.041875	11.003813	1.71403846	0.51511052
Alb	71	53	89	63	0.91096153	3		84	2	6
					8					
M_	170.81151	29.926901	136.56781	233.09926	-0.165625	0.57116060	24.041875	11.003813	1.371875	0.65775454
Alb	32	02	26	89		6		84		5
L_A	148.60479	29.129721	105.56089	927.75055	-	0.55670666	24.041875	11.003813	2.35222222	0.71466952
lb	23	03	38	08	0.44266666	7		84	2	4
					7					
U_	140.59348	4.0829836	104.09553	645.62245	-2	0.149	20.752272	7.0810568	4.95833333	0.24241666
Apt		64	43	91			73	18	3	7
L_A	151.12760	9.9312801	112.50271	362.29298	-2.325	0.66125	20.752272	7.0810568	3.35	2.645
pt	91	33	2	13			73	18		
Bar	162.29746	12.912409	112.15844	495.95911	-	0.37017831	21.55	0.81	1.01016923	0.65131784
	58	72	34	62	0.62156923	3			1	3
					1					
Hau	152.66057	200.36687	119.50145	615.26078	0.35837349	0.17403034	19.6375	8.285625	1.09380368	0.38082339
	27	24	59	66	4	5			1	9
Val	92.959089	207.59072	68.734862	394.25355	-	0.44640011	20.8975	9.3501259	0.50402965	0.75075317
	68	01	29	96	0.04273584	2		62		1
					9					
Ber	121.04137	27.039011	91.951696	603.62262	-	1.02660505	21.4825	31.720612	0.45040322	1.28149195
	93	55	55	94	1.22403225	7		5	6	4
					8					

Supplementary Table 16 | Environmental metrics used in this paper.

From left to right: (i) mean value of the long term sea level curve (all sea level data from a digitized version of Haq³⁷); (ii) variance of the long term sea level curve; (iv) mean value of the short term sea level curve; (ii) variance of the short term sea level curve; (v) weighted mean d¹⁸O value (all isotopic values from Prokoph et al.³⁸), (vi) variance of d¹⁸O values; (vii) mean sea surface temperatures from Martin et al.³⁹; (viii) variance of the sea surface temperatures from Martin et al.³⁹; (viii) variance of the d13C value.

Full dataset			Early Cretaceou	s dataset	
Correlation	Pearson	p value	Correlation	Pearson	p value
	coefficient			coefficient	
Sum of	0.634	0.036	Observed	0.743	0.022
Variances			diversity ~		
(equal) ~ Long			Mean long-term		
term eustatic			eustasy		
variance					
Sum of	-0.622	0.041	Observed	0.698	0.037
Variances			diversity ~		
(equal) ~			Mean short-		
Prokoph d13C			term eustasy		
Evolutionary	-0.739	0.009	Sum of	0.679	0.044
rate			Variances		
(constrained) ~			(equal)~ Long		
Martin Sea			term eustatic		
surface			variance		
temperature					
Evolutionary	-0.831	0.002	Sum of	-0.685	0.042
rate			Variances		
(unconstrained)			(equal)~		
~ Martin Sea			Prokoph d13C		
surface					
temperature					
Extinction rate	0.612	0.045			
~ Short term					
eustatic					
variance					
Per capita	0.742	0.014			
extinction rate					
~ Short term					
eustatic					
variance					
Per capita	0.815	0.004			
extinction rate					
~ Prokoph d180					
variance					
Per capita	0.644	0.045			
extinction rate					

Supplementary Table 17 | Results of pairwise correlations tests with a ≥ 0.05 p value.

~ Metazoan				
Collections				
Per capita	0.706	0.022		
extinction rate				
~ Metazoan				
Occurrences				
Per capita	0.652	0.041		
extinction rate				
~ Metazoan				
Formations				
Per capita	0.796	0.006		
extinction rate				
~ Vertebrate				
Collections				
Per capita	0.821	0.004		
extinction rate				
~ Vertebrate				
Occurrences				
Per capita	0.787	0.007		
extinction rate				
~ Vertebrate				
Formations				
Per capita	0.755	0.012		
extinction rate	0.722	0.012		
~ Aquatic				
Callections				
Collections	0.005	0.005		
Per capita	0.805	0.005		
extinction rate				
~ Aquatic				
vertebrate				
Occurrences				
Per capita	0.739	0.015		
extinction rate				
~ Aquatic				
vertebrate				
Formations				
Origination rate	-0.604	0.049		
~ Martin Sea				
surface				

temperature			

Model	AICc	AICc	\mathbf{R}^2	Phi	Slope	Slope n	Intercent
	inht		IX.	1	blope	slope p	intercept
	weight	score				value	
Observed diversity ~ 1	0.323	49.5707	0	0.358	NA	NA	3.027
Observed diversity ~ Prokoph	0.159	50.9884	0.138	0.269	-0.4	0.647	3.464
d13C variance							
Observed diversity ~ Prokoph	0.144	51.1855	0.123	0.43	0.483	0.452	3.612
d180							
Observed diversity ~ Prokoph	0.127	51.4393	0.102	0.534	-	0.361	3.897
d13C					0.483		
Observed diversity ~ Prokoph	0.087	52.1855	0.039	0.355	0.048	0.926	2.979
d180 variance							
Observed diversity ~ Martin	0.069	52.66	-	0.654	-	0.248	9.911
Sea surface temperatures			0.003		0.296		
Phylogenetically adjusted	0.261	53.3441	0.293	-	-0.84	0	27.529
diversity ~ Martin Sea surface				0.048			
temperatures							
Phylogenetically adjusted	0.203	53.8523	0.26	1	-0.93	0.13	7.498
diversity ~ Prokoph d13C							
Phylogenetically adjusted	0.179	54.1021	0	1	NA	NA	5.75
diversity ~ 1							
Phylogenetically adjusted	0.156	54.3698	0.224	1	0.931	0.247	7.814
diversity ~ Prokoph d180							
Phylogenetically adjusted	0.106	55.1395	0.168	1	-	0.451	6.645
diversity ~ Prokoph d13C					0.634		
variance							
Phylogenetically adjusted	0.053	56.5222	0.056	1	-	0.902	5.863
diversity ~ Prokoph d180					0.071		
variance							
Sum of variances (basic) ~	0.209	51.4935	0.271	0.655	-	0.176	8.408
Prokoph d13C					0.995		
Sum of variances (basic) ~ 1	0.198	51.6007	0	0.624	NA	NA	6.494
Sum of variances (basic) ~	0.175	51.8515	0.245	0.577	0.991	0.329	7.711
Prokoph d180							
Sum of variances (basic) ~	0.155	52.0917	0.226	0.648	-	0.444	7.255
Prokoph d13C variance					0.843		
Sum of variances (basic) ~	0.122	52.5758	0.188	0.504	-	0.319	7.465
Prokoph d180 variance					0.723		
Sum of variances (basic) ~	0.081	53.3802	0.12	0.236	-	0.159	22.274

Supplementary Table 18. Best models (AICc weight > 0.1 * weight of the best model).

Martin Sea surface temperatures					0.687		
Sum of variances (equal) ~	0.265	44.9348	0.285	1	-0.8	0.097	9.678
Prokoph d13C							
Sum of variances (equal) ~ 1	0.228	45.2343	0	1	NA	NA	8.188
Sum of variances (equal) ~	0.177	45.7424	0.225	1	0.799	0.223	9.664
Prokoph d180							
Sum of variances (equal) ~	0.091	47.0624	0.116	1	-	0.376	9.392
Prokoph d180 variance					0.445		
Sum of variances (equal) ~	0.081	47.2906	0.095	1	0.001	0.999	8.187
Prokoph d13C variance							
Sum of variances (equal) ~	0.054	48.1253	0.016	1	-	0.855	10.191
Martin Sea surface temperatures					0.083		
Sum of variances (equal) ~	0.028	49.4614	-	1	-	0.154	11.23
Martin Sea surface temperatures			0.124		0.107		
variance							
Cladogenesis rate (Max Parsim)	0.55	31.1244	0	0.583	NA	NA	0.524
~ 1							
Cladogenesis rate (Max Parsim)	0.145	33.7918	0.035	0.479	0.297	0.243	0.922
~ Prokoph d180							
Cladogenesis rate (Max Parsim)	0.09	34.746	-	0.554	0.044	0.889	0.479
~ Prokoph d13C variance			0.053				
Cladogenesis rate (Max Parsim)	0.065	35.4009	-	0.474	-	0.605	0.754
~ Prokoph d13C			0.117		0.109		
Cladogenesis rate (Max Parsim)	0.061	35.523	-0.13	0.54	-0.07	0.729	0.601
~ Prokoph d180 variance							
Cladogenesis rate (Max Parsim)	0.057	35.6535	-	0.539	-0.11	0.233	3.157
~ Martin Sea surface			0.143				
temperatures							
Cladogenesis rate (Bayesian,	0.758	8.7123	0	1	NA	NA	0.438
constrained) ~ 1							
Cladogenesis rate (Bayesian,	0.761	8.281	0	1	NA	NA	0.443
unconstrained) ~ 1							
Evolutionary rate (constrained)	0.741	-19.9549	0	0.971	NA	NA	0.764
~ 1							
Evolutionary rate (constrained)	0.195	-17.2796	0.037	0.984	0.038	0.012	0.831
~ Prokoph d180							
Evolutionary rate	0.875	-24.3286	0	1	NA	NA	0.744
(unconstrained) ~ 1							
Extinction rate~ 1	0.324	48.8026	0	-	NA	NA	2.013

				0.076			
Extinction rate~ Prokoph d13C	0.171	50.0817	0.149	-	0.432	0.633	1.615
variance				0.106			
Extinction rate~ Prokoph d180	0.154	50.2922	0.133	-0.09	0.51	0.256	1.528
variance							
Extinction rate~ Prokoph d180	0.093	51.3061	0.049	-	-	0.693	1.774
				0.061	0.201		
Extinction rate~ Prokoph d13C	0.072	51.8168	0.004	0.021	-	0.786	2.244
					0.117		
Extinction rate~ Aquatic	0.045	52.7498	-	-	0.079	0.07	0.593
vertebrates Formations			0.084	0.071			
Extinction rate~ Vertebrates	0.03	53.5743	-	0.05	0.062	0.082	0.871
Formations			0.169				
Per capita extinction rate ~	0.4	9.8152	0.294	-	0.22	0.002	0.098
Prokoph d180 variance				0.291			
Per capita extinction rate ~ 1	0.322	10.2471	0	0.928	NA	NA	0.501
Per capita extinction rate ~	0.107	12.458	0.081	0.54	0.111	0.026	-2.19
Martin Sea surface temperatures							
Per capita extinction rate ~	0.048	14.0426	-	0.551	-	0.132	0.165
Prokoph d180			0.077		0.151		
Origination rate ~ 1	0.466	36.263	0	0.817	NA	NA	0.953
Origination rate ~ Martin Sea	0.17	38.276	0.09	1	-	0.076	7.08
surface temperatures					0.264		
Origination rate ~ Prokoph	0.096	39.4181	-	0.786	0.179	0.606	1.323
d180			0.009				
Origination rate ~ Prokoph	0.09	39.5586	-	0.772	-	0.986	1.077
d13C variance			0.022		0.007		
Origination rate ~ Prokoph	0.069	40.0822	-	0.828	-	0.775	1.077
d13C			0.072		0.078		
Origination rate ~ Prokoph	0.06	40.3645	-0.1	0.775	-	0.914	1.094
d180 variance					0.027		
Turnover rate ~ 1	0.326	48.884	0	0.004	NA	NA	2.53
Turnover rate ~ Prokoph d13C	0.16	50.3099	0.138	-	0.279	0.757	2.269
variance				0.006			
Turnover rate ~ Prokoph d13C	0.126	50.786	0.1	0.006	-	0.302	3.438
					0.427		
Turnover rate ~ Prokoph d180	0.107	51.1149	0.072	0.09	0.355	0.466	2.166
variance							
Turnover rate ~ Prokoph d180	0.1	51.2441	0.061	0.078	0.237	0.667	2.799

Turnover rate ~ Aquatic	0.046	52.7789	-	-	0.08	0.067	1.104
vertebrates Formations			0.079	0.056			
Turnover rate ~ Martin Sea	0.044	52.8788	-	0.145	-	0.366	6.307
surface temperatures			0.089		0.163		

Results from generalised least squares regressions incorporating a first-order autoregressive model, using the full dataset. Other variables were tested and resulted in models with negligible AICc-weights (see Supplementary Data 9 GLS_results).

Model	AICc	AICc	R^2	Phi	Slope	Slope p	Intercept
	weight	score				value	
Observed diversity ~ 1	0.603	42.1942	0	0.839	NA	NA	4.227
Observed diversity ~ Martin	0.121	45.4141	0.357	0.255	0.796	0.029	-14.03
Sea surface temperatures							
Phylogenetically adjusted	0.65	44.7324	0	0.69	NA	NA	9.36
diversity ~ 1							
Phylogenetically adjusted	0.093	48.6306	0.307	0.629	0.657	0.759	9.011
diversity ~ Prokoph d180							
variance							
Phylogenetically adjusted	0.087	48.7631	0.297	0.609	-	0.119	10.695
diversity ~ Prokoph d13C					0.827		
Sum of variances (basic) ~ 1	0.631	50.9365	0	0.508	NA	NA	7.15
Sum of variances (basic) ~	0.13	54.0948	0.362	0.486	-	0.994	7.176
Prokoph d180 variance					0.025		
Sum of variances (equal) ~ 1	0.693	45.3157	0	1	NA	NA	9.213
Sum of variances (equal) ~	0.094	49.3111	0.3	1	0.055	0.979	9.182
Prokoph d180 variance							
Cladogenesis rate (Max Parsim)	0.802	32.2745	0	0.552	NA	NA	0.616
~ 1							
Cladogenesis rate (Bayesian,	0.931	14.3994	0	1	NA	NA	0.438
constrained) ~ 1							
Cladogenesis rate (Bayesian,	0.934	14.0544	0	1	NA	NA	0.444
unconstrained) ~ 1							
Evolutionary rate (constrained)	0.96	-12.1583	0	0.893	NA	NA	0.784
~ 1							
Evolutionary rate	0.993	-21.1458	0	0.625	NA	NA	0.801
(unconstrained) ~ 1							
Extinction rate~ 1	0.747	42.2323	0	-	NA	NA	1.84
				0.234			
Extinction rate~ Prokoph d180	0.096	46.3391	0.291	-	-	0.913	1.936
variance				0.236	0.217		
Per capita extinction rate ~ 1	0.965	6.1419	0	-	NA	NA	0.188
				0.481			
Per capita extinction rate ~	0.014	14.6668	-	-	-	0.716	0.221
Prokoph d180 variance			0.159	0.463	0.074		
Origination rate ~ 1	0.826	32.4348	0	1	NA	NA	1.5
Turnover rate ~ 1	0.73	42.7738	0	0.118	NA	NA	2.565

Supplementary Table 19. Best models (AICc weight > 0.1 * weight of the best model)

Turnover rate ~ Prokoph d180	0.095	46.8532	0.293	0.102	0	1	2.561
variance							

Results from generalised least squares regressions incorporating a first-order autoregressive model, using the Early Cretaceous dataset. Other variables were tested and resulted in models with negligible AICc-weights (see Supplementary Data 9 GLS_results).

SUPPLEMENTARY NOTES

Supplementary note 1. Specimens considered in Figure 4 of the main paper.

(1) incorporates indeterminate ophthalmosaurines from the Late Albian of the Cambridge Greensand Member³⁶; (2) incorporates the large Late Albian platypterygiines of the Vocontian Basin (RGHP PR 1), from the Gault and Upper Greensand formations, from the Late Albian to earliest Cenomanian of the Cambridge Greensand Member³⁶, and from the Late Cenomanian of the Boulonnais⁴⁰. (3) incorporates indeterminate ophthalmosaurines from the Late Albian of Saratov region (SSU 14/37 837/46) and from the Albian–Cenomanian boundary of western Russia (see Supplementary Methods). (4) incorporates large platypterygiines from Stoilensky quarry and the Cenomanian of western Russia (see Supplementary Methods). (5) incorporates Early Cenomanian material from Texas (DMNH 11843⁴¹). (6) incorporates the Early Cenomanian specimen(s) mentioned by^{42,43}. (7) incorporates platypterygiine material from India (see Supplementary Methods below).

SUPPLEMENTARY METHODS

INSTITUTIONAL ABBREVIATIONS

The following institutional abbreviations are used: BRSMG, City of Bristol Museum and Art Gallery, Bristol, UK; CAMSM, Sedgwick Museum of Earth Sciences, Cambridge University, Cambridge, CM, Carnegie Museum of Natural History, Pittsburgh, PA, USA; UK; DON, Museo Geológico José Royo y Gómez del Instituto de Investigaciones en Geociencias, Minería y Química, Ingeominas, Colombia; GLAHM, The Hunterian Museum, University of Glasgow, Glasgow, UK; IRSNB, Royal Belgian Institute of Natural Sciences, Brussels, Belgium; LMR, Lyme Regis Museum, Lyme Regis, Dorset, UK; MGRI, Moscow Geological Prospecting Institute, Vernadskii State Geological Museum, Moscow, Russia; MHNH, Muséum d'Histoire Naturelle du Havre, Le Havre, France; MNHN, Muséum national d'Histoire naturelle, Paris, France; MJML, Museum of Jurassic marine life, Ashfield, Kimmeridge, Dorset, UK; MOZ, Museo Professor J. Olsacher, Dirección Provincial de Minería, Zapala, Neuquén, Argentina; NHMUK, Natural History Museum, London, UK; RGHP, Réserve naturelle géologique de Haute-Provence, Digne-les-Bains, France; SMNS, Staatliches Museum für Naturkunde Stuttgart, Stuttgart, Germany; SMSS, Städtisches Museum Schloss Salder, Salzgitter, Germany; SNHM, Staatliches Naturhistorisches Museum, Braunschweig, Germany; SSU, Geological Museum, Saratov State University, Saratov, Russia; U.W., University of Wyoming, Laramie, Wyoming; YKM, Ульяновский областной краеведческий музей им И.А. Гончарова [Ulyanovsk Regional Museum of Local Lore named after I.A. Goncharov], Ulyanovsk, Ulyanovsk Region, Russian Federation.

REVISED TAXONOMY OF CRETACEOUS ICHTHYOSAURS FROM EURASIA

Species taxonomically revaluated here are marked with asterisks and taxa incorporated in our phylogenetic analysis are written in bold.

Valid taxa

Ichthyosauria Blainville, 1835⁴⁴ Thunnosauria Motani, 1999⁴⁵ *Malawania anachronus* Fischer et al., 2013⁴ Baracromia Fischer et al., 2013⁴ Ophthalmosauridae Baur, 1887⁴⁶ Ophthalmosaurinae Baur, 1887⁴⁶ sensu Fischer et al.³ Acamptonectes densus Fischer et al., 2012³ *Leninia stellans* Fischer et al., 2014⁴⁷ Platyptervgiinae Arkhangelsky, 2001⁴⁸ sensu Fischer et al.³ Caypullisaurus bonapartei Fernández, 1997⁴⁹ Simbirskiasaurus birjukovi Ochev & Efimov, 1985⁵⁰ Sveltonectes insolitus Fischer et al., 2011⁵¹ 'Platypterygius' hauthali Huene 1927⁵² *Platypterygius platydactylus* (Broili 1907)⁵³ 'Platypterygius' sachicarum Páramo, 1997³⁵ *Platypterygius' hercynicus* Kuhn, 1946³³ Athabascasaurus bitumineus Druckenmiller & Maxwell, 2010⁵⁴ Maiaspondylus lindoei Maxwell & Caldwell, 2006⁵⁵ 'Platypterygius' australis (M'Coy, 1867)⁵⁶ 'Platypterygius' americanus (Nace, 1939)⁵⁷ Sisteronia seeleyi Fischer et al., 2014³⁶ Cetarthrosaurus walkeri (Seeley, 1869)⁵⁸ 'Platypterygius' campylodon (Carter, 1846)⁵⁹ Pervushovisaurus bannovkensis Arkhangelsky, 1998⁶⁰

Invalid taxa

Cf. Acamptonectes: Ichthyosaurus brunsvicensis Broili, 1908⁶¹. See treatment in ³.

Ophthalmosauridae indet.: *Ichthyosaurus doughtyi* **Seeley, 1869**⁵⁸. See treatment in ³⁶.

Ophthalmosauridae indet.: *Delphinosaurus kiprijanoffi/kiprianoffii* Eichwald, 1853. Eichwald⁶² erected *Delphinosaurus kiprijanoffii* on remains (eight mandible fragments, twelve teeth, one rib, two centra, one humerus and one ulna) from the iron-rich sands of the Kursk area (Albian–Cenomanian boundary). He interpreted these remains as those of amphibians, because of the presence of dolphin and reptile features, suggesting an intermediate form in between these groups, hence the name. Nevertheless, he already recognized close affinities with "*Ichthyosaurus*" (see Eichwald, 1853) and he clearly listed *Delphinosaurus* as belonging to the "Ichthyosaures" family in his monograph (Eichwald, 1865).

There are numerous issues with the name *Delphinosaurus kiprijanoffii*. In Eichwald⁶², the specific name is written "*kiprijanoffii*", whereas it is written "*kiprianoffii*" in the 1865 monograph. This taxon became rapidly forgotten and later authors erected similar generic and specific names, sometimes on totally different material: Merriam ⁶⁴ erected *Delphinosaurus* as a new generic name for reception of the Carnian (Late Triassic) species *Ichthyosaurus perrini*⁶⁵. Kuhn⁶⁶ noted this generic name was preoccupied and proposed a new replacement name, *Californosaurus*, for the species *I. perrini*. The same year, Kuhn⁶⁷(p116) listed *Delphinosaurus kiprijanoffi* (with a single "i" at the end) as problematic taxon included within polycotylid plesiosaurs.

In parallel, Kiprijanoff described numerous remains of ichthyosaurs ("*Ichthyosaurus campylodon*") and plesiosaurs from the Lower Cenomanian phosphorite horizon^{68–71} (incorrectly considered as "Neocomian" in the literature⁷²). However, the horizon containing these specimens is a bone-bed similar and contemporaneous to the 'greensands' of western Europe; any supposedly articulated remains should therefore be considered with extreme caution. Romer³⁴ considered a skull reconstruction of *Ichthyosaurus campylodon* figured by Kiprijanoff⁶⁸ to be distinct from the British remains and erected the specific name "*kiprijanoffi*" (with a single "i" at the end), without first-hand examination of the material.

Both specific names *kiprijanoffi* and *kiprianoffii* have the same origin and etymology: they honour the Colonel W. Kiprijanoff for his research on the marine reptiles from the Albian–Cenomanian boundary phosphatic sand of the Kursk region, which started much before his 1880's publications. However, both these species have been erected independently and on different 'specimens' of Kiprijanoff's collection: isolated rostral fragments and postcranial skeleton for *Delphinosaurus kiprijanoffii* Eichwald, 1853 and a supposedly articulated skull for *Myopterygius kiprijanoffi* Romer, 1968.

The remains from Kursk Albian–Cenomanian sand are isolated in a bonebed-like deposit. There is a strong possibility that the remains of *D. kiprijanoffii* figured by Eichwald⁶³ (in Pl XXXVIII; XL) are actually a composite of the several taxa found in this deposit: some teeth are referable to cf. *Sisteronia*, because of their markedly rectangular cross-section of the root³⁶. The partial humerus shows the large trochanters unlike in *Sisteronia*³⁶ (and V.F. pers. obs. on new material from France) and the large radial and ulnar facets parallel to the sagittal plane. The "ulna" is an ophthalmosaurid epipodial element. Similarly, the articulated skull in Kiprijanoff⁶⁸ is most probably a composite, given the nature of their hosting sediments. Whereas the upper part of the Cambridge Greensand Member contains non-reworked early Cenomanian fossils³⁶, this has never been proved yet for the Kursk bone-bed. Accordingly,

Delphinosaurus kiprijanoffi and *Platypterygius kiprijanoffi* are considered here as a nomina dubia. The specimen referred to as *Platypterygius* cf. *kiprijanoffi* by Bardet⁴⁰ possesses large teeth whose roots have a squared cross-section. This material thus differs from the material figured by Eichwald⁶² and should not be assigned to *D./P. kiprijanoffi*.

Ichthyosauria indet.: *Ichthyosaurus hildesiensis* **Koken, 1883**. *Ichthyosaurus hildesiensis* is based on three isolated centra from the "Neocom" of two different localities (Hildesheim and Braunschweig), and a fragmentary snout with a few teeth from Braunschweig⁷³. The material is indeterminate, and considered here as Ichthyosauria indet.

Ichthyosauria indet.: *Ichthyosaurus kurskensis* **Gutzeit**, **?** Both Eichwald⁶² and Meyer⁷⁴ cited "H. Gutzeit" as the authority for the name *I. kurskensis*, but were unable to provide a reference of a paper by Gutzeit to support this claim. Accordingly, the first mention of that name is found in Eichwald⁶² and Storrs et al.⁷⁵ cited indeed Eichwald, 1853 as the authority of this species. The species is established on large teeth and a large centrum, apparently found together in the "Iron sand" from the Kursk area (western Russia). As will be discussed above, this deposit is reworked; the claim of articulated element is thus doubtful. Moreover, the elements described by Eichwald 1853 lack distinctive features and are to be considered as a nomen dubium and the material transferred to as Ichthyosauria indet.

Ichthyosauria indet.: *Ichthyosaurus polyptychodon* Koken, 1883. This taxon is based on a single partial skull and a few centra from the 'Speeton Clays' of the Hannover area (Germany), so it is likely to come from the same beds as one of the paratypes of *Acamptonectes densus*, SNHM 1284-R³. The external exposure of the maxilla is low and appears separated from the margin of the naris by the lacrimal and the premaxilla, unlike in the platypterygine ophthalmosaurids '*Platypterygius' australis* and *Athabascasaurus bitumineus*^{31,54}. The prefrontal does not contact the margin of the naris either, unlike in *Aegirosaurus* or *Sveltonectes*^{29,51}. The naris is incompletely preserved and the shape of its dorsal surface cannot be used from a taxonomic point of view. Only maxillary teeth are preserved. More than 10 maxillary teeth are present. The crown appears relatively small and blunt, which may be due to the slight heterodonty in ophthalmosaurids tooth rows. Koken⁷³ indicates that the teeth possess a square shaped cross-section, which may suggest platypterygine affinities, if genuine. In the absence of other evidence, this taxon is considered here as Ichthyosauria indet.

Ichthyosauria indet.: *Ichthyosaurus steleodon* Bogolubow, 1909. The Barremian strata of the Ulyanovsk region had already yielded ichthyosaur remains prior to *Sveltonectes insolitus* and *Simbirskiasaurus birjukovi*: these remains in questions where described by Bogolubow⁷⁶ as *Ichthyosaurus steleodon*. The type and only specimen comprises a fragmentary snout with poorly preserved teeth and a few centra. This material lacks diagnostic features but appears to be twice the size as the small platypterygiines *Sveltonectes insolitus* and *Simbirskiasaurus birjukovi*. Nevertheless, this material is considered here as Ichthyosauria indet. According to Storrs et al.⁷⁵, the holotype is housed at the Moscow Geological Prospecting Institute (Vernadskii State Geological Museum, Moscow, Russia). Rozhdestvenskiy¹¹ considers this material as Late Jurassic in age.

Ichthyosauria indet.: *Ichthyosaurus strombecki* Meyer, 1862. *Ichthyosaurus strombecki* is based on an incomplete teeth-bearing rostrum from Lower Cretaceous of the Braunschweig area (Germany, same locality as *Acamptonectes densus*). The specimen lacks diagnostic features, but Meyer⁷⁴ describes the teeth as having a rounded to oval cross-section, presumably throughout, suggesting affinities with Ophthalmosaurinae or *Aegirosaurus*^{3,19,77}. However, only the cross-section of the root may have a taxonomic value and Meyer does not mention where he observed that rounded cross-section. The specimen otherwise lacks other diagnostic features. Accordingly, it is considered here as Ichthyosauria indet.

Ichthyosauria indet.: *Gavialis vassiacensis* **Cornuel, 1851.** Cornuel⁷⁸ described a fossil from the Hauterivian of Haute-Marne (France) that he identified as a gavial and proposed the name "*vassiacensis*" for this specimen if it turned to be a new species. This specimen is actually a fragmentary ichthyosaur snout and Cornuel then recognized his mistake⁷⁹. The snout is thin and tubular. The rostrum and the mandible are semi-circular in cross-section and the bones are thick. There is no trace of the lateral fossae, but the dental grooves form pseudo-alveoli⁷⁸. The teeth are conical, elongated and appear to be less than 20 mm high. Only the crown is ridged⁷⁸. This material is too scant and lacks diagnostic features to be identify more precisely than Ichthyosauria indet. It is unclear whether this material or some other was used as part of a composite specimen considered as the holotype of the iguanodontid dinosaur *Heterosaurus neocomensis* by Cornuel⁸⁰. Lapparent & Stchepinsky⁸¹ found evidence for remains belonging to plesiosaurs, *Iguanodon*, and ichthyosaur in the holotype series.

Vertebrata Indet.: *Plesiosaurus nordmanni* Eichwald, 1865. This taxon is based on fragmentary propodial from the 'Neocomian' of Crimea, Russia, originally considered as plesiosaurian by Eichwald⁶³. However, both Ryabinin (1946 see Storrs et al.⁷⁵) and Storrs et al.⁷⁵ regarded it as indeterminate ichthyosaur. The material was figured by Eichwald⁶³ and cannot be determined more precisely than Vertebrata indet.

Species inquirenda: *Plutoniosaurus bedengensis* Efimov, 1997. Efimov⁸² reported a new stenopterygiine ichthyosaur from the Speetoniceras versicolor Zone (upper Hauterivian) of the Ulyanovsk area, for which he proposed a new genus and species, Plutoniosaurus bedengensis. Maisch & Matzke⁸³ assigned *Plutoniosaurus bedengensis* to *Platypterygius* on the basis of several shared features, including the high number of digits (including anterior and posterior accessory digits), the tight mosaic formed by the phalanges, the presence of a preaxial accessory epipodial element, the large trochanter dorsalis of the humerus and the rectangular cross-section of the roots. All these features are now known to be widespread in a clade of ophthalmosaurids, Platypterygiinae. Additional features support this assignation, such as the seemingly strongly reduced extracondylar area of the basioccipital, the unnotched coracoids, and the reduced naris⁸⁴. The material seems well preserved, but Efimov⁸² only provides 'idealized' and highly simplified drawings of the specimen. These drawings suggest highly unusual features for P. bedengensis, including wide frontals with large temporalis process that are excluded from the temporal fenestra; a lacrimal forming the entire margin of the naris, even anteriorly; teeth with extremely reduced and rounded roots but are described by Efimov⁸² as having a subrectangular cross-section. Moreover, the description is succinct and emphasizes features common in post-Triassic ichthyosaurs. Accordingly, the features of this taxon are to be taken with caution until a better redescription.

Plutoniosaurus bedengensis lacks trustworthy diagnostic features and is possibly a representative of the platypterygiine ophthalmosaurid *Simbirskiasaurus birjukovi*, from the same area and nearly coeval strata. Efimov⁸² indicated the nares of *Plutoniosaurus bedengensis* were different from *Simbirskiasaurus birjukovi*, but the holotype of *Simbirskiasaurus birjukovi* was described by Ochev & Efimov (1985) before preparation of the naris⁸⁴. Accordingly, *Plutoniosaurus bedengensis* is considered here as species inquirenda, and will not be counted as an additional platypterygiine taxon in diversity analyses. Examination of old photographs of the holotype of *Plutoniosaurus bedengensis* (I. Stenshin, pers. com. July 2015) indicates this taxon possesses a large frontal forming the

anteromedial margin of the supratemporal fenestra, as in Platypterygiinae; we found no notable morphological differences with the coeval taxon *Simbirskiasaurus birjukovi*.

Species inquirenda: *Ichthyosaurus ceramensis* **Martin, 1888.** Martin⁸⁵ described a moderately large ichthyosaur rostrum from the purported Cretaceous of the Seram Island (also known as Ceram) near Timor and New Guinea. The age of the Cretaceous shales of this area are said to be coeval with the Upper Greensand Formation of England and Utatúr Group in India in Martin's paper. The morphology of the teeth, however, appear similar to that of *Temnodontosaurus platyodon, T. trigonodon* or even large specimens of *Ichthyosaurus communis*^{86–88}, with the presence of numerous continuous apicobasal ridges extending from the top of the crown to the root and a reduced to absent distinct layer of acellular cementum. These features markedly contrast with known ophthalmosaurids^{89,90}. Accordingly, while *I. ceramensis* cannot be considered as a nomen dubium, it is regarded here as a nomen inquirendum, and will not be counted as a valid species in this work, because the morphological and stratigraphic evidence considering this taxon as a distinct Cretaceous species is too scant.

Species inquirenda: *Platypterygius ochevi* **Arkhanglesky et al., 2008.** Arkhangelsky et al.⁹¹ reported a new species, *Platypterygius ochevi*, from Albian–Cenomanian boundary glauconitic sands of the Voronezh area, in between Saratov and Kursk. This taxon is however based on fragmentary remains from a juvenile individual, as evidenced by the presence of unfinished bone on humerus and quadrate and the small size of the centra: the largest anterior caudal centrum is c. 6cm wide, most centra are between 3 and 4cm wide). Because this taxon exhibits some particular features, such as the architecture of the forefin, we consider this taxon as valid, but did not assess its phylogenetic position until more complete unambiguously adult material is found. Indeed, ophthalmosaurids develop numerous features of their forefin during ontogeny, as evidenced by a foetal specimen of '*Platypterygius*' *australis* specimen possessing a humerus more similar to those of early ophthalmosaurids and ophthalmosaurines than to those of platypterygiines⁹².

Species inquirenda: *Platypterygius campylodon* (Carter, 1846). Carter⁵⁹ established the name *Ichthyosaurus campylodon* in a conference abstract. His initial description is based on an articulated rostrum with numerous teeth that he described in a paper the same year⁹³. In that paper, he figured two teeth and made clear that his collection contained several

specimens, coming from both the Cambridge Greensand Member and the overlying chalk (Grey Chalk Subgroup). Since Carter's publications, nearly every Cretaceous ichthyosaur remain from Eurasia has been referred to *Platypterygius campylodon* by default^{68,70,94–97}. Other remains were referred to the species *kiprijanoffi*^{34,40}, but these were subsequently assigned to as *Platypterygius campylodon* by McGowan & Motani⁹⁸. At the current state of knowledge, '*Platypterygius' campylodon* is a vague entity with no clear-cut morphology nor any valid diagnostic feature. A probable type series has been located in the CAMSM while examining ichthyosaurs for the present paper; a re-description of these specimens is currently being undertaken.

ICHTHYOSAURS FROM THE RUSSIAN EARLY-LATE CRETACEOUS BOUNDARY

A diversified assemblage of vertebrates is preserved within this greensand-like bed. The first marine reptile remains from the Kursk region were described by Eichwald^{62,63} and Kiprijanoff^{68–71}. In recent years, remains of terrestrial biota have been described from the Stoilensky quarry as well⁹⁹. The composition of the fauna may be summarized as containing numerous ichthyosaurs, plesiosaurs (*Polyptychodon interruptus*, Polycotylidae indet., Elasmosauridae indet.) and hadrosaurs.

Description of selected remains. Interclavicles (SSU 14/8 137/176, SSU 14/8 137/177). The interclavicle is markedly T-shaped, although there is a thin bony sheet laterally to the junction of the anterior transverse bar with the posterior median stem, forming a gently concave edge as in *Caypullisaurus*⁴⁹, and unlike the abrupt angle seen in *Sveltonectes insolitus*⁵¹. The posterior median stem is slender and flat: in SSU 14/8 137/176, the dorsal (internal) surface of the median stem is slightly concave, although not as much as in *Sveltonectes insolitus* (V.F., pers. obs. on holotype). This surface is slightly convex on SSU 14/8 137/177.

Humeri (SSU 14/37 837/46; SSU 14/37). The capitulum is missing in both specimens. The humerus is short and no constricted, which may suggest a juvenile condition. Both the ventral and dorsal trochanters are well developed. There are numerous minute foramina on the shaft of specimen SSU 14/37. There are three distal facets, presumably for anterior accessory element, radius and ulna. The semi-oval anterior facet is the smallest, the square radial facet is the largest and the ulnar facet is semicircular. The ulnar facet is markedly deflected posteromedially while the radial facet faces laterally, a feature of *Arthropterygius* and

ophthalmosaurine ophthalmosaurids^{3,100}. These humeri correspond to the 'HM4 morphotype' of the English greensands deposits and are referred to as Ophthalmosaurinae indet. by ³⁶.

Femur (SSU 14/44 137/122). The femur has well developed trochanters, a marked triangular cross-section of the capitulum and an elongated shaft. The fibular facet is slightly deflected posteromedially. The tibial facet is the largest and is deflected anteromedially. The facet for the anterior accessory element is small and nearly in the same plane as the tibial facet. This morphology correspond to the 'FM1 morphotype' in the English greensands deposits and is referred to as *Platypterygius* sp. by ³⁶.

Teeth (SSU GPV 2/). Four distinct morphotypes can be recognized in the assemblage. Three correspond to the morphotypes TM1, TM2 and TM3 defined by Fischer et al.³⁶ the English greensands deposits. TM1 teeth are the largest, have a squared cross-section and lack prominent angles, unlike in *Pervushovisaurus bannovkensis* and '*Platypterygius*' $campylodon^{60,84}$; we refer these teeth to '*Platypterygius*' sp. TM2 teeth have a markedly rectangular root, a smooth acellular cementum ring, and well-marked ridges on the enamel, as in Sisteronia seelevi. In the absence of cranial remains, we refer these teeth to cf. Sisteronia. Possible small TM3 are also present; these are referred to this morphotype because of the rounded-cross-section of the root and recurved crown. This morphotype was assigned to Ophthalmosaurinae indet. by Fischer et al.³⁶. Diagnostic feature can be hardly discernable on smaller teeth (either from juvenile individuals or from the back of the mandible); yet, because other isolated elements referable to Ophthalmosaurinae are present in Stoilensky, we refer these teeth to as cf. Ophthalmosaurinae. A fourth morphotype is abundant (Supplementary Figure 3) and appears distinct from the three others; the crown and acellular cementum ring are elongated, pointed and slightly recurved, the enamel is only weakly ridged, the root is apicobasally shortened with a slightly quadratic cross-section. These features recall leptonectid ichthyosaurs of the Early Jurassic and more generally soft-prey specialised marine reptiles.

THE CENOMANIAN RECORD OF ICHTHYOSAURS

Europe

The most abundant material from the Cenomanian comes from the lower part of the Grey Chalk Subgroup in England, but rarely contains articulated material. Nearly all ichthyosaur specimens from that deposit have been referred to as '*Platypterygius*' campylodon, by default^{59,72,93,96,101,102}. While the status of this species is unclear and currently under investigation, all the available material is compatible with large macrophageous

platypterygiine ophthalmosaurids and indicate low taxonomic diversity, probably a single species (V.F. & N.B., pers. obs.). On the contrary, the basal part of the Grey Chalk Subgroup, formed by the Cambridge Greensand Member, contains a higher diversity³⁶. Numerous remains have been described from the western part of Paris Basin as well. Morière¹⁰³ reported a fragmentary skeleton with teeth, rostrum and centra from the chalk of near Villers-sur-Mer. Blain et al.¹⁰⁴ reported two skull roof elements referred to as cf. *Platypterygius* from the lower Cenomanian (Hypoturrilites carcitanensis or Mantelliceras saxbii Zones) of the Falaises des Vaches Noires locality (Villers-sur-mer, Calvados). Bardet⁴⁰ described a fragmentary but associated skull (referred to as 'Platypterygius' cf. kiprijanoffi) from the upper part of the early Cenomanian Mantelliceras dixoni Zone of the Petit Blanc-Nez Formation. Cenomanian teeth from Le Havre, possibly belonging to 'Platypterygius' campylodon, are present in the Muséum national d'Histoire naturelle (Paris, France) collections (MNHN 135). Germany yielded a large number of isolated finds, mainly teeth, of ichthyosaurs ranging from the basal to middle Cenomanian^{105–108}. Bardet et al¹⁰⁹ reported the youngest ichthyosaur known so far, from the upper Cenomanian of Bavaria. Finally, Bardet¹¹⁰ regards the specimens of Capellini^{111,112} from Emilia, Italia, as being Cenomanian in age.

Russia

The fossil-rich strata of the neighbouring Kursk and Belgorod regions^{62,63,68–71} have yielded a diversified assemblage, which can be compared to those of the Cambridge Greensand Member (UK) and the Annopol anticline (Poland)^{16,113}. Our reassessment indicates that the Stoilensky assemblage (Appendix) and other late Albian-Cenomanian localities of the Saratov area contain cranial and postcranial remains referable to as 'Platypterygius' sp., cf. Sisteronia and cf. Ophthalmosaurinae. Teeth from the Stoilensky quarry suggest the presence of a fourth, currently indeterminate taxon. This taxon is not counted as an additional valid species in our analyses because of the scarcity of the remains (isolated teeth). Our preliminary assessment indicates that relative abundances greatly vary but ichthyosaurs dominate the ecosystem (Fig. S 5). Of course, the specie abundance signal is biased by three factors: the total number of teeth for each taxon, the shedding frequency, and sedimentological sorting. Thus, additional material is crucial to gain a less biased insight of the top predator assemblages within the Kursk area at the Early-Late Cretaceous transition. As in the upper Gault/Cambridge Greensand Member ecosystem³⁶, the Stoilensky ichthyosaur assemblage display three distinct tooth morphotypes, suggesting as much feeding guilds colonised by ichthyosaurs. However, the absence of articulated specimen prevents a complete assessment of the ecology of these taxa. A notable feature of the Stoilensky fauna is the strong presence of polycotylid teeth, likely belonging to a 'pierce' guild, in conjunction with the ubiquitous but rare apex predator *Polyptychodon* (Fig. S 4-5). Few remains are known from the Cenomanian of Russia besides those of the Kursk and Belgorod regions discussed above. Many isolated and undetermined finds are reported in Pervushov et al.¹¹⁴ (fourteen specimen in total from the Volga region). The best material comes from the Saratov region, with an articulated rostrum of one of the youngest ichthyosaur species known, the middle Cenomanian platypterygiine *Pervushovisaurus bannovkensis*^{60,84}.

North America

Both Gilmore and Merriam reported the presence of isolated centra from the 'Benton Cretaceous'^{115,116}. However, Slaughter & Hoover¹¹⁷ consider this material as probably Albian in age. Since then, more complete material has been recovered from early–middle Cenomanian deposits of the Western Interior seaway, belonging to '*Platypterygius*' *americanus* and '*Platypterygius*' sp.^{41,57,118,119}.

Australia and India

The rare Cenomanian remains from Australia and India complete the current picture of distribution of Cenomanian ichthyosaurs. Kear⁴³ mentions the presence of ichthyosaur remains in the early Cenomanian of Australia; the material is a specimen consisting of a single phalanx and worn centra⁴², that we regard as Ichthyosauria indet. Lydekker¹²⁰ reported centra from the Utatúr Group of Trichinopolí, India, which he considered as coeval to the Upper Greensand Formation of England. He referred these centra to a new species, although he was not "absolutely certain of the specific distinctness of the India form"^{120: 28}. Moreover, Lydekker formally erected the species name, *Ichthyosaurus indicus*, nine years later¹²¹. The description and figuration of these centra indicate that they lack diagnostic features and the material should be regarded as Ichthyosauria indet. Recently, additional material from the early Cenomanian of India has been attributed to this taxon (although under a novel combination, *Platypterygius indicus*) by ¹²², uniquely on the basis of biogeography. Part of this material (DUGF/41) is referable to as Platypterygiinae indet. because of the squared cross-section of the root. Tooth size and shape appear variable, but all other teeth should be referred to as Ichthyosauria indet. Verma¹²³ indicates the presence of Cenomanian to early Turonian ichthyosaurs in the Cauvery Basin, southeast India. However, the material supporting this claim appears to be that of 122 , which is restricted to the early Cenomanian.

PHYLOGENETIC DATASET AND METHODS

Review of recent phylogenetic data on ophthalmosaurids

The dataset of ³ has been used in many analyses and has undergone a number of modifications since its publication. A wealth of taxa, characters and character states have been added or modified, but some characters and characters states have been misinterpreted or miscoded. Here, we review the two most important recent modifications.

Roberts et al. 2014 dataset:

- New character: Anterior margin of the jugal: terminates prior to anterior end of lacrimal (0), reaches or surpasses anterior end of lacrimal (1). *Incorporated*. Derived state in *Stenopterygius* is erroneous¹²⁴.
- New character: Posterior margin of the jugal: articulates with the postorbital and quadratojugal (0), excluded from the quadratojugal by the postorbital (1). *Not incorporated*. Needs to be redefined as *Macgowania* and many other Triassic ichthyosaur exhibit both states 0 and 1¹²⁵. Coding for *Sveltonectes* should be "?" ⁵¹ and coding in *Athabascasaurus* should be "0" or more conservatively "?"⁵⁴. As a result, on *Janusaurus* unambiguously possesses the derived state and the character is therefore not informative.
- New character: Broad postfrontal-postorbital contact: absent (0), present (1). *Incorporated*. Coding for *Ichthyosaurus* should be "0"⁸³.
- New character: Stapedial shaft in adults: thick (0), slender and gracile (1). *Incorporated with modification.* We added "in posterior view" to the character definition as the derived state is not visible in dorsal or ventral view.
- New character: Ventral process on femur: smaller than dorsal process (0), more prominent (1). *Not incorporated*. We feel the states for this character are ambiguously defined and, as a result, we were unable to code it for many ophthalmosaurids.
- Character state modification of *Stenopterygius quadriscissus*: we feel the state 0&1 better captures the evidence here.
- Character state modifications for *Arthropterygius*. Character 24 stapes head size: facets on the basioccipital indicates state 1¹⁰⁰. We also found the coding for characters 36, 44, and 51⁵ to be erroneous.
- Character state modification of the pelvic girdle of *Caypullisaurus bonapartei*. We do not agree with this interpretation, following ⁶.

• Character state modification of the quadratojugal and squamosal of *Platypterygius hercynicus*. We consider the extreme depth and changing angle of the facets on the lateral surface of the quadratojugal¹²⁶ as strong evidence for inferring the presence of a squamosal.

Arkhangelsky & Zverkov 2014 dataset

- New character: Medial facet for the scapula on coracoid: absent (0), present and well prominent (1). *Not incorporated*. Not parsimony informative in the present dataset (derived state only found in *Stenopterygius aalensis*, and it is 0&1 in *Stenopterygius quadriscissus*). We also found this character to be not independent with the next one.
- New character: Coracoid shape in adults: rounded (length to width ratio less than 1.3 and often close to 1) (0), elongated (length to width ratio greater or equal to 1.5) (1). *Incorporated with modification.* We added « anteroposteriorly » elongated in the character definition to make the difference with the mediolaterally elongated coracoids seen in some shastasaurids for example.
- New character: Intermedium/distal carpal2 contact: absent (0), present (1). *Not incorporated*. We note this character is very likely to vary with ontogeny, so it cannot be unambiguously coded for poorly represented taxa. Moreover, the derived state is directly dependent of the presence or absence of polygonal proximal elements in adults (char74 of the novel dataset) and is also dependent of the forefin architecture (latipinnate/longipinnate, char 71 of the novel dataset).

Additional modifications. In addition of merging recent datasets^{3-6,84}, we incorporated new morphological data from recent sources^{28,127,128} and first hand examination of several OTUs. We also added five Cretaceous taxa (*Platypterygius platydactylus*, '*Platypterygius*' *sachicarum*, '*Platypterygius*' *americanus*, *Sisteronia seeleyi*) and corrected a number of misinterpreted and miscoded character states. We modified five characters and adding seventeen new ones (see below). Furthermore, we think Broili⁵³ and subsequent authors wrongly oriented the forefin of *Platypterygius platydactylus*. The humerus in his figure 16a in table XIII shows a long, axial trochanter on the left and a fine trailing blade on the right: this strongly suggest it depicts a right humerus in ventral view. Indeed, the humeral trochanter that is axially oriented and closer to the edge is the deltopectoral crest in ophthalmosaurids; additionally, ophthalmosaurid humeri also frequently have a posterior trailing edge, but never

anteriorly^{36,129,130}. Thus, the preserved humerus and forefin of *Platypterygius platydactylus* belong to the right side of the animal, not the left one. This substantially alters a number of character states (number of anterior and posterior accessory digits, zeugopodial elements, etc.).

We modified the following characters:

- Character 4 (novel dataset) deep apicobasal grooves on roots, not the very common fine striations. The primitive state is thus restricted to *Macgowania janiceps*, *Eurhinosaurus longirostris*, *Suevoleviathan disinteger*, *Temnodontosaurus* spp. and *Ichthyosaurus communis*.
- Character 9 (novel dataset) anterior process of the maxilla. We feel this character (character 7 in ⁵¹) was hard to code and could result in distinct character states because of slight modifications of the premaxilla-nasal suture. Thus, we redefined this character as follows: external part of the anterior process of the maxilla, in lateral view: extends anteriorly to the anterior border of the naris (including reduced anterior narial opening, if present) (0), don't (1).
- We also split the previously multistate ordered character related to naris shape in two: Character 13: naso-maxillary pillar dividing the naris in two (regardless of the reduction of the anterior portion): absent (0), present (1). Character 14: narialis process of the nasal: absent (0), present (1).
- We split the character related to the anterior part of the coracoid in two (characters 53 and 54 in the novel dataset), because it encompassed two different, independent structures: the shape anteromedial process and the anterior notch.

We added the following characters:

- Character 7: Subnarialis process of the premaxilla: ends anteriorly to posterior end of naris (0), reaches posterior end of naris (1).
- Character 12: Naris size: large, $\geq \frac{1}{2}$ orbit diameter (0), small, $\ll \frac{1}{2}$ orbit diameter (1).
- Character 16: lacrimal-prefrontal suture in external view: straight (0), strongly crenulated (1).
- Character 19: External prefrontal-parietal contact: absent (0), present (1). The derived state is a feature unique to *Leptonectes tenuirostris*, *Ichthyosaurus* and *Stenopterygius* 128,131,132

- Character 21: Anterior part of the postfrontal: simple, unpaired (0), bifurcated in a medial and anterolateral processes (1).
- Character 24: Anterolateral parietal process that connects to parietal: absent (0), present (1).
- Character 26: Supratemporal-stapes contact: absent, the posteroventral process of the supratemporal does not extend up to the shaft of the stapes (0), present (1). The derived state was previously found uniquely in *Ophthalmosaurus* spp. ^{25,26}, but is also found in *Leninia stellans* ⁴⁷.
- Character 31: Occipital lamella of the quadrate: present, giving the quadrate a U-shape in posterior view (0), reduced, the dorsal part of the quadrate is a simple transversely-compressed lamella (1).
- Character 34: Basioccipital condyle peripheral groove: absent (0), present laterally (1); present laterally and ventrally (2).
- Character 37: Raised opisthotic facet of the basioccipital: absent (0), present (1).
- Character 41: Supraoccipital shape: semioval with reduced ventral notch (0), squared and markedly U-shaped with a deep ventral notch (1).
- Character 64: Posterior accessory epipodial element posterior to ulna: absent (0), present (1); present with associated facet on humerus (2). We interpret the condition in *Caypullisaurus bonapartei* as derived (state 1), possessing a posterior accessory epipodial element and a pisiform, rather than a pisiform and a neomorph ¹³³.
- Character 73: Compact and tightly packed epi- and mesopodial rows: absent, elements are loosely connected (0), present (1).
- Character 83: Wide distal femoral blade: present (0), absent, the distal extremity of the femur being smaller than the proximal one in dorsal view (1).

OTU list. *Mikadocephalus gracilirostris*, the best known euichthyosaurian close to Parvipelvia⁸³, is used as the outgroup for this analysis. Our coding for *Temnodontosaurus spp.* is based on the two best-known species included in that genus: *T. platyodon* (mostly) and *T. trigonodon.* Of the thirty-six OTUs, twenty-two taxa have been personally examined and four additional ones have been examined using high-resolution photographs provided by colleagues.

We did not assess the phylogenetic position of the following Cretaceous taxa, because of the scarcity of their remains: '*Platypterygius*' *hauthali* (partial forefin), *Cetarthrosaurus*

walkeri (two highly peculiar propodials), 'Platypterygius' ochevi (partial forefin and fragmentary skeleton of a probably juvenile individual), 'Platypterygius' campylodon (teeth and partial rostrum), Maiaspondylus lindoei (diagnostic material is a partial forefin and a partial skeleton from unborn individual, thereby lacking full expression of its characters and carrying a potentially misleading signal¹³⁴). Some Late Jurassic genera were also omitted for the same reasons: Nannopterygius enthekiodon (one strongly weathered skeleton and referred isolated fins²⁵) and the controversial ophthalmosaurines Paraophthalmosaurus (whose distinctness from Ophthalmosaurus is still debated^{6,83}) and Undorosaurus (U. trautscholdi is based on an incomplete forelimb and U. gorodischensis has been diagnosed and described on doubtful grounds⁸³. We direct the reader to Arkhangelsky & Zverkov⁶ for an assessment of the phylogenetic relationships of these ophthalmosaurine taxa. The exclusion of these Late Jurassic taxa from our analyses also slightly mitigate the strong impact of laggerstätten in diversity analyses^{135,136}. Indeed, with several highly productive formations all over the world^{6,25,29,127,137,138}, the Tithonian can be considered as a laggerstätte for pelagic marine reptiles, biasing the results towards high diversity and disparity. Also, the exclusion of these Tithonian taxa should not result in significant alteration of the disparity analyses, as both Paraophthalmosaurus and Undorosaurus have been regarded as junior or senior synonyms of other ophthalmosaurine genera^{6,83}, suggesting these taxa do not exhibit extreme morphologies that would be ignored by our disparity analyses.

Outgroup

1. Mikadocephalus gracilirostris Maisch & Matzke, 1997

Stratigraphic range: Tschermakfjellet Formation, Ladinian; Grenzbitumenzone of the Besano Formation, Anisian–Ladinian boundary, Middle Triassic.

Geographic range: Middelhook, Isfjord, Spitsbergen; Monte San Giorgio, Tessin, Switzerland.

Data sources: ^{83,139,140}.

Specimen personally examined: None.

Terminal taxa

2. Hudsonelpidia brevirostris McGowan, 1995

Stratigraphic range: *Epigondolella quadrata* conodont zone of the Pardonet Formation, lower Norian, Upper Triassic.

Geographic range: Williston Lake, British Columbia, Canada.
Data sources: ^{98,141}.

Specimen personally examined: None.

3. Macgowania janiceps (McGowan, 1996b)

Stratigraphic range: *Epigondolella multidentata* and *Epigondolella elongata* conodont Zones (\approx *Drepanites rutherfordi* and lower *Mesohimavatiyes columbianus* ammonite Zones of the Pardonnet Formation, middle Norian, Upper Triassic.

Geographic range: Williston Lake, British Columbia, Canada. Data sources: ^{83,98,125,142}.

Specimen personally examined: None.

4. Leptonectes tenuirostris (Conybeare, 1822)

Stratigraphic range: 'Pre-Planorbis' beds, lowermost Hettangian; upper Pliensbachian, Lower Jurassic.

Geographic range: Street, Somerset and Lyme Regis, Dorset, UK; Baden-Württemberg, Germany; Hauenstein area, Switzerland.

Data sources: ^{83,88,131,143–147}.

Specimen personally examined: MNHN AC.9937; NHMUK R498; NHMUK R3612.

5. Excalibosaurus costini McGowan, 1986

Stratigraphic range: Bucklandi Zone of an unnamed formation, lower Sinemurian, Lower Jurassic.

Geographic range: Lilstock, Somerset, UK.

Data sources: ^{148–150}.

Specimen personally examined: BRSMG Cc881.

6. Eurhinosaurus longirostris von Jäger, 1856

Stratigraphic range: Lower-middle Toarcian.

Geographic range: Banz, Bavaria and numerous localities in Baden-Württemberg, Germany; Whitby, Yorkshire, UK; Dudelange, Luxembourg; Staffelegg (Canton Aargau), Switzerland; Pic-Saint-Loup (Montagne Noire), Noirefontaine (Franche-Comté), and Marcoux (Vocontian Basin), France.

Data sources: ^{83,98,151–160}.

Specimen personally examined: MNHN 1946-20; NHMUK R3938; NHMUK 5465; RGHP MA 1.

7. Suevoleviathan disinteger Maisch, 1998

Stratigraphic range: Lower Toarcian, Lower Jurassic.

Geographic range: Holzmaden, Baden-Württemberg, Germany; la Robine-sur-Galabre, Vocontian Basin, France.

Data sources: ^{83,156,161,162}.

Specimen personally examined: RGHP PR 1.

8. Temnodontosaurus spp. Lydekker, 1889

Stratigraphic range: Hettangian; upper Toarcian.

Geographic range: Lyme Regis, Dorset and Whitby, Yorkshire, England; Banz, Bavaria and numerous localities in Baden-Württemberg, Germany; Arlon, Belgium; Yonne, Millau, and Belmont areas, France.

Data sources: ^{83,86,156,159,163–169}

Specimen personally examined: CAMSM J 46989; IRSNB R 122: IRSNB R 123; LMR material; NHMUK 2003*; NHMUK R1158.

9. Hauffiopteryx typicus Maisch, 2008

Stratigraphic range: Early Toarcian, Early Jurassic.

Geographic range: Holzmaden, Bande-Württemberg, Germany; Dudelange, Luxemburg; Ilminster, Somerset, UK.

Data sources: ^{128,152,170,171}.

Specimen personally examined: None.

10. Malawania anachronus Fischer et al., 2013

Stratigraphic range: late Hauterivian–Barremian (range uncertainty of one specimen).

Geographic range: Chia Gara, Kurdistan, Iraq.

Data sources: ⁴.

Specimen personally examined: NHMUK R6682.

11. Ichthyosaurus communis de la Bèche & Conybeare, 1821

Stratigraphic range: 'Pre-Planorbis' beds, lowermost Hettangian–late Sinemurian, Early Jurassic. Congeneric specimens have been found in the Pliensbachian.

Geographic range: Street, Somerset and Lyme Regis, Dorset, UK; Lorraine, Belgium. Bennett et al. ¹⁷² argues that *I. communis* extends up to the Pliensbachian; however, the specimen they described, NHMUK R15907, which V.F. personally examined, differs from other specimens currently referred to as *I. communis* in a number of features of the braincase and hind fin; moreover, their interpretation of numerous bones is incorrect, mixing up scapulae for quadratojugals and clavicles for scapulae. Accordingly we do not consider this specimen as a valid post-Sinemurian occurrence of *I. communis* until more robust arguments are presented. Data sources: ^{83,87,143,144,172–177}.

Specimen personally examined: GLAHM V1180a; GLAHM V1190; LMR material and private collections in Lyme Regis; MNHN 9862; numerous specimens from NHMUK including NHMUK R1664, NHMUK R5595.

12. Stenopterygius quadriscissus (Quenstedt, 1856)

Stratigraphic range: Lower Toarcian; Lower Jurassic.

Geographic range: Holzmaden, Baden-Württemberg; Dobbertin, Germany; Dudelange, Luxembourg.

Data sources: ^{124,152,170,178–180}.

Specimen personally examined: IRSNB 22669; NHMUK R4086.

13. Stenopterygius/Chacaicosaurus cayi Fernández, 1994

Stratigraphic range: *Emileia giebeli* Subzone, *E. multiformis* Zone of the Los Molles Formation, lower Bajocian, Middle Jurassic. Geographic range: Chacaico Sur, Neuquén Basin, Argentina.

Data sources: ^{181,182}.

Specimen personally examined: MOZ 5803.

14. Stenopterygius aalensis Maxwell et al., 2012

Stratigraphic range: *Torulosum* Subzone, *opalinum* Zone of the Opalinuston Formation, Lower Aalenian, Middle Jurassic.

Geographic range: Near Zell am Aichelberg, Baden-Württemberg, Germany. Data sources: ¹²⁸.

Specimen personally examined: SMNS 90699 (photographs provided by P. Vincent, pers. com. 2012).

15. Ophthalmosaurus icenicus Seeley, 1874

Stratigraphic range: Oxford Clay Formation (middle Callovian); Kimmeridge Clay Formation (*cymodoce* to *pectinatus* zones, lower Kimmeridgian–lower Tithonian), Upper Jurassic. Possible congeneric specimens have been reported from the lower Berriasian.

Geographic range: Southeastern England, UK; possibly northern France.

Data sources: ^{3,25,183–191}.

Specimen personally examined: Multiple specimens in CAMSM; GLAHM V1874, GLAHM V1870; MJML material (yet unnumbered); Multiple NHMUK specimens including NHMUK R2133, NHMUK R3702.

16. Ophthalmosaurus natans (Marsh, 1878)

Stratigraphic range: "*Sauranodon* beds" = Red Water shale Member, Sundance Formation, upper Callovian–middle Oxfordian, Middle–Upper Jurassic (Massare & Young 2005; Massare et al. 2006; Wahl 2009).

Geographic range: Numerous localities in Wyoming, USA (Massare et al. 2006}). Data sources: ^{26,54,187,192–199}.

Specimen personally examined: Multiple CM specimens including CM 603.

17. Mollesaurus perialus Fernández, 1999

Stratigraphic range: *Emileia giebeli* ammonite Zone of the Los Molles Formation, lower Bajocian, Middle Jurassic.

Geographic range: Chacaico Sur, Neuquén Basin, Argentina.

Data sources: ^{28,138,181,200}.

Specimen personally examined: MOZ 2282 V (photographs provided by and examined with M. Fernández pers. com. September 2014).

18. Acamptonectes densus Fischer et al., 2012

Stratigraphic range: D2D horizon of the Speeton Clay Formation, basal Hauterivian; C7F–C7D horizons of the Speeton Clay Formation, lower–middle Hauterivian; *Simbirskites concinnus/staffi* Zone, upper Hauterivian, Lower Cretaceous.

Geographic range: Speeton and Filey, North Yorkshire, UK; Cremlingen, Lower Saxony, Germany.

Data sources: ^{3,36}.

Specimen personally examined: GLAHM 132855; NHMUK R11185; SNHM1284-R.

19. Leninia stellans

Stratigraphic range: *Deshayesites volgensis* Zone, Lower Aptian, Lower Cretaceous. Geographic range: Kriushi, Sengiley district, Ulyanovsk Region, Russia. Data sources: ⁴⁷.

Specimen personally examined: YKM 65931.

20. Brachypterygius extremus (Boulenger, 1904)

Stratigraphic range: *Aulcostephanoides mutabilis* and *Pectinates wheatleyensis* zones of the Kimmeridge Clay Formation, middle Kimmeridgian and lower Tithonian, respectively (McGowan & Motani 2003).

Geographic range: Weymouth, Dorset; Stowbridge, Norfolk, UK.

Data sources: ^{25,27,98,183,201–205}.

Specimen personally examined: BRSMG Cc 16696; CAMSM J68516; NHMUK R3177. V.F. have also examined a cast of the type specimen of *Ichthyosaurus cuvieri* Valenciennes, 1861 (eudoxus Zone Kimmeridgian) ²⁰³ held at the MNHN; this taxon is regarded as a possible specimen of *Grendelius* (=*Brachypterygius*) par Bardet et al. ¹⁸³. We agree with this assignation, however, only the specimens referable to the species *B. extremus* were used to code this taxon in the dataset.

21. Arthropterygius chrisorum (Russell, 1993)

Stratigraphic range: Ringnes Formation, Oxfordian to Kimmeridgian, Upper Jurassic (one specimen). Congeneric specimens have been found in Tithonian strata.

Geographic range: Cape Grassy, Melville Island, Northwest Territories, Canada. Congeneric specimens have been found in Argentina and Russia.

Data sources: ^{100,206–208} (with a strong focus on the remains referable to *A. chrisorum*). Specimen personally examined: None.

22. Caypullisaurus bonapartei Fernández, 1997

Stratigraphic range: Numerous horizons within the Vaca Muerta Formation, lower Tithonian, Upper Jurassic to lower Berriasian, Lower Cretaceous.

Geographic range: Numerous localities in Neuquén Basin (Neuquén and Mendoza Provinces), Argentina.

Data sources: 49,133,138,209.

Specimen personally examined: MOZ 6139 and photographs of MOZ 6067 provided by M. Fernández (pers. com. September 2014).

23. Aegirosaurus leptospondylus (Wagner, 1853)

Stratigraphic range: Solnhofen Formation, Malm ζ2b, lowermost Tithonian.

Geographic range: Solnhofen; Eichstätt, Bavaria, Germany. A congeneric specimen has been reported from the Upper Valanginian.

Data sources: ^{19,29,77,210–213}

Specimen personally examined: NHMUK 42833 and RGHP LA 1; although the coding is primarily based on the specimens referred to *Aegirosaurus leptospondylus*.

24. Athabascasaurus bitumineus Druckenmiller & Maxwell, 2010

Stratigraphic range: Wabiskaw Member of the Clearwater Formation, lowermost Albian, Lower Cretaceous.

Geographic range: Syncrude Canada Ltd. base mine, near Mildred Lake, Alberta, Canada. Data sources: ^{54,199}.

Specimen personally examined: None, photographs of holotype (TMP 2000 2901) provided by A. Wolniewicz (pers. com. April 2015).

25. Sveltonectes insolitus Fischer et al., 2011

Stratigraphic range: Unknown formation, upper Barremian, Lower Cretaceous.

Geographic range: Ulyanovsk area, Ulyanovsk region, Russia.

Data sources: ⁵¹.

Specimen personally examined: IRSNB R269.

26. Simbirskiasaurus birjukovi Ochev & Efimov, 1985

Stratigraphic range: Probably *Praeoxyteuthis pugio* Zone, Lower Barremian, Lower Cretaceous.

Geographic range: Right bank of the Volga River, 25 km above the town of Ulyanovsk, between the Zakhar'yevskoye mine and the Detskiy sanatorium. Russia. Data sources: ^{50,84}.

Specimen personally examined: YKM 65119.

27. Platypterygius australis (McCoy, 1867)

Stratigraphic range: Bulldog Shale, Aptian; Wallumbilla Formation, lower Aptian–upper Albian; Darwin Formation, late Aptian–Albian; Allaru Mudstone, middle–upper Albian; Toolebuc Formation, upper Albian; Alinga Formation, upper Albian–Cenomanian; Molecap Greensand, Cenomanian–Turonian, Lower–Upper Cretaceous ²¹⁴ and references therein</sup>. Kear ⁴³, however, considers *P. australis* to be restricted to the middle–upper Albian.

Geographic range: Numerous localities across Australia, see Kear⁴³ for a review. Data sources: ^{31,32,56,214–216}.

Specimen personally examined: NHMUK unnumbered, two juvenile specimens.

28. Pervushovisaurus bannovkensis Arkhangelsky, 1998

Stratigraphic range: Probably Melovatskaya Formation, Lower-middle Cenomanian, Upper Cretaceous.

Geographic range: Nizhnaya Bannovka, Krasnoarmeisk District, Saratov Region, Russia. Data sources: ^{60,84,114}.

Specimen personally examined: SSU 104a/24.

29. Platypterygius hercynicus (Kuhn, 1946)

Stratigraphic range: Neocomer Erzhorizont, upper Aptian; lower *Callihoplites auritus* ammonite Subzone (*Mortoniceras inflatum* ammonite Zone), upper Albian, Lower Cretaceous.

Geographic range: Salzgitter, Lower Saxony, Germany; Saint-Jouin-Bruneval, Seine-Maritime, France.

Data sources: ^{33,126,217}.

Specimen personally examined: Cast of SMSS 'SGS'; MHNH 2010.4.

30. Platypterygius americanus (Nace, 1939)

Stratigraphic range: Mowry Shale Member of the Graneros Formation, upper Albian; Ashville Formation, Albian-Cenomanian; Belle Fourche Shale; Lower Cenomanian, Lower– Upper Cretaceous.

Geographic range: Crook County, Wyoming; Southern Saskatchewan, Canada. Data sources: ^{34,57,118,119}.

Specimen personally examined: U.W 2421 (photographs provided by E. Maxwell, pers. com. February 2015).

31. Platypterygius platydactylus Broili, 1907

Stratigraphic range: *Deshayesites deshayesi* Zone, Lower Aptian, Lower Cretaceous.
Geographic range: Castendamm, near Hannover, Lower Saxony, Germany.
Data sources: ⁵³, reinterpreted here; see above.
Specimen personally examined: None.

32. Platypterygius sachicarum Páramo, 1997

Stratigraphic range: Arcillolitas Abigarradas Member of the Paja Formation, early Aptian. Geographic range: Loma Pedro Luis, near Villa de Leiva, Boyacá, Columbia. Data sources: ^{21,35,218}.

Specimen personally examined: DON-19671 (photographs provided by E. Maxwell, pers. com. February 2015).

33. Palvennia hoybergeti Druckenmiller et al., 2012

Stratigraphic range: Dorsoplanites ilovaiskyi to Dorsoplanites maximus zones, Slottsmøya Member, Agardhfjellet Formation, Tithonian, Upper Jurassic (one specimen). Geographic range: Janusfjellet, Spitsbergen, Norway.

Data sources: ^{5,127}.

Specimen personally examined: none.

34. Cryopterygius kristiansenae Druckenmiller et al., 2012

Stratigraphic range: Dorsoplanites ilovaiskyi to Dorsoplanites maximus zones, Slottsmøya Member, Agardhfjellet Formation, Tithonian, Upper Jurassic (one specimen). Geographic range: Janusfjellet, Spitsbergen, Norway.

Data sources: ^{5,127}.

Specimen personally examined: none.

35. Janusaurus lundi Roberts et al., 2014

Stratigraphic range: Slottsmøya Member, Agardhfjellet Formation, Tithonian, Upper Jurassic. Geographic range: Janusfjellet, Spitsbergen, Norway.

Data sources: ⁵.

Specimen personally examined: none.

36. Sisteronia seeleyi Fischer et al., 2014

Stratigraphic range: Middle Albian–earliest Cenomanian.

Geographic range: Sisteron and Bevons, Vocontian Basin, France; Cambridgeshire, UK. Possible congeneric specimens are found in Russia (this work). Data sources: ³⁶.

Specimen personally examined: Several tens of specimens at CAMSM, NHMUK, GLAHM, and RGHP; see Fischer et al. ³⁶ for a complete list.

Character list. Characters are polarized with respect to *Mikadocephalus gracilirostris* as outgroup. As a general rule, we tried to avoid continuous characters, characters clearly related to ecology such as crown shape, or characters based on ratios with ambiguous state boundaries. We illustrate some character states. Characters are polarized with respect to *Mikadocephalus gracilirostris* as outgroup. As a general rule, we tried to avoid continuous characters, characters clearly related to ecology such as crown shape, or characters are polarized with respect to *Mikadocephalus gracilirostris* as outgroup. As a general rule, we tried to avoid continuous characters, characters clearly related to ecology such as crown shape, or characters based on ratios with subjective state boundaries. We illustrate the states of selected characters.

Dentition

1. **Crown striations**: presence of deep axial ridges (0), crown enamel subtly ridged or smooth (1) ⁵⁴: character 25.



Teeth in lateral view illustrating character 1.

2. **Base of enamel layer on crown**: weakly defined, invisible (0), well defined, precise (1). This appears variable along the rostrum/jaw in *T. platyodon* (IRSNB R 122): the crown enamel is well defined in the anterior-most teeth and then becomes poorly defined in the rest of the jaw. Therefore, only take the teeth from the middle part of the rostrum/jaw. It seems however rather constant for all other ichthyosaurs we have examined. ⁵¹: character 2.

3. **Root cross-section in mid-jaw teeth of adults**: rounded (0), quadrangular (1). ⁵¹: character 3

4. **Deep apicobasal grooves in root**: present (0), absent (1).

Skull

- 5. **Overbite**: absent or slight (0), clearly present (1) 45 : character 33.
- 6. **Processus supranarialis of the premaxilla**: present (0), absent (1) ⁸³: character 10.





Skull in lateral view illustrating character 6.

- 7. **Subnarialis process of the premaxilla**: ends anteriorly to posterior end of naris (0), reaches posterior end of naris (1).
- 8. **Processus postpalatinis of the pterygoid**: absent (0), present (1) ⁸³: character 38.



Skull in ventral view illustrating character 8.

- External part of the anterior process of the maxilla, in lateral view: extends anteriorly to the anterior border of the naris (including reduced anterior narial opening, if present) (0), don't (1).⁵¹:character 7, modified.
- 10. **External exposure of the maxilla:** large, well visible (0), extremely reduced, nearly absent in external view by processes of the premaxilla and the lacrimal (1).
- 11. Processus narialis of the maxilla in external view: present (0), absent (1). ⁵¹: character
 9, modified by⁴



Skull in lateral view illustrating character 11.

- 12. Naris size: large, $\geq \frac{1}{2}$ orbit diameter (0), small, $\ll \frac{1}{2}$ orbit diameter (1).
- 13. Naso-maxillary pillar dividing the naris in two (regardless of the reduction of the anterior portion): absent (0), present (1).
- 14. Narialis process of the nasal: absent (0), present (1).





Skull in lateral view illustrating character 14.

15. Processus narialis of prefrontal: absent (0), present (1). ⁵¹: character 11.





Skull in lateral view illustrating character 15.

- 16. Lacrimal-prefrontal suture in external view: straight (0), strongly crenulated (1).
- 17. **Anterior margin of the jugal**: tapering, running between lacrimal and maxilla (0), broad and fan-like, covering large area of maxilla ventrolaterally (1) ⁵⁴: character 6.



Skull in lateral view illustrating character 17.

- 18. Anterior margin of the jugal II: terminates prior to anterior end of lacrimal (0), reaches or surpasses anterior end of lacrimal (1). ⁵ : character 11
- 19. External prefrontal-parietal contact: absent (0), present (1).
- 20. Processus temporalis of the frontal: absent (0), present (1). ⁵¹: character 14



Skull in dorsal view illustrating character 20.

- 21. Anterior part of the postfrontal: simple, unpaired (0), bifurcated in a medial and anterolateral processes (1).
- 22. **Supratemporal-postorbital contact**: absent (0), present (1) (²¹⁹: character 27, inverted coding).
- 23. Broad postfrontal-postorbital contact: absent (0), present (1). ⁵: character 16.
- 24. Anterolateral parietal process that connects to parietal: absent (0), present (1).
- 25. **Sagittal eminence of the parietal**: present (0), absent (1) (²⁰⁹: character 5, inverted coding).
- 26. **Supratemporal–stapes contact:** absent, the posteroventral process of the supratemporal does not extend up to the shaft of the stapes (0), present (1).

- 27. **Supratemporal fenestra reduction**: absent, the supratemporal fenestra is large, elongated and its anterior margin is set at the level of the parietal foramen or more anteriorly (0), reduced, the supratemporal fenestra is small, rounded, and its anterior margin is set posterior to the parietal foramen (1). ¹²⁸: characters 14 & 15, modified.
- 28. Squamosal shape: square (0), triangular (1), squamosal absent (2). ⁵¹: character 16, inverted coding.
- 29. **Quadratojugal exposure**: extensive (0), small, largely covered by squamosal and postorbital (1) ⁸³: character 30, modified.
- 30. Lower temporal embayment between jugal and quadratojugal (=jugalquadratojugal notch or incisura postjugalis): present (0), lost (1) ²¹⁹: character 25, modified.
- 31. Occipital lamella of the quadrate: present, giving the lateral surface of the quadrate a U-shape in posterior view (0), reduced, the dorsal part of the quadrate is a simple transversely-compressed lamella (1).



Right quadrate in posterior view illustrating character 31.

32. **Basipterygoid processes**: short, giving basisphenoid a square outline in dorsal view (0), markedly expanded laterally, being wing-like, giving basisphenoid a marked pentagonal shape in dorsal view (1). ⁵¹: character 18.



Basisphenoid in ventral view illustrating character 32.

- 33. **Extracondylar area of basioccipital**: wide (0), reduced but still present ventrally and laterally (1); extremely reduced, being non-existent at least ventrally (2) ²⁰⁹: character 10, modified.
- 34. **Basioccipital condyle peripheral groove:** absent (0), present laterally (1); present laterally and ventrally (2).
- 35. **Basioccipital peg**: present (0), absent (1) ⁴⁵: character 29, modified by ⁵¹.
- 36. Ventral notch in the extracondylar area of the basioccipital: present (0), absent (1).³.
- 37. Raised opisthotic facet of the basioccipital: absent (0), present (1).
- 38. **Shape of the paroccipital process of the opisthotic:** short and robust (0), elongated and slender (1). ³:character 20.
- 39. **Stapedial shaft in posterior view in adults**: thick (0), slender and gracile (1). ⁵, definition modified.
- 40. **Stapes proximal head**: slender, much smaller than opisthotic proximal head (0), massive, as large or larger than opisthotic (1) ²¹⁹: character 34, modified by ⁵¹



Skull in posterior view illustrating character 40.

41. Supraoccipital shape: semioval with reduced ventral notch (0), squared and markedly U-shaped with a deep ventral notch (1).



Partial basicranium in posterior view illustrating character 41.

Mandible

42. **Angular lateral exposure**: much smaller than surangular exposure (0), extensive (1) ⁴⁵: character 32, inverted coding.



Skull in lateral view illustrating character 42.

Axial skeleton

- 43. **Posterior dorsal/anterior caudal centra**: 3.5 times or less as high as long (0), four times or more as high as long (1) 100 : character 15, inverted coding.
- 44. **Tail fin centra**: strongly laterally compressed (0), as wide as high (1) ¹⁰⁰: character 16, inverted coding.
- 45. Neural spines of atlas-axis: completely overlapping, may be fused (0), functionally separate, never fused (1) 54 : character 26.
- 46. Chevrons in apical region: present (0), lost (1) 219 : character 72.

- 47. **Rib articulation in thoracic region**: predominantly unicapitate (0), exclusively bicapitate (1) ⁸³: character 53.
- 48. **Rib cross-section at mid-shaft**: rounded and robust (0), '8'-shaped (1) ²¹⁹: character 73, modified.
- 49. **Ossified haemapophyses**: present (0), absent (1) ⁸³: character 63.
- 50. **Tail size**: as long or longer than the rest of the body (0) distinctly shorter (1) ⁸³: character 65.
- 51. Lunate tailfin: no (0) well-developed (1) ⁸³: character 66.



Illustration of character 51.

Scapular girdle and forefin

- 52. Coracoid shape in adults: rounded (length to width ratio less than 1.3 and often close to 1) (0), anteroposteriorly elongated (length to width ratio greater or equal to 1.5) (1). ⁶: character 53, definition modified
- 53. Anteromedial process of the coracoid: absent (0), present (1).



Right coracoid in ventral view illustrating character 53.

- 54. Anterior notch of the coracoid: present (0); absent (1) ⁵¹: character 29, modified.
- 55. Glenoid contribution of the scapula: extensive, being at least as large as the coracoid facet (0), reduced, being markedly smaller than the coracoid facet (1). ³: character 27.



Partial scapular girdle in ventral view illustrating character 54.

56. **Prominent acromion process of scapula:** absent (0), present (1). ⁵¹: character 28.



Partial scapular girdle in ventral view illustrating character 55.

57. Plate-like dorsal ridge on humerus: absent (0), present (1) ⁴⁵: character 56.



Humerus in proximal view illustrating character 57.

58. **Protruding triangular deltopectoral crest on humerus**: absent (0), present (1); present and very large, matching in height the trochanter dorsalis, and bordered by concave areas (2). ⁵¹: character 31, modified by ³.



Humerus in proximal view illustrating character 58.

- 59. Humerus distal and proximal ends in dorsal view (thus regardless of the size of the dorsal and ventral processes): distal end wider than proximal end (0), nearly equal or proximal end slightly wider than distal end (1)⁴⁵: character 55, modified by ⁵¹.
- 60. Anterior accessory epipodial element anterior to radius: absent (0), present (1); present with associated facet on humerus (2) 220 : character 10, modified by 51 .



Partial forefin in dorsal view illustrating character 60.

61. Humerus with posterodistally deflected ulnar facet and distally facing radial facet: absent (0), present (1). ⁵¹: character 34, modified by ³.



Humerus in dorsal view illustrating character 61.

62. Humerus/intermedium contact: absent (0), present (1) ²⁰⁹: character 15.



Partial forefin in dorsal view illustrating character 62.

63. Anterodistal extremity of the humerus: prominent leading edge tuberosity (0), acute angle (1). ⁴: character 44.



Partial forefin in dorsal view illustrating character 63.

64. **Posterior accessory epipodial element posterior to ulna**: absent (0), present (1); present with associated facet on humerus (2).



Partial forefin in dorsal view illustrating character 64.

65. **Shape of the posterior surface of the ulna**: rounded or straight and nearly as thick as the rest of the element (0), concave with a thin, blade-like margin (1). ³ :character 36.



Partial forefin in dorsal view illustrating character 65.

- 66. **Spatium interosseum between radius and ulna**: present as a space or foramen (0), absent (1) ⁸³: character 84, modified by ³.
- 67. Manual pisiform: absent (0), present (1) ⁴⁵: character 67, inverted coding.
- 68. Notching of anterior facet of leading edge elements of forefin in adults: present (0), absent (1) ⁴⁵: characters 59 and 65, modified by ⁵¹.
- 69. **Preaxial accessory digits on forefin**: absent (0), one (1); two or more (2) ⁸³: character 91, modified.
- 70. Posterior enlargement of forefin: number of postaxial accessory 'complete' digits: none (0), one (1), two or more (2) ⁸³: character 89, modified by ⁵¹.
- 71. **Longipinnate or latipinnate forefin architecture**: one (0), two (1) digit (s) directly supported by the intermedium. ⁵¹: character 40.



Partial forefin in dorsal view illustrating character 71.

- 72. **Zeugo- to autopodial elements**: flattened and plate-like (0), strongly thickened (1). ⁸³: character 94.
- 73. Compact and tightly packed epi- and mesopodial rows: absent, elements are loosely connected (0), present (1).
- 74. **Tightly packed rectangular phalanges**: absent, phalanges are mostly rounded (0), present (1) ⁸³: character 102, modified.
- 75. Digital bifurcation: absent (0), frequently occurs in digit IV (1). ⁵¹: character 43.
- 76. Manual digit V: lost or reduced to small floating elements (0), present (1) ⁴⁵: character 73, modified.
- 77. **Forelimb–hind limb ratio**: nearly equal (0), forelimb longer twice as much as hind limb ²²⁰: character 5, modified by ⁴.

Pelvic girdle and hind fin

78. Ischium-pubis fusion in adults: absent or minute (0), present with an obturator foramen (1); present with no obturator foramen (2) ²²¹: character 13, modified by ⁵¹.



Ischium and pubis in lateral view illustrating character 78.

79. Ischium or ischiopubis shape: plate-like, flattened (0), rod-like (1) 45 : character 87, modified by 51 .



Ischium (or ischiopubis) in lateral view illustrating character 79.

- 80. Iliac anteromedial prominence: absent (0), present (1) ⁴⁵: character 84.
- 81. **Ilium proximal region:** expanded (0), narrow proximally and distally, rib-like (1) ²¹⁹: character 106, modified by ¹²⁸.



Ilium in lateral view illustrating character 81.

82. Prominent, ridge-like dorsal and ventral processes demarcated from the head of the femur and extending up to mid-shaft: absent (0), present (1). ⁵¹ : character 46.



Femur in proximal (above) and anterior (below) views illustrating character 82.

- 83. **Wide distal femoral blade**: present (0), absent, the distal extremity of the femur being smaller than the proximal one in dorsal view (1).
- 84. Astragalus/femoral contact: absent (0), present (1) ¹⁰⁰: character 33.



Partial hind fin in dorsal view illustrating character 84.

- 85. Femur anterodistal facet for accessory zeugopodial element anterior to tibia: absent
 - (0), present (1). ⁵¹ : character 48.



Partial hind fin in dorsal view illustrating character 85.

- 86. **Spatium interosseum between tibia and fibula**: present (0), absent (1). ⁸³: character 114, modified.
- 87. Hind fin leading edge element in adults: notched (0), straight (1). ⁴⁵ : character 92, modified by ⁴.
- 88. **Postaxial accessory digit**: absent (0), present (1). ⁵¹: character 50.

Maximum parsimony analytical details. Maximum parsimony analyses were carrier both in TNT v1.1²²² and PAUP* v4.0a142²²³. We used the exact parsimony searches of TNT 1.1 to analyse the character matrix (20,000 trees in memory, max ram=1000, heuristic search, tree bisection reconnection (TBR) as swapping algorithm with 10 trees saved per replication) and calculate the Bremer support ('suboptimal'=5), Jacknife (removal probability = 36, with 1000 replications), and bootstrap (standard, 1000 replications) values. We timescaled and plotted our consensus tree using various branch length reconstruction methods ('basic', 'equal', 'minimum'; see details below) and calculated stratigraphic congruence using a RCI and GER indexes using the packages ape $v3.2^{23}$ and strap v1.4⁷ in R v.3.1.3²²⁴.

As analyses of ophthalmosaurid relationship are characterised by moderately high homoplasy^{3,4}, we also ran a maximum parsimony analysis using implied weighting in TNT (K=3).

Analytical details of the Bayesian analyses. We used MrBayes v3.2.4²²⁵. Characters 33, 34 and 78 were ordered, as in the maximum parsimony analysis. Coding was considered as informative (reflecting the exclusion of autapomorphies) and we set used the following parameters: gamma rates and uncorrelated relaxed clock (igr). Our root calibration assumes Parvipelvia originated after the Permian but before the end of the Early Triassic (uniform distribution between 252.17 and 247.2 Ma) and we calibrated each tip using a uniform

distribution of first appearance datum ages to account for uncertainty in dating (except for a few taxa dated as a the ammonite zone or subzone, whose ages were obtained in Scott²²⁶ and set as fixed). We set four chains, three replicate runs and 40,000,000 generations, sampling every 1000; a burn-in of 25% was applied.

BIODIVERSITY DATA

Time bins

We divided the largest stages (Aptian and Albian) into their widely accepted substages (lower and upper Aptian; lower, middle, and upper Albian), based on ammonite stratigraphy^{12,227–232}. The lower Aptian encompasses the ammonite zones from the *oglanlensis* Zone to the *furcata* Zone; the upper Aptian from *subdonosocostatum* Zone to the *Jacobi* Zone; the lower Albian from the *schrammeni/tardefurcata* Zone to the *mammlilatum/auritiformis* Zone; the middle Albian to the *dentatus* Zone to the *lautus* Zone; the upper Albian from the *cristatum* Zone to the *dispar/briacensis* Zone. Using numerical ages from Kuhnt & Moullade²³³, Scott²³¹ and the 2014 updated data of Cohen et al.²³⁴, time bins for the stages from the Hettangian to the Turonian have a mean duration 5.06 My, and a moderate standard deviation (± 2.25 My).

Disparity

We use the R packages strap ape $v3.2^{23}$ to run the principal coordinate analyses on the phylogeny-reconstructed dataset (using Mesquite²³⁵), applying the Cailliez correction for negative eigenvalues.

PCOA

See nexus file ("phy_rec.nex") for the phylogenetically-reconstructed dataset and the files "pcoa.txt" and "pcoa.csv" for the PCoA results.

ECOLOGICAL DIVERSITY

Note on tooth wear quantification

We used articulated rostra to count the relative occurrence of three stages of wear that we defined qualitatively as follows: (i) no wear, the crown apex is pointed and still possesses its

enamel microtexture; (ii) slight wear, the crown apex is rounded and the microtexture of the enamel is lost; (iii) intense wear, the crown apex is broken and/or spalled and this section is polished and smoothed by further food processing, so that we are confident this feature is not diagenetic or due to preparation damage. We gave a weight to each category (1, 2, 3 respectively) and quantified wear as the relative proportion of each wear stage multiplied by its weight.

Ecological metrics employed

- 1. Absolute tooth size
 - a. Mid-rostrum tooth, total apico-basal size
 - b. In mm; e.g. 55
- 2. Crown shape ratio
 - a. Crown apicobasal height divided by crown basal diameter (at the start of enamel covering)
 - b. E.g. 1.65
- 3. Crown relative size
 - a. Crown apicobasal height divided by basioccipital diameter (which is a good proxy for intraquadrate length/gullet size
 - b. E.g. 0.304
- 4. Relative symphysial length
 - a. Symphysis length divided by mandible length
 - b. In %, e.g. 41
- 5. Relative snout depth (from McGowan²⁷)
 - a. Snout depth at midpoint divided by jaw length
 - b. E.g. 0.484
- 6. Absolute sclerotic aperture
 - a. Diameter of the aperture (=inner opening) of the sclerotic ring
 - b. In mm; e.g. 31.5
- 7. Tooth wear
 - a. Assign a weight to each wear stage of each functional (=fully erupted) crown:
 - i. 1=pristine: with details of texture intact and/or apex pointed
 - ii. 2=polished: crown texture lost and/or apex slightly rounded
 - iii. 3=heavy wear: crown apex (or more) broken off and the break is polished so that we are sure this is a diagenetic/preparation artefact

b. Value is the sum of % of each stage; e.g. 0.5*1+025*2+0.25*3=1.75

Confidence assessment. Because we restricted our data to ecologically relevant measurements and with a strong emphasis on Cretaceous forms, the resulting dataset is small and contain a non-negligible proportion of missing values (33%), which renders usual bootstrapping methods inadequate. To cope with this issue, we assessed the statistical support of our cluster using the "Approximately Unbiased P-value" method of the pvclust v1.3-2 package²³⁶ in R. This method employs multiscaled bootstrapping: instead of simply bootstrapping the dataset, it creates multiple datasets that are smaller, equal and larger than the original dataset. We ran it from 0.5 times to 5 times the size of the original dataset, with 0.1 increments and 10,000 bootstrap per increment.

CORRELATIONS

We used the nlme v3.1²³⁷ and AICcmodavg v2.0²³⁸ packages in R to compute the Akaike Information Criterion for finite sample sizes (AICc²³⁹). Results from the pairwise correlation tests and from the generalised least square tests, for both the Early Cretaceous and Full (Cretaceous) dataset can be found in the "Supplementary Data 8 Pairwise_results.xlsx" and "Supplementary Data 9 GLS_results.xlsx" files.

SUPPLEMENTARY REFERENCES

- Huelsenbeck, J. P. Comparing the Stratigraphic Record to Estimates of Phylogeny. *Paleobiology* 20, 470–483 (1994).
- 2. Wills, M. A. Congruence Between Phylogeny and Stratigraphy: Randomization Tests and the Gap Excess Ratio. *Syst. Biol.* **48**, 559–580 (1999).
- 3. Fischer, V. *et al.* New ophthalmosaurid ichthyosaurs from the European Lower Cretaceous demonstrate extensive ichthyosaur survival across the Jurassic-Cretaceous boundary. *PLoS One* **7**, e29234 (2012).
- 4. Fischer, V. *et al.* A basal thunnosaurian from Iraq reveals disparate phylogenetic origins for Cretaceous ichthyosaurs. *Biol. Lett.* **9**, 1–6 (2013).
- Roberts, A. J., Druckenmiller, P. S., Sætre, G.-P. & Hurum, J. H. A New Upper Jurassic Ophthalmosaurid Ichthyosaur from the Slottsmøya Member, Agardhfjellet Formation of Central Spitsbergen. *PLoS One* 9, e103152 (2014).
- 6. Arkhangelsky, M. S. & Zverkov, N. G. On a new ichthyosaur of the genus Undorosaurus. Proc. Zool. Inst. RAS 318, 187–196 (2014).
- Bell, M. a. & Lloyd, G. T. strap: an R package for plotting phylogenies against stratigraphy and assessing their stratigraphic congruence. *Palaeontology* 58, 379–389 (2015).
- Gabdullin, R. R. Rhythms of Upper Cretaceous Deposits in the Russian Plate, Northwestern Caucasus and Southwestern Crimea (Structure, Classification, Models of Formation). *Geology* (Moscow University, 2002).
- Košťák, M. & Weise, F. Remarks to geographic distribution and phylogeny of the Upper Cretaceous belemnite genus Praectinocamax Naidin. Acta Univ. Carolinae Geol. 49, 135–139 (2006).
- Wilmsen, M., Niebuhr, B., Wood, C. J. & Zawischa, D. Fauna and palaeoecology of the Middle Cenomanian Praeactinocamax primus Event at the type locality, Wunstorf quarry, northern Germany. *Cretac. Res.* 28, 428–460 (2007).
- Rozhdestvenskiy, A. K. The study of Cretaceous Reptiles in Russia. *Paleontol. J.* 2, 206–214 (1973).
- 12. Juignet, P. La transgression crétacée sur la bordure orientale du Massif armoricain.

Aptien, Albien, Cénomanien de Normandie et du Maine. Le stratotype du Cénomanien. **Thèse de d,** (Université de Caen, 1974).

- Cookson, I. C. & Hughes, N. F. Microplankton from the Cambridge Greensand (mid-Cretaceous). *Palaeontology* 7, 37–59 (1964).
- Hopson, P. M. A stratigraphical framework for the Upper Cretaceous Chalk of England and Scotland with statements on the Chalk of Northern Ireland and the UK Offshore Sector. *Br. Geol. Surv. Res. Reports* RR/05/01, 1–102 (2005).
- 15. Hopson, P. M., Wilkinson, I. P. & Wood, M. A. A stratigraphical framework for the Lower Cretaceous of England. *Br. Geol. Surv. Res. Reports* **RR/08/03**, 1–87 (2008).
- Bardet, N., Fischer, V. & Machalski, M. Large predatory marine reptiles from the Albian–Cenomanian of Annopol, Poland. *Geol. Mag.* 1–16 (2015). doi:10.1017/S0016756815000254
- Hüsing, S. K., Deenen, M. H. L., Koopmans, J. G. & Krijgsman, W. Magnetostratigraphic dating of the proposed Rhaetian GSSP at Steinbergkogel (Upper Triassic, Austria): Implications for the Late Triassic time scale. *Earth Planet. Sci. Lett.* 302, 203–216 (2011).
- Wotzlaw, J.-F. *et al.* Towards accurate numerical calibration of the Late Triassic: Highprecision U-Pb geochronology constraints on the duration of the Rhaetian. *Geology* 42, 571–574 (2014).
- Fischer, V., Clément, A., Guiomar, M. & Godefroit, P. The first definite record of a Valanginian ichthyosaur and its implication for the evolution of post-Liassic Ichthyosauria. *Cretac. Res.* 32, 155–163 (2011).
- 20. Ogg, J. G., Ogg, G. & Gradstein, F. M. A concise geologic timescale. Cambridge University Press (2008).
- 21. Hampe, O. Considerations on a *Brachauchenius* skeleton (Pliosauroidea) from the lower Paja Formation (late Barremian) of Villa de Leyva area (Colombia). *Foss. Rec. Mitteilungen aus dem Museum dür Naturkd. Berlin, Geowissenschaften* 8, 37–51 (2005).
- 22. Druckenmiller, P. S. & Maxwell, E. E. A Middle Jurassic (Bajocian) ophthalmosaurid (Reptilia, Ichthyosauria) from the Tuxedni Formation, Alaska and the early

diversification of the clade. Geol. Mag. 151, 41–48 (2014).

- 23. Paradis, E., Claude, J. & Strimmer, K. APE: Analyses of phylogenetics and evolution in R language. *Bioinformatics* **20**, 289–290 (2004).
- 24. Bapst, D. W. paleotree: an R package for paleontological and phylogenetic analyses of evolution. *Methods Ecol. Evol.* **3**, 803–807 (2012).
- 25. Kirton, A. M. A review of British Upper Jurassic ichthyosaurs. **Ph.D. diss**, (University of Newcastle upon Tyne, 1983).
- 26. Gilmore, C. W. Osteology of *Baptanodon* (Marsh). *Mem. Carnegie Museum* II, 77–129 (1905).
- 27. McGowan, C. The description and phenetic relationships of a new ichthyosaur genus from the Upper Jurassic of England. *Can. J. Earth Sci.* **13**, 668–683 (1976).
- Fernández, M. & Talevi, M. Ophthalmosaurian (Ichthyosauria) records from the Aalenian–Bajocian of Patagonia (Argentina): an overview. *Geol. Mag.* 151, 49–59 (2014).
- 29. Bardet, N. & Fernández, M. A new ichthyosaur from the Upper Jurassic lithographic limestones of Bavaria. *J. Paleontol.* **74**, 503–511 (2000).
- 30. Kear, B. P., Boles, W. E. & Smith, E. T. Unusual gut contents in a Cretaceous ichthyosaur. *Proc. R. Soc. London B Biol. Sci.* **270**, S206–S208 (2003).
- Kear, B. P. Cranial morphology of *Platypterygius longmani* Wade, 1990 (Reptilia: Ichthyosauria) from the Lower Cretaceous of Australia. *Zool. J. Linn. Soc.* 145, 583– 622 (2005).
- Wade, M. A review of the Australian Cretaceous longipinnate ichthyosaur *Platypterygius* (Ichthyosauria, Ichthyopterygia). *Mem. Queensl. Museum* 28, 115–137 (1990).
- Kuhn, O. Ein skelett von Ichthyosaurus hercynicus n. sp. aus dem Aptien von Gitter. Berichte der Naturforschenden Gesellschaft Bamb. 29, 69–82 (1946).
- 34. Romer, A. S. An ichthyosaur skull from the Cretaceous of Wyoming. *Contrib. to Geol.Wyoming Univ.* 7, 27–41 (1968).
- 35. Paramo, M. E. Platypterygius sachicarum (Reptilia, Ichthyosauria) nueva especie del

Cretácio de Colombia. Rev. Ingeominas 6, 1–12 (1997).

- 36. Fischer, V., Bardet, N., Guiomar, M. & Godefroit, P. High Diversity in Cretaceous Ichthyosaurs from Europe Prior to Their Extinction. *PLoS One* **9**, e84709 (2014).
- 37. Haq, B. U. Cretaceous eustasy revisited. *Glob. Planet. Change* **113**, 44–58 (2014).
- Prokoph, A., Shields, G. A. & Veizer, J. Compilation and time-series analysis of a marine carbonate δ18O, δ13C, 87Sr/86Sr and δ34S database through Earth history. *Earth-Science Rev.* 87, 113–133 (2008).
- 39. Martin, J. E., Amiot, R., Lécuyer, C. & Benton, M. J. Sea surface temperature contributes to marine crocodylomorph evolution. *Nat Commun* **5**, 1–7 (2014).
- 40. Bardet, N. Un crâne d'Ichthyopterygia dans le Cénomanien du Boulonnais. *Mémoires la Société académique du Boulonnais* **6**, 1–32 (1989).
- 41. Adams, T. L. & Fiorillo, A. *Platypterygius* Huene, 1922 (Ichthyosauria, Ophthalmosauridae) from the Late Cretaceous of Texas, USA. *Palaeontol. Electron*. 14, 19A (2011).
- 42. Choo, B. Cretaceous ichthyosaurs from Western Australia. *Rec. West. Aust. Museum, Suppl.* **57**, 207–218 (1999).
- 43. Kear, B. P. Cretaceous marine reptiles of Australia: a review of taxonomy and distribution. *Cretac. Res.* 24, 277–303 (2003).
- 44. Blainville de, H. M. D. Description de quelques espèces de reptiles de la Californie, précédée de l'analyse d'un système général d'érpetologie et d'amphibiologie. *Nouv. Ann. du Muséum d'Histoire Nat. Paris* 4, 233–296 (1835).
- 45. Motani, R. Phylogeny of the Ichthyopterygia. J. Vertebr. Paleontol. 19, 473–496 (1999).
- 46. Baur, G. On the morphology and origin of the Ichthyopterygia. *Am. Nat.* **21**, 837–840 (1887).
- 47. Fischer, V., Arkhangelsky, M. S., Uspensky, G. N., Stenshin, I. M. & Godefroit, P. A new Lower Cretaceous ichthyosaur from Russia reveals skull shape conservatism within Ophthalmosaurinae. *Geol. Mag.* 151, 60–70 (2014).
- 48. Arkhangelsky, M. S. The historical sequence of Jurassic and Cretaceous ichthyosaurs.

Paleontol. J. 35, 521–524 (2001).

- 49. Fernández, M. A new ichthyosaur from the Tithonian (Late Jurassic) of the Neuquén Basin (Argentina). J. Paleontol. 71, 479–484 (1997).
- 50. Ochev, V. G. & Efimov, V. M. A new genus of Ichthyosaur from the Ul'Yanovsk area of the Povolzh'ye Region. *Paleontol. J.* **4**, 87–91 (1985).
- Fischer, V., Masure, E., Arkhangelsky, M. S. & Godefroit, P. A new Barremian (Early Cretaceous) ichthyosaur from western Russia. J. Vertebr. Paleontol. 31, 1010–1025 (2011).
- 52. Huene, F. von. Beitrag zur Kenntnis mariner mesozoicher Wirbeltiere in Argentinien. *Cent. für Mineral. Geol. und Paläntologie, B* **1927,** 22–29 (1927).
- Broili, F. Ein neuer Ichthyosaurus aus der norddeutschen Kreide. *Palaeontographica* 54, 139–162 (1907).
- 54. Druckenmiller, P. S. & Maxwell, E. E. A new Lower Cretaceous (lower Albian) ichthyosaur genus from the Clearwater Formation, Alberta, Canada. *Can. J. Earth Sci.* 47, 1037–1053 (2010).
- 55. Maxwell, E. E. & Caldwell, M. W. A new genus of ichthyosaur from the Lower Cretaceous of Western Canada. *Palaeontology* **49**, 1043–1052 (2006).
- M'Coy, F. On the occurrence of Ichthyosaurus and Plesiosaurus in Australia. Ann. Mag. Nat. Hist. third Ser. 19, 355–356 (1867).
- 57. Nace, R. L. A new ichthyosaur from the Upper Cretaceous Mowry Formation of Wyoming. *Am. J. Sci.* 237, 673–686 (1939).
- 58. Seeley, H. G. Index of the fossil remains of Aves, Ornithosauria and Reptilia, from the Secondary System of Strata Aranged in the Woodward Museum of the University of Cambridge. (1869).
- 59. Carter, J. Notice of the jaws of an Ichthyosaurus from the chalk in the neighbourhood of Cambridge. *Reports Br. Assoc. Adv. Sci.* **1845**, 60 (1846).
- Arkhangelsky, M. S. On the ichthyosaurian genus *Platypterygius*. *Paleontol. J.* 32, 611–615 (1998).
- 61. Broili, F. Ichthyosaurierreste aus der Kriede. Neues Jahrb. für Mineral. Geol. und

Paläontologie. Beilage 25, 422–442 (1908).

- 62. Eichwald, K. E. Einige paläontologische Bemerkungen über den Eisensand von Kursk. *Bull. la Société Impériale des Nat. Moscou* **2**, 209–231 (1853).
- 63. Eichwald, K. E. Lethaea Rossica ou Paléontologie de la Russie. Second Volume. Période Moyenne. (1865).
- 64. Merriam, J. C. The types of limb-structure in the Triassic Ichthyosauria. *Am. J. Sci. Fourth Ser.* **19**, 23–30 (1905).
- Merriam, J. C. Triassic Ichthyopterygia from California and Nevada. Univ. Calif. Publ. Bull. Dep. Geol. 3, 63–108 (1902).
- 66. Kuhn, O. Ichthyosauria. Fossilium Catalogus I: Animalia 63, (W. Junk, 1934).
- 67. Kuhn, O. Sauropterygia. Fossilium Catalogus I: Animalia 69, (W. Junk, 1934).
- Kiprijanoff, W. Studien über die fossilen Reptilien Russlands. Theil 1, Gattung Ichthyosaurus König aus dem severischen Sandstein oder Osteolith der Kreide-Gruppe. Mémoires l'Académie impériale des Sci. St.-Pétersbourg, VIIe série 28, 1–103 (1881).
- Kiprijanoff, W. Studien uber die fossilen Reptilien Russlands. 2. Theil. Gattung Plesiosaurus Conybeare aus dem Sewerschen Sandstein oder Osteolith der Keridegruppe. Mémoires l'Académie impériale des Sci. St.-Pétersbourg, VIIe série 30, 1–55 (1882).
- Kiprijanoff, W. Studien uber die fossilen Reptilien Russlands. 3. Theil. Gruppe Thaumatosauria n. Aus der Kreide-Formation und dem Moskauer Jura. Mémoires l'Académie impériale des Sci. St.-Pétersbourg, VIIe série 31, 1–57 (1883).
- Kiprijanoff, W. Studien uber die fossilen Reptilien Russlands. 4. Theil. Ordung Crocodilia Oppel. Indeterminirte fossile Reptilien . Mémoires l'Académie impériale des Sci. St.-Pétersbourg, VIIe série 31, 1–29 (1883).
- 72. McGowan, C. The systematics of Cretaceous ichthyosaurs with particuliar reference to the material from North America. *Contrib. to Geol.* **11**, 9–29 (1972).
- Koken, E. Die Reptilien der norddeutschen unteren Kreide. Zeitschrift der Dtsch. Geol. Gesellschaft 35, 735–827 (1883).
- 74. Meyer von, H. Ichthyosaurus strombecki aus dem Eisenstein der unteren Kreide bei

Gross-Döhren. Palaeontographica 10, (1862).

- Storrs, G. W., Arkhangelsky, M. S. & Efimov, V. M. in *The Age of Dinosaurs in Russia and Mongolia* (eds. Benton, M. J., Shiskin, M. A., Unwin, D. M. & Kurochkin, E. N.) 187–210 (Cambridge University Press, 2000).
- 76. Bogolubov, N. N. Sur quelques restes de deux reptiles (*Cryptoclidus simbirskensis* n. sp. et *Ichthyosaurus steleodon* n. sp.) trouvés par Mr. le Profess. P. Pavlow sur les bords de la Volga dans les couches mesozoïques de Simbirsk. *Annu. géologique minéralogique Russ.* 11, 42–64 (1909).
- Scheyer, T. M. & Moser, M. Survival of the thinnest: rediscovery of Bauer's (1898) ichthyosaur tooth sections from Upper Jurassic lithographic limestone quarries, south Germany. Swiss J. Geosci. 104, S147–S157 (2011).
- Cornuel, M. J. Note sur deux portions de mâchoire fossile rapportées à un Gavial et recueillies dans le terrain crétacé inférieur du département de la Haute-Marne. *Bull. La* société géologique Fr. série 2 8, 170–174 (1851).
- Cornuel, M. J. Description de débris de poissons fossiles provenant principalement du calcaire néocomien du département de la Haute-Marne. *Bull. la Société géologique Fr. série 3* 5, 604–626 (1877).
- Cornuel, M. J. Note sur les ossements fossiles découverts dans le calcaire de néocomien de Wassy (Haute-Marne). Bull. la Société géologique Fr. deuxième série 7, 702–704 (1850).
- Lapparent, A. F. de & Stchepinsky, V. Les Iguanodons de la région de Saint-Dizier (Haute-Marne). Comptes Rendus l'Académie des Sci. Paris, série D 266, 1370–1372 (1968).
- 82. Efimov, V. M. A new genus of ichthyosaurs from the Late Cretaceous of the Ulyanovsk Volga region. *Paleontol. J.* **31**, 422–426 (1997).
- Maisch, M. W. & Matzke, A. T. The Ichthyosauria. *Stuttgarter Beiträge zur Naturkd*. Ser. B (Geologie und Paläontologie) 298, 1–159 (2000).
- 84. Fischer, V. *et al. Simbirskiasaurus* and *Pervushovisaurus* reassessed: implications for the taxonomy and cranial osteology of Cretaceous platypterygiine ichthyosaurs. *Zool. J. Linn. Soc.* 171, 822–841 (2014).

- Martin, K. Ein Ichthyosaurus von Ceram. Jaarb. van het Mijnwezen, Ned. Oost-Indië 17, 3–19 (1888).
- Godefroit, P. Les grands ichthyosaures sinémuriens d'Arlon. Bull. l'Institut R. des Sci. Nat. Belgique Sci. la Terre 63, 25–71 (1993).
- Maisch, M. W., Reisdorf, A., Schlatter, R. & Wetzel, A. A large skull of *Ichthyosaurus* (Reptilia: Ichthyosauria) from the Lower Sinemurian (Lower Jurassic) of Frick (NW Switzerland). *Swiss J. Geosci.* 101, 617–627 (2008).
- Vincent, P. *et al.* Mary Anning's legacy to French vertebrate palaeontology. *Geol.* Mag. 151, 7–20 (2014).
- Maxwell, E. E., Caldwell, M. W. & Lamoureux, D. O. Tooth histology in the Cretaceous ichthyosaur *Platypterygius australis*, and its significance for the conservation and divergence of mineralized tooth tissues in amniotes. *J. Morphol.* 272, 129–135 (2011).
- 90. Maxwell, E. E., Caldwell, M. W. & Lamoureux, D. O. Tooth histology, attachment, and replacement in the Ichthyopterygia reviewed in an evolutionary context. *Paläontologische Zeitschrift* 86, 1–14 (2012).
- Arkhangelsky, M. S., Averianov, A. O., Pervushov, E. M., Ratnikov, V. Y. & Zozyrev, N. Y. On ichthyosaur remains from the Cretaceous of the Voronezh region. *Paleontol. J.* 42, 287–291 (2008).
- Kear, B. P. & Zammit, M. In utero foetal remains of the Cretaceous ichthyosaurian *Platypterygius*: ontogenetic implications for character state efficacy. *Geol. Mag.* 151, 71–86 (2014).
- 93. Carter, J. On the occurence of a new species of Ichthyosaurus in the Chalk. London Geol. J. 1, (1846).
- Sauvage, H. E. Recherches sur les reptiles trouvées dans le Gault de l'Est du bassin de Paris. Mémoires la Société géologique Fr. 3e série 2, 21–24 (1882).
- 95. Buffetaut, E. Remarques préliminaires sur l'ichthyosaure de Saint-Jouin (76). *Bull. la Société Géologique Normandie Amis du Muséum du Havre* **64,** 17–19 (1977).
- 96. Buffetaut, E. *et al.* Les vertébrés de la partie moyenne du Crétacé en Europe. *Cretac*. *Res.* 2, 275–281 (1981).
- 97. Buffetaut, E., Tomasson, R. & Tong, H. Restes fossiles de grands reptiles jurassiques et crétacés dans l'Aube (France). *Bull. d'information des géologues du bassin Paris* 40, 33–43 (2003).
- McGowan, C. & Motani, R. Part 8. Ichthyopterygia. Handbook of Paleoherpetology 8, (Verlag Dr. Friedrich Pfeil, 2003).
- Arkhangelsky, M. S. & Averianov, A. O. On the find of a primitive hadrosaurid dinosaur (Ornitishia, Hadrosauroidea) in the Cretaceous of the Belgorod Region. *Paleontol. J.* 37, 58–61 (2003).
- 100. Maxwell, E. E. Generic reassignment of an ichthyosaur from the Queen Elizabeth Islands, Northwest Territories, Canada. J. Vertebr. Paleontol. **30**, 403–415 (2010).
- 101. Owen, R. A monograph on the fossil Reptilia of the Cretaceous formations. (The Palæntological Society, 1851).
- Milner, A. C. in *Fossils of the Chalk* (eds. Owen, E. & Smith, A. B.) 2, 266–280 (The Palaeontological Association field guides to fossils, 1987).
- 103. Morière, J. Découverte d'une tête incomplète de saurien dans un bloc de craie tombée de la partie supérieure de la falaise située entre Auberville et Villers-sur-mer. Bull. la Société Linéenne Normandie, troisième série 1, 129–130 (1877).
- 104. Blain, H.-A., Pennetier, G. & Pennetier, E. Présence du genre *Platypterygius* (Ichthyosauria, Reptilia) dans le Cénomanien inférieur de Villers-sur-Mer (Normandie, France. *Echos des falaises* 7, 35–50 (2003).
- 105. Zawischa, D. Saurierzähne aus Wunstorf. Arbeitskr. Paläontologie Hann. 10, 16–17 (1982).
- 106. Wittler, F. A. & Roth, R. Ein Ichthyosaurier aus dem Cenoman des Münsterlandes. Arbeitskr. Paläontologie Hann. 29, 76–81 (2001).
- 107. Wittler, F. A. Besonderheiten aus der Oberkreide von Dortmund I: Ein Ichthyosaurierzahn aus dem südwestfälischen Cenoman. Dortmunder Beitrage zue Landeskunde-Naturwissenschaftliche Mitteilungen 42, 59-61 (2010).
- 108. Diedrich, C. G. New ichthyosaur remains of Platypterygius cf. campylodon (Carter 1846) (Ichthyopterygia, Reptilia) from the Cenomanian of NW Germany. *Münstersche Forschungen zur Geol. und Paläontologie* **93**, 97–108 (2002).

- 109. Bardet, N., Wellnhofer, P. & Herm, D. Discovery of ichthyosaur remains (Reptilia) in the upper Cenomanian of Bavaria. *Mitteilungen der Bayer. Staatssammlung für Paläontologie und Hist. Geol.* 34, 213–220 (1994).
- Bardet, N. Stratigraphic evidence for the extinction of the ichthyosaurs. *Terra Nov.* 4, 649–656 (1992).
- 111. Capellini, G. Ichthyosaurus campylodon e tronchi di cicadee nelle argille scagliose dell emilia. *Mem. della R. Accad. delle Sci. di Bol. Ser. IV* **10**, 431–450 (1890).
- Sirotti, A. & Papazzoni, C. On the Cretaceous ichthyosaur remains from the Northern Apennines (Italy). *Boll. della Soc. Paleontol. Ital.* 41, 237–248 (2002).
- 113. Machalski, M., Komorowski, A. & Harasimiuk, M. Nowe perspektywy poszukiwan morskich kregowców kredowych w nieczynnej kopalni fosforytów w Annopolu nad Wisla. *Prz. Geol.* 57, 1–4 (2009).
- Pervushov, E. M., Arkhangelsky, M. S. & Ivanov, A. V. Catalog of the locations of the remainders of sea reptiles in the Jurassic and Cretaceous of the Lower Volga Region. (Saratov University, 1999).
- Merriam, J. C. The occurrence of ichthyosaur-like remains in the Upper Cretaceous of Wyoming. *Science* (80-.). 22, 640–641 (1905).
- 116. Gilmore, C. W. A second occurence of ichthyosaurian remains in the Benton Cretaceous. *Science (80-.).* **39,** 210 (1914).
- Slaughter, B. H. & Hoover, B. R. Occurences of Ichthyosaurian Remains in the Cretaceous of Texas. *Texas J. Sci.* 15, 339–343 (1963).
- Nace, R. L. A new ichthyosaur from the Late Cretaceous of northeastern Wyoming. Am. J. Sci. 239, 908–914 (1941).
- Maxwell, E. E. & Kear, B. P. Postcranial anatomy of *Platypterygius americanus* (Reptilia: Ichthyosauria) from the Cretaceous of Wyoming. *J. Vertebr. Paleontol.* 30, 1059–1068 (2010).
- Lydekker, R. Indian pre-Tertiary Vertebrata. Fossil Reptilia and Batrachia. *Mem. Geol. Surv. India* 1, 1–36 (1879).
- 121. Lydekker, R. Note on the classification of the Ichthyopterygia with a notice of two new species. *Geol. Mag. third Ser.* **5**, 309–314 (1888).

- 122. Underwood, C. J., Goswami, A., Prasad, G. V. R., Verma, O. & Flynn, J. J. Marine vertebrates from the 'Middle' Cretaceous (Early Cenomanian) of South India. J. Vertebr. Paleontol. 31, 539–552 (2011).
- 123. Verma, O. Cretaceous vertebrate fauna of the Cauvery Basin, southern India: Palaeodiversity and palaeobiogeographic implications. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* (2015). doi:10.1016/j.palaeo.2015.04.021
- Maxwell, E. E. New metrics to differentiate species of *Stenopterygius* (Reptilia: Ichthyosauria) from the Lower Jurassic of southwestern Germany. *J. Paleontol.* 86, 105–115 (2012).
- 125. McGowan, C. A new and typically Jurassic ichthyosaur from the Upper Triassic of Birtish Columbia. *Can. J. Earth Sci.* **33**, (1996).
- 126. Fischer, V. New data on the ichthyosaur *Platypterygius hercynicus* and its implications for the validity of the genus. *Acta Palaeontol. Pol.* **57**, 123–134 (2012).
- 127. Druckenmiller, P. S., Hurum, J., Knutsen, E. M. & Nakrem, H. A. Two new ophthalmosaurids (Reptilia: Ichthyosauria) from the Agardhfjellet Formation (Upper Jurassic: Volgian/Tithonian), Svalbard, Norway. Nor. J. Geol. 92, 311–339 (2012).
- 128. Maxwell, E. E., Fernández, M. S. & Schoch, R. R. First diagnostic marine reptile remains from the Aalenian (Middle Jurassic): a new ichthyosaur from southwestern Germany. *PLoS One* 7, e41692 (2012).
- 129. Maxwell, E. E., Zammit, M. & Druckenmiller, P. S. Morphology and orientation of the ichthyosaurian femur. *J. Vertebr. Paleontol.* **32**, 1207–1211 (2012).
- Motani, R. On the evolution and homologies of ichthyosaurian forefins. J. Vertebr. Paleontol. 19, 28–41 (1999).
- Maisch, M. W. & Matzke, A. T. The cranial osteology of the ichthyosaur Leptonectes </i>
 </i>
 cf.<i>> tenuirostris from the Lower Jurassic of England. J. Vertebr. Paleontol. 23, 116–127 (2003).
- Motani, R. True skull roof configuration of *Ichthyosaurus* and *Stenopterygius* and its implications. *J. Vertebr. Paleontol.* 25, 338–342 (2005).
- Fernández, M. Dorsal or ventral? Homologies of the forefin of *Caypullisaurus* (Ichthyosauria: Ophthalmosauria). J. Vertebr. Paleontol. 21, 515–520 (2001).

- Motani, R. *et al.* First evidence of centralia in Ichthyopterygia reiterating bias from paedomorphic characters on marine reptile phylogenetic reconstruction. *J. Vertebr. Paleontol.* 1–6 (2015). doi:10.1080/02724634.2014.948547
- 135. Benson, R. B. J., Butler, R. J., Lindgren, J. & Smith, A. S. Mesozoic marine tetrapod diversity: mass extinctions and temporal heterogeneity in geological megabiases affecting the vertebrates. *Proc. R. Soc. B Biol. Sci.* 277, 829–834 (2010).
- Benson, R. B. J. & Butler, R. J. in *Comparing the geological and fossil records: implications for biodiversity studies* (eds. McGowan, A. J. & Smith, A. B.) **358**, 191– 208 (Geological Society, Special Publications, 2011).
- Gasparini, Z. & Fernández, M. in *The Neuquén Basin, Argentina: A case study in sequence stratigraphy and basin dynamics* (eds. Veiga, G. D., Spalletti, L. A., Howell, J. A. & Schwarz, E.) 252, 279–294 (Geological Society, special Publications, 2005).
- Fernández, M. in *Patagonian Mesozoic Reptiles* (eds. Gasparini, Z., Salgado, L. & Coria, R. A.) 271–291 (Indiana University Press, 2007).
- Maisch, M. W. & Matzke, A. T. Mikadocephalus gracilirostris n. g. n. sp., a new ichthyosaur from the Grenzbitumenzone (Anisian-Ladinian) of Monte San Giorgio (Switzerland). Paläontologische Zeitschrift 71, 267–289 (1997).
- 140. Maisch, M. W. Observations on Triassic ichthyosaurs; Part V, The skulls of Mikadocephalus and Wimanius reconstructed. *Neues Jahrbuch für Geologie und Paläontologie. Monatshefte* 1999, 345–356 (1999).
- McGowan, C. A remarkable small ichthyosaur from the Upper Triassic of British Columbia, representing a new genus and species. *Can. J. Earth Sci.* 32, 292–303 (1995).
- 142. McGowan, C. An ichthyosaur forefin from the Triassic of British Columbia exemplifying Jurassic features. *Can. J. Earth Sci.* **28**, 1553–1560 (1991).
- 143. von Hillebrandt, A. & Krystyn, L. On the oldest Jurassic ammonites of Europe (Northern Calcareous Alps, Austria) and their global significance. *Neues Jahrb. für Geol. und Paläontologie, Abhandlungen* 253, 163–195 (2009).
- 144. Benson, R. B. J., Evans, M. & Druckenmiller, P. S. High diversity, low disparity and small body size in plesiosaurs (Reptilia, Sauropterygia) from the Triassic–Jurassic

boundary. PLoS One 7, e31838 (2012).

- 145. Maisch, M. W. & Reisdorf, A. G. Evidence for the longest stratigraphic range of a post-Triassic Ichthyosaur: a *Leptonectes tenuirostris* from the Pliensbachian (Lower Jurassic) of Switzerland. *Geobios* 39, 491–505 (2006).
- 146. Godefroit, P. Présence de *Leptopterygius tenuirostris* (Reptilia, Ichthyosauria) dans le Lias moyen de Lorraine belge. *Bull. l'Institut R. des Sci. Nat. Belgique Sci. la Terre* 62, 163–170 (1992).
- 147. Conybeare, W. D. Additional notes on the fossil genera *Ichthyosaurus* and *Plesiosaurus*. *Trans. Geol. Soc. London* **2**, 103–123 (1822).
- McGowan, C. Computed tomography reveals further details of *Excalibosaurus*, a putative ancestor for the swordfish-like ichthyosaur *Eurhinosaurus*. J. Vertebr. Paleontol. 9, 269–281 (1989).
- McGowan, C. A putative ancestor for the swordfish-like ichthyosaur *Eurhinosaurus*. *Nature* 322, 454–456 (1986).
- McGowan, C. A new specimen of *Excalibosaurus* from the English Lower Jurassic. J. Vertebr. Paleontol. 23, 950–956 (2003).
- 151. Reisdorf, A., Maisch, M. W. & Wetzel, A. First record of the leptonectid ichthyosaur Eurhinosaurus longirostris from the Early Jurassic of Switzerland and its stratigraphic framework. Swiss J. Geosci. 104, 211–224 (2011).
- 152. Godefroit, P. Les reptiles marins du Toarcien (Jurassique inférieur) belgoluxembourgeois. *Mémoires pour Serv. à l'Explication des Cart. Géologiques Minières la Belgique* **39**, 98 (1994).
- Lamaud, P. Les Ichthyosaures et la mer toarcienne du Pic Saint-Loup. *Minéraux Foss.* Le Guid. du Collect. 58, 42–49 (1979).
- Pharisat, A., Contini, D. & Frikert, J.-C. Early Jurassic (Lower Toarcian) 'ichthyosaurs' from France-Comté, France. *Rev. Paléobiologie, Vol. spécial* 7, 189– 198 (1993).
- Pharisat, A. L'ichthyosaure de la base des schistes-cartons du Toarcien inférieur de Noirefontaine (Doubs). Société d'Histoire Nat. du Pays Montbéliard 1993, 193–198 (1993).

- 156. Fischer, V., Guiomar, M. & Godefroit, P. New data on the palaeobiogeography of Early Jurassic marine reptiles: the Toarcian ichthyosaur fauna of the Vocontian Basin (SE France). *Neues Jahrb. für Geol. und Paläontologie* 261, 111–127 (2011).
- 157. Huene, F. von. *Die Ichthyosaurier des Lias und ihre Zusammenhänge. Monographien zur Geologie und Paläontologie* **1**, (Verlag von Gebrüder Borntraeger, 1922).
- 158. Huene, F. von. Ein neuer Fund von Eurhinosaurus longirostris. Neues Jahrb. für Geol. und Paläontologie, Abhandlungen **93**, 277–283 (1951).
- McGowan, C. A revision of the Lower Jurassic ichthyosaurs of Germany with descriptions of two new species. *Palaeontogr. Abteilung A. Paläozoologie, Stratigr.* 166, 93–135 (1979).
- Jäger, G. über eine neue species von Ichthyosauren (*Ichthyosaurus longirostris* Owen & Jäger). Nebst Bemerkungen über die übrigen in der Liasformation Würtembergs aufgefundenen Reptiliien. *Novum actorum Acad. caesarae Leopoldino-Carolinae naturae curiosorum* 25, 937–967 (1856).
- 161. Maisch, M. W. A new ichthyosaur genus from the Posidonia Shale (Lower Toarcian, Jurassic) of Holzmaden, SW-Germany with comments on the phylogeny of post-Triassic ichthyosaurs. *Neues Jahrb. für Geol. und Paläontologie, Abhandlungen* 209, 47–78 (1998).
- Maisch, M. W. Neue Exemplare der seltenen Ichthyosauriergattung Suevoleviathan Maisch 1998 aus dem Unteren Jura von Südwestdeutschland. Geol. Palaeontol. 35, 145–160 (2001).
- Martin, J. E., Fischer, V., Vincent, P. & Suan, G. A longirostrine *Temnodontosaurus* (Ichthyosauria) with comments on Early Jurassic ichthyosaur niche partitioning and disparity. *Palaeontology* 55, 995–1005 (2012).
- 164. McGowan, C. A revision of the longipinnate ichthyosaurs of the Lower Jurassic of England, with description of the new species (Reptilia, Ichthyosauria). *Life Sci. Contrib. R. Ontario Museum* 97, 1–37 (1974).
- McGowan, C. *Temnodontosaurus risor* is a juvenile of *T. platyodon* (Reptilia: Ichthyosauria). J. Vertebr. Paleontol. 14, 472–479 (1994).
- 166. Maisch, M. W. & Hungerbühler, A. New evidence for a discrete supratemporal bone in

the Jurassic Ichthyosaur Temnodontosaurus. Hist. Biol. 15, 335–345 (2001).

- Maisch, M. W. A braincase of *Temnodontosaurus nuertingensis* cf. *trigonodon* (von Theodori, 1843) (Ichthyosauria) from the Lower Jurassic of Germany. *Geol. Palaeontol.* 36, 115–122 (2002).
- 168. Gaudry, A. L'Ichthyosaurus burgundiæ. Bull. la Société d'Histoire Nat. d'Autun 5, 1–9 (1892).
- 169. Lydekker, R. Catalogue of the fossil Reptilia and Amphibia in British Museum (Natural History). Part II. containing the orders Ichthyopterygia and Sauropterygia. (Printed by Orders of the Trustees of the British Museum, London, 1889).
- Maisch, M. W. Revision der Gattung *Stenopterygius* Jaekel, 1904 emend. von Huene, 1922 (Reptilia: Ichthyosauria) aus dem unteren Jura Westeuropas. *Palaeodiversity* 1, 227–271 (2008).
- Caine, H. & Benton, M. J. Ichthyosauria from the upper Lias of Strawberry Bank, England. *Palaeontology* 54, 1069–1093 (2011).
- Bennett, S. P. *et al.* A new specimen of *Ichthyosaurus communis* from Dorset, UK, and its bearing on the stratigraphical range of the species. *Proc. Geol. Assoc.* 123, 146–154 (2012).
- 173. Godefroit, P. Un crâne d'*Ichthyosaurus communis* (Reptilia, Ichthyosauria) du Sinémurien supérieur de Lorraine belge. *Bull. la Société belge Géologie* 104, 77–89 (1996).
- Sollas, W. J. The skull of Ichthyosaurus, studied in serial sections. *Philos. Trans. R. Soc. London, Ser. B* 208, 63–126 (1916).
- 175. Delair, J. B. Unusual preservation of fibrous elements in an ichthyosaur skull. *Nature* 212, 575–576 (1966).
- McGowan, C. The cranial morphology of the Lower Liassic latipinnate ichthyosaurs of England. *Bull. Br. Museum (Natural Hist. Geol.* 24, 1–109 (1973).
- 177. de la Beche, H. T. & Conybeare, W. D. Notice of the discovery of a new fossil animal, forming a link between the *Ichthyosaurus* and Crocodile, together with general remarks on the Osteology of the Ichthyosaurus. *Trans. Geol. Soc. London* **5**, 559–594 (1821).
- 178. Dechaseaux, C. L'arrière-crâne d'un ichthyosaurien du Lias. Ann. Paléontologie 40,

67-77 (1954).

- 179. Maisch, M. W. & Ansorge, J. The Liassic ichthyosaur Stenopterygius cf. S. quadrissicus from the lower Toarcian of Dobbertin (NE Germany) and some considerations on lower Toarcian marine reptile palaeobiogeography. Paläontologische Zeitschrift 78, 161–171 (2004).
- 180. Quenstedt, F. A. Der Jura. (1856).
- 181. Spalletti, L., Gasparini, Z. & Fernández, M. Facies, ambientes y reptiles marinos de la transición entre las formaciones Los Molles y Lajas (Jurasico medio), cuenca nequina, Argentina. Acta Geol. Leopoldensis 39, 329–344 (1994).
- Fernández, M. A new long-snouted ichthyosaur from the early Bajocian of Neuquén basin (Argentina). *Ameghiniana* 31, 291–297 (1994).
- 183. Bardet, N. et al. Découverte de l'ichthyosaure Ophthalmosaurus dans le Tithonien (Jurassique supérieur) du Boulonnais, Nord de la France. Neues Jahrb. für Geol. und Paläontologie, Abhandlungen 205, 339–354 (1997).
- 184. Seeley, H. G. On the pectoral arch and fore limb of *Ophthalmosaurus*, a new ichthyosaurian genus from the Oxford Clay. Q. J. Geol. Soc. London 30, 696–707 (1874).
- Andrews, C. W. Note on the osteology of *Ophthalmosaurus icenicus* Seeley an ichthyosaurian Reptile from the Oxford Clay of Peterborough. *Geol. Mag.* 4, 202–208 (1910).
- 186. Andrews, C. W. A descriptive catalogue of the Marine Reptiles of the Oxford Clay, part II. (British Museum of Natural History, 1913).
- Appleby, R. M. The osteology and taxonomy of the fossil reptile *Ophthalmosaurus*. *Proc. Zool. Soc. London* **126**, 403–447 (1956).
- 188. Appleby, R. M. On the cranial morphology of ichthyosaurs. *Proc. Zool. Soc. London* 137, 333–370 (1961).
- Maisch, M. W. Variationen im Verlauf der Gerhinnerven bei Ophthalmosaurus (Ichthyosauria, Jura). Neues Jahrb. für Geol. und Paläontologie, Monatshefte 1997, 425–433 (1997).
- 190. Maisch, M. W. The temporal region of the Middle Jurassic ichthyosaur

Ophthalmosaurus: further evidence for the non-diapsid cranial architecture of the Ichthyosauria. *Neues Jahrb. für Geol. und Paläontologie. Monatshefte* **1998**, 401–414 (1998).

- 191. Araújo, R., Smith, A. S. & Liston, J. The Alfred Leeds fossil vertebrate Collection of the National Museum of Ireland–Natural History. *Irish J. Earth Sci.* **26**, 17–32 (2008).
- Massare, J. A. & Young, H. A. Gastric contents of an ichthyosaur from the Sundance formation (Jurassic) of central Wyoming. *Paludicola* 5, 20–27 (2005).
- 193. Massare, J. A., Buchholtz, E. A., Kenney, J. & Chomat, A.-M. Vertebral morphology of *Ophthalmosaurus natans* (Reptilia: Ichthyosauria) from the Jurassic Sundance Formation of Wyoming. *Paludicola* 5, 242–254 (2006).
- 194. Wahl, W. R. Taphonomy of a nose dive: bone and tooth displacement and mineral accretion in an ichthyosaur skull. *Paludicola* **7**, 107–116 (2009).
- 195. Marsh, O. C. A new Order of Extinct Reptiles (Sauronodonta), from the Jurassic Formation of the Rocky Mountains. *Am. J. Sci. Third Ser.* **17**, 85–86 (1878).
- 196. Gilmore, C. W. Discovery of teeth in *Baptanodon*, an ichthyosaurian from the Jurassic of Wyoming. *Science* (80-.). **16**, 913–914 (1902).
- 197. Gilmore, C. W. Notes on osteology of *Baptanodon. Mem. Carnegie Museum* II, 325–337 (1906).
- 198. Gilmore, C. W. New species of *Baptanodon. Am. J. Sci. Fourth Ser.* 23, 193–198 (1907).
- 199. Maxwell, E. E. & Druckenmiller, P. S. A small ichthyosaur from the Clearwater Formation (Alberta, Canada) and a discussion of the taxonomic utility of the pectoral girdle. *Paläontologische Zeitschrift* 85, 457–463 (2011).
- Fernández, M. A new ichthyosaur from the Los Molles Formation (Early Bajocian), Neuquén basin, Argentina. J. Paleontol. 73, 677–681 (1999).
- 201. Boulenger, G. A. On a new species of ichthyosaur from Bath. *Proc. Zool. Soc. London* 1904, 424–426 (1904).
- 202. McGowan, C. The taxonomic status of the Late Jurassic ichthyosaur *Grendelius mordax*: a preliminary report. *J. Vertebr. Paleontol.* **17**, 428–430 (1997).

- Sauvage, H. E. Catalogue des reptiles trouvées dans le terrain jurassique supérieur du Boulonnais. *Comptes rendus l'Association française pour l'avancement des Sci.* 28, 416–419 (1899).
- 204. Lennier, G. Description des fossiles du Cap de la Hève. Bull. la Société géologique Normandie 12, 17–98 (1887).
- 205. Valenciennes, M. A. D'une tête de grand Ichthyosaure, trouvée dans l'argile de Kimmeridge par M. Lennier, au cap de la Hève, près du Havre. C. R. Hebd. Seances Acad. Sci. 53, 276–273 (1861).
- 206. Russell, D. A. in *The Geology of Melville Island, Artic Canada* (eds. Christie, R. L. & McMilan, N. J.) 450, 195–201 (Bulletin of the Geological Survey of Canada, 1993).
- 207. Fernández, M. S. & Maxwell, E. E. The genus Arthropterygius Maxwell (Ichthyosauria: Ophthalmosauridae) in the Late Jurassic of the Neuquén Basin, Argentina. Geobios 45, 535–540 (2012).
- Zverkov, N. G., Arkhangelsky, M. S., Pardo-Pérez, J. & Beznosov, P. A. On the Upper Jurassic ichthyosaur remains from the Russian North. *Proc. Zool. Inst. RAS* **319**, 81–97 (2015).
- 209. Fernández, M. Redescription and phylogenetic position of *Caypullisaurus* (Ichthyosauria: Ophthalmosauridae). *J. Paleontol.* **81**, 368–375 (2007).
- 210. Wagner, A. Die Characteristic einer neuen Art von Ichthyosaurus aus den lithographischen Schiefern und eines Zahnes von Polyptychodon aus dem Gründsandsteine von Kelheim. Bull. der königlische Akad. der Wissenschaft, Gelehrt. Anzeigen 3, 25–35 (1853).
- Meyer von, H. Ichthyosaurus leptospondylus aus dem lithographischen Schiefer von Eichstätt. *Palaeontographica* 11, 222–225 (1863).
- 212. Fraas, E. E. Ichthyosaurier der Süddeutschen Trias und Jura-Ablagerungen. (H. Laupp, 1891).
- 213. Gasparini, Z. *et al.* Reptiles from Lithographic Limestones of the Los Catutos Member (Middle-Upper Tithonian), Neuquén Province, Argentina: an essay on its taxonomic composition and preservation in an environmental and geographic context. *Ameghiniana* 52, 1–28 (2015).

- 214. Zammit, M. A review of Australasian ichthyosaurs. Alcheringa 34, 281–292 (2010).
- 215. Wade, M. Platypterygius australis, an Australian Cretaceous ichthyosaur. *Lethaia* 17, 99–113 (1984).
- 216. Zammit, M., Norris, R. M. & Kear, B. P. The Australian Cretaceous ichthyosaur *Platypterygius australis*: a description and review of postcranial remains. J. Vertebr. *Paleontol.* 30, 1726–1735 (2010).
- 217. Kolb, C. & Sander, P. M. Redescription of the ichthyosaur *Platypterygius hercynicus* (Kuhn 1946) from the Lower Cretaceous of Salzgitter (Lower Saxony, Germany). *Palaeontogr. Abteilung A (Paläozoologie, Stratigr.* 288, 151–192 (2009).
- Hoedemaeker, P. J. On the Barremian lower Albian stratigraphy of Colombia. Scr. Geol. 128, 3–15 (2004).
- 219. Sander, P. M. Ichthyosauria: their diversity, distribution, and phylogeny. *Paläontologische Zeitschrift* 74, 1–35 (2000).
- 220. Godefroit, P. The skull of *Stenopterygius longifrons* (Owen, 1881). *Rev. Paléobiologie Genève Vol. spécial* **7**, 67–84 (1993).
- 221. Mazin, J.-M. Affinités et phylogénie des Ichthyopterygia. *Geobios, mémoire spécial* 6, 85–98 (1982).
- 222. Goloboff, P., Farris, J. & Nixon, K. T.N.T. 1.1: Tree Analysis Using New Technology. Available at www.zmuc.dk/public/phylogeny/TNT/. (2010).
- 223. Swofford, D. L. PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4. (2002).
- 224. R Core Team. R: A language and environment for statistical computing. (2015).
- 225. Ronquist, F. & Huelsenbeck, J. P. MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* **19**, 1572–1574 (2003).
- Scott, R. W. A Cretaceous chronostratigraphic database: construction and applications. *Notebooks Geol.* 14, 15–37 (2014).
- 227. Travassac, F. Stratigraphie, sédimentologie et géochimie d'une série d'âge barrémien supérieur à albien pro parte du bassin vocontien (SE France): implications paléoenvironnmentales. DEA, (Ecole doctorale Sciences de l'Environnement d'Aix-

Marseille, 2004).

- 228. Amédro, F. Support for a Vraconnian Stage between the Albien sensu stricto and the Cenomanien (Cretacous System). *Notebooks Geol.* Memoir 200, 83 (2008).
- 229. Amédro, F. & Robaszynski, F. Zonation by ammonites and foraminifers of the Vraconnian-Turonian interval: A comparison of the Boreal and Tethyan domains (NW Europe / Central Tunisia). *Notebooks Geol. Lett.* 2008/02, 5 (2008).
- 230. Lehmann, J., Heldt, M., Bachmann, M. & Hedi Negra, M. E. Aptian (Lower Cretaceous) biostratigraphy and cephalopods from north central Tunisia. *Cretac. Res.* 30, 895–910 (2009).
- 231. Scott, R. W. Uppermost Albian biostrigraphy and chronostratigraphy. *Notebooks Geol.*2009/03, 1–16 (2009).
- 232. Owen, H. G. The Gault Group (Early Cretaceous, Albian), in East Kent, S.E. England; its lithology and ammonite biozonation. *Proc. Geol. Assoc.* **123**, 742–765 (2012).
- 233. Kuhnt, W. & Moullade, M. The Gargasian (Middle Aptian) of La Marcouline section at Cassis-La Bédoule (SE France): Stable isotope record and orbital cyclicity. *Notebooks Geol.* 2007/02, 1–9 (2007).
- 234. Cohen, K. M., Finney, S. C., Gibbard, P. L. & Fan, J. The ICS International Chronostratigraphic Chart. *Episodes* **36**, 199–204 (2013).
- 235. Maddison, W. P. & Maddison, D. R. Mesquite: A modular sytem for evolutionary analysis. (2011).
- Suzuki, R. & Shimodaira, H. Hierarchical Clustering with P-Values via Multiscale Bootstrap Resampling. 1–13 (2014).
- 237. Pinheiro, J., Bates, D., DebRoy, S. & Sarkar, D. Package 'nlme'. (2015).
- 238. Mazerolle, M. J. Package 'AICcmodavg'. (2015).
- 239. Burnham, K. P. & Anderson, D. Model Selection and Multi-Model Inference: A Practical Information- Theoretic Approach. (Springer, 2001).