

# CONTRASTING MACROEVOLUTIONARY PATTERNS IN PELAGIC TETRAPODS ACROSS THE TRIASSIC–JURASSIC TRANSITION

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## ABSTRACT

The iconic marine raptorial predators Ichthyosauria and Eosauropterygia co-existed in the same ecosystems throughout most of the Mesozoic Era, facing similar evolutionary pressures and environmental perturbations. Both groups seemingly went through a massive macroevolutionary bottleneck across the Triassic–Jurassic (T/J) transition that greatly reduced their morphological diversity, leaving pelagic lineages as the only survivors. However, analyses of marine reptile disparity across the T/J transition have usually employed coarse morphological and temporal data. We comprehensively compare the evolution of ichthyosaurian and eosauropterygian morphology and body size across the Middle Triassic to Early Jurassic interval and find contrasting macroevolutionary patterns. The ecomorphospace of eosauropterygians predominantly reflects a strong phylogenetic signal, resulting in the clustering of three clades with clearly distinct craniodental phenotypes, suggesting ‘leaps’ towards novel feeding ecologies. Ichthyosaurian diversification lacks a discernible evolutionary trend, as we find evidence for a wide overlap of craniodental morphologies between Triassic and Early Jurassic forms. The temporal evolution of ecomorphological disparity, fin shape and body size of eosauropterygians and ichthyosaurians during the Late Triassic does not support the hypothesis of an abrupt macroevolutionary bottleneck near the T/J transition. Rather, an important turnover event should be sought earlier, during times of rapid sea level falls.

**KEYWORDS:** Ichthyosauria, Eosauropterygia, Triassic, Early Jurassic, evolutionary trajectory, disparity

## INTRODUCTION

During the Mesozoic, reptiles notably occupied upper trophic levels in the marine realm for more than 180 million years (Motani 2009; Bardet et al. 2014). Several independent lineages rapidly invaded the seas in the aftermath of the catastrophic end-Permian mass extinction, each experiencing an ‘early-burst’ radiation that led to the exploration of vacant or novel ecological guilds in shallow-marine environments (Benton et al. 2013; Stubbs and Benton 2016; Cheng et al. 2019; Huang et al. 2020; Moon and Stubbs 2020; Reeves et al. 2021; Qiao et al. 2022). These radiations resulted in a wide range of body sizes, swimming adaptations, and feeding specializations (Stubbs and Benton 2016; Sander et al. 2021; Gutarra et al. 2023; Laboury et al. 2023). Among these reptile lineages, Eosauropterygia (including the speciose post-Triassic plesiosaurians), and Ichthyosauria (the ‘fish-shaped’ reptiles) became the most successful and longest-lived clades of raptorial predators of the Mesozoic (Motani 2009; Bardet et al. 2014). These animals evolved into very distinctive body plans due to strong differences in their craniodental architecture and locomotion style. Indeed, eosauropterygians were paraxial swimmers (e.g., the underwater flying plesiosaurians) characterized by repeated variations in neck length (O’Keefe 2002), while the fusiform ichthyosaurians adopted a tail-propelled swimming mode (Motani 2009; Krahl 2021; Gutarra and Rahman 2021). Often sympatrically distributed (Motani 2009; Bardet et al. 2014), they were affected by the same environmental and ecological pressures, making them a meaningful example for evolutionary comparison. The morphological diversity of both clades peaked during the Middle and early Late Triassic due to the presence of many forms that were adapted to coastal environments. However, many of these coastal forms disappeared by the end of the Triassic and their niches were never reoccupied during the subsequent radiations of these two clades (Dick and Maxwell 2015; Stubbs and Benton 2016; Moon and Stubbs 2020; Reeves et al. 2021).

Indeed, the second half of the Triassic represents a key period in the history of the Mesozoic marine ecosystems, marked by rapid sea level changes that likely drove nearshore marine tetrapods to extinction (Benson and Butler 2011; Kelley et al. 2014). This ultimately left only pelagic lineages to survive and to diversify (Benson et al. 2010, 2012; Thorne et al. 2011; Dick and Maxwell 2015) throughout the rest of the Mesozoic: Plesiosauria within eosauropterygians and Parvipelvia within ichthyosaurians. These extinctions are thought to represent a macroevolutionary bottleneck at the T/J transition (Benson et al. 2010, 2012; Thorne et al. 2011; Dick and Maxwell 2015), because the disparity of speciose assemblages recorded at the start of the Jurassic is generally considered to be very small in comparison to their Triassic predecessors (Thorne et al. 2011; Benson et al. 2012; Stubbs and Benton 2016; Moon and Stubbs 2020; Reeves et al. 2021). Yet, most studies suggesting the existence of a bottleneck in marine reptile disparity were either based on phylogenetic characters (Thorne et al. 2011; Moon and Stubbs 2020) or investigated marine reptile diversification dynamics on a broad scale (Dick and Maxwell 2015; Stubbs and Benton 2016; Reeves et al. 2021; Gutarra et al. 2023), potentially confounding different temporally or phylogenetically isolated events. Here, we reinvestigate the end-Triassic macroevolutionary bottleneck hypothesis by comprehensively analysing the evolution of eosauropterygians and ichthyosaurians in terms of ecomorphospace occupation, fluctuation of disparity and evolution of fin shape, and body size.

## Material and methods

### A) TAXONOMIC AND MORPHOLOGICAL SAMPLING

We gathered a series of functionally important continuous traits for a total of 326 specimens of ichthyosaurians and eosauropterygians, ranging from Middle Triassic to the end of the Early Jurassic (see supplementary materials, Figures S1 and S2). Some functional traits are unique to one clade (e.g., the relative overbite length, which can greatly vary in ichthyosaurians, but not in eosauropterygians), difficult to measure depending on the state of preservation (e.g., crown curvature in ichthyosaurians, as most of their teeth are labio-lingually oriented and thus hardly measurable in teeth preserved *in situ*) or were not well preserved (e.g., sclerotic ring in eosauropterygians). As a result, we always analysed trends for both groups separately (214 eosauropterygian and 112 ichthyosaurian specimens, representing 51 and 32 species respectively). Morphological data were collected through first-hand observation of specimens, and measurements on high precision three-dimensional surface scans using MeshLab v2023.12 (Cignoni et al. 2008). When no other alternatives were available, we populated our datasets by taking measurement from first-hand photographs and figured specimens from the literature by using ImageJ (v.1.53) (Schneider et al. 2012), as well as by using published measurements (see supplementary material: Tables S1–S2 and S4–S5 for the full taxonomic sampling including all the studied specimens, ages of taxa and sources of the data). Measurements were used to generate 31 dimensionless ratios (with only 29 applicable for eosauropterygians; see supplementary material: Morphofunctional ratios and traits section), which have clear craniodental and postcranial morphofunctional implications (Stubbs and Benton 2016; Fischer et al. 2020; MacLaren et al. 2022; Laboury et al. 2023). The apicobasal height of the tooth crown, a proxy determining the range of possible prey items (Fischer et al. 2022), represents the only absolute trait in both ichthyosaurian and eosauropterygian datasets. Finally, we also incorporated six binary discrete traits. Therefore, in total we used 35 for eosauropterygians and 37 traits for ichthyosaurians. We applied a completeness threshold of 40% to each taxa by calculating the percentage of non-missing data for both the craniodental and postcranial regions as well as for the whole body architecture (craniodental and postcranial regions combined) for each group. This procedure serves to remove incomplete taxa (those with less than 40% of data for the corresponding morphological region) and thus minimizes the risk of distortions to our morphospace. However, it also leads to the removal of important but partially known Late Triassic taxa (e.g., *Paludidraco* or *Rhaeticosaurus* for eosauropterygians and *Californosaurus*, *Hudsonelpidia*, *Shonisaurus*, *Shastasaurus* for ichthyosaurians). Nevertheless, even if these taxa could not be integrated into our morphospace and disparity analyses, they are included within the body size and fin shape analyses (see supplementary material: Tables S1–S6). We also temper our interpretations of the results in the light of the absence of these taxa.

### B) PHYLOGENETIC DATA

We analysed the phylogenetic relationships of eosauropterygians and ichthyosaurians in order to generate phylomorphospaces and phenograms. To date, no cladistic matrices or analyses have thoroughly investigated the phylogenetic relationships of all eosauropterygians (both non-plesiosaurians and plesiosaurians) together. Therefore, we created a composite phylogenetic tree by combining topologies generated separately for Triassic eosauropterygians and for Early Jurassic plesiosaurians. Recent studies have recovered two main topologies for Triassic taxa: one where nothosauroids are either closely related to pachypleurosauroids (Hu et al. 2024) and another where they are more closely related to the pistosauroids (Xu et al. 2022). To test the influence of these conflicting topologies on our disparity and ordination analyses, we used datasets from both Hu et al. (2024) and Xu et al. (2022) and grafted their respective Triassic eosauropterygian topologies onto phylogenetic trees generated for the Early Jurassic with the dataset of Wintrich et al. (2017). Results from the composite tree using

the Triassic dataset of Hu et al. (2024) are discussed in the main text, whereas results involving the Triassic dataset of Xu et al. (2022) are very similar and presented in the supplementary material.

For ichthyosaurians, we used the character-taxon matrix of Laboury et al. (2022), derived from the original dataset of Moon (2017), which appears to be most suitable for our analyses. The recent dataset of Bindellini et al. (2021), which comprehensively reinvestigated the phylogenetic relationships of Triassic ichthyosaurians appears to be an appropriate alternative but was not used as it does not incorporate most of the Early Jurassic taxa present in our ecomorphological dataset. We modified our cladistic matrix by incorporating revised scores for *Cymbospondylus nichollsi* and *Cymbospondylus petrinus* [from Klein et al. (2020)] and adding *Cymbospondylus duelferi* and *Cymbospondylus youngorum* [from Klein et al. (2020) and Sander et al. (2021)].

All phylogenetic analyses were performed in TNT (v1.6) (Goloboff et al. 2023) using an implied weighting maximum parsimony framework to reduce the impact of homoplasy and with a concavity constant  $k$  of 12. In each cladistic datasets, multi-states characters were unordered. The number of trees was set to 100,000 and we used the New Technology Search (ratchet activated: 200 iterations; drift activated: 10 cycles; 5 hits and 10 trees per replication) followed by a tree bisection-reconnection (TBR) algorithm (trees can be seen in supplementary material, Figures S3–S12); a single most parsimonious tree was then randomly selected for subsequent analyses. Since the cladistic datasets used do not include all eosauroptrygian and ichthyosaurian specimens sampled in our ecomorphological datasets, we grafted missing taxa on trees using the phytools (v2.0-3) and paleotree (v3.4.5) packages (Bapst 2012; Revell 2012) in the R statistical environment (v4.2.3) (R Core Team 2023). For eosauroptrygians, we manually added Triassic taxa missing from the phylogenetic matrices of Hu et al. (2024) and Xu et al. (2022), as in Laboury et al. (2023) (see supplementary material: Supplementary methods section). Furthermore, we also added *Microcleidus melusinae* to the phylogenetic tree generated for plesiosaurians, as the most basal member of *Microcleidus* (Vincent et al. 2017). For ichthyosaurians, the synonymy of *Temnodontosaurus platyodon* and the smaller '*Temnodontosaurus risor*' (McGowan 1994) has been recently questioned due to numerous morphological differences (Bennion et al. 2024) and we therefore decided to separate these two taxa by adding '*T. risor*' as the sister lineage of *T. platyodon*.

To ensure consistent results, our composite eosauroptrygian and ichthyosaurian trees were timescaled using the minimum branch length approach (Bapst 2012) (supplementary material: Figures S5, S8 and S11) and the Hedman algorithm, which constraints the age of a clade based on the ages of consecutive older groups that act as the clade outgroup (Hedman, 2010; Lloyd et al., 2016) (supplementary material: Figures S4, S7, S10 and S12). All analyses presented in the results section are based on trees timescaled with the Hedman method. Other results are presented in the supplementary materials.

### **C) ORDINATION METHODS AND TEMPORAL DISPARITY ANALYSES.**

All analyses were conducted in the R statistical environment (v4.2.3) (R Core Team 2023). We analysed eosauroptrygians and ichthyosaurians separately, and we also separated skeletal regions (craniodental and postcranial). Continuous traits of all morphological datasets were z-transformed, and these datasets were used to generate a distance matrix by using Gower (for datasets containing continuous and discrete traits) (Gower 1971) or Euclidean (for datasets containing only continuous traits) distances. We generated morphospaces using non-multidimensional scaling (nMDS, dimension=2) with the vegan package (v.2.6- 4) (Oksanen et al. 2022) and principal coordinate analysis (PCoA) with Caillez correction for negative eigenvalues, using the ape package (v.5.7-1) (Paradis et al. 2004). In order to test the influence of phylogeny on the clustering of taxa in our ordination analyses, we computed Mantel tests by using the vegan package (v.2.6-4) (Oksanen et al. 2022) based on tanglegrams (supplementary material: Figures S17–S22) generated with our timescaled phylogenetic trees and cluster dendrograms (see detailed description of these analyses in supplementary materials). To compare the

amount of disparity between different key time periods, we computed morphofunctional disparity for the following time bins: Anisian– Ladinian (Middle Triassic); Carnian–Norian (Late Triassic); Hettangian–Sinemurian (earliest Jurassic) and Pliensbachian–Toarcian (latest Early Jurassic). These bins have uneven temporal durations but were selected to ensure sufficient sampling. Because of the very limited amount of data available for the Rhaetian–no well-preserved and complete specimens have been found from this stage (Fischer et al. 2014; Wintrich et al. 2017; Sander et al. 2022)–it was excluded from our analyses. Nevertheless, the scarcity of its fossil record was considered when discussing our results. The significance of both taxonomical group and temporal differences across morphospace axes was tested by using nonparametric multivariate analyses of variance (NPMANOVA). The p-values resulting from the pairwise comparisons (see supplementary material: Tables S7–S10) were corrected using the Benjamini–Hochberg adjustment for controlling the false discovery rate (FDR), which is the expected proportion of falsely rejected hypotheses (Benjamini and Hochberg 1995). We generated phylomorphospaces superimposed on the density of taxon occupation by using the modified *ggphylomorphospace* function provided in Fischer et al. (2020). We used all axes of the PCoAs to compute the bootstrapped disparity (1,000 replications for bootstraps iterations, sum of variances) for each time bin using the *dispRity* package (v.1.7.0) (Guillerme 2018). We primarily focus on presenting and discussing the craniodental results in the main text, but all other tables and morphospaces can be found in the supplementary material.

To address issues associated with under-sampled time intervals such as the late Norian and Rhaetian and the uneven length of time bins, we used a ‘time-slicing’ approach to sample ghost lineages and estimate ancestors and compute disparity-through-time (Guillerme and Cooper 2018). For ichthyosaurians, we randomly selected a timescaled tree in which ancestral character states were estimated with a likelihood of  $\geq 0.95$  for each node by using the *claddis* package (v.0.6.6) (Lloyd 2016). This method uses cladistic data to compute disparity, which, although not ideal, allows for better sampling during the latest Triassic. This was our main goal in this analysis, as it incorporates partially known taxa that could not be added to our ecomorphological dataset (see the Taxonomic and morphological sampling section for ichthyosaurian examples). Reconstructed ancestral character states could not be estimated for eosauropterygians because we used a composite phylogenetic tree arising from different cladistic matrices. Therefore, we extracted morphospace coordinate positions of ancestral nodes and tips from the phylomorphospace generated with all ecomorphological data. For both eosauropterygians and ichthyosaurians, time-sliced sum of variance disparity was calculated through time at ten equidistant intervals and bootstrapped (1,000 iterations for replications). This procedure ensures sufficient taxon sample size for each interval and reliable comparison not biased by the unequal duration of the different stages. We adopted the gradual splits model of evolution, which selects for a given branch the ordination score from the ancestral node or the descendant with a probability function defined by the distance along the branch where the time slice samples the latter (Guillerme and Cooper 2018). Other models, such as proximity and equal splits, were also tested and are detailed in the supplementary material (Figures S46, S47 and S50).

#### **D) CONVERGENCE ANALYSES**

Our ichthyosaurian ordination analyses hinted at possible craniodental convergences between distantly related taxa. We tested the strength of these morphological convergences between pre- and post- T–J species by applying the Ct1, Ct2, Ct3 and Ct4 metrics (Grossnickle et al. 2024) to selected pairs of taxa. We randomly selected one of our most parsimonious phylogenetic trees and p-values were generated

through 1,000 Brownian simulations with the *convevol* package (v. 2.0.0) (Brightly and Stayton 2023) with the first two, the first five, and all axes of the PCoA. To fully explore these patterns of morphological convergences, in addition to the Ct metrics, we also used the method developed by Castiglione et al. (2019) implemented in the

RRphylo package (v.2.8.0) (Castiglione et al. 2018). All convergence analyses are further detailed in the supplementary material.

## E) LIMB ARCHITECTURE AND BODY SIZE

Brachial and crural indexes were calculated as the length of the zeugopodial bones (radius and tibia) relative to the length of the corresponding propodial bones (humerus and femur). They therefore represent the outlever/inlever ratio of the fore- and the hindlimb (Caldwell 2002; Gutarra et al. 2023). Lower values reflect a higher degree of adaptation to aquatic environments and pelagic taxa are characterized by a relative shortening of the epipodial bones (Gutarra et al. 2023). We used our previously generated timescaled phylogenies (see above) to infer the ancestral node values in a maximum likelihood framework using the phytools (v.2.0-3) package (Revell 2012) and to generate brachial and crural phenograms for eosauropterygians and ichthyosaurians.

Dimensions of dorsal vertebrae have often been used to estimate the overall body size of aquatic tetrapods when highly incomplete specimens or isolated centra are found in the fossil record (Romer and Price 1940; Currie 1978; Sennikov and Arkhangelsky 2010; Fischer et al. 2014; Li and Liu 2020; Sander et al. 2022). To investigate the evolution of body size from the Late Triassic to the Early Jurassic, we gathered a dataset of dorsal vertebra height based on articulated specimens as well as numerous isolated vertebrae of ichthyosaurians and eosauropterygians mentioned in the literature (supplementary material: Tables S3 and S6).

# Results

## A) MORPHOSPACE OCCUPATION AND CONVERGENCE

For the principal coordinate analysis (PCoA) of eosauropterygian and ichthyosaurian craniodental characters, the combination of the first two axes captures 28.71% and 32.65% of the total variance respectively. Eosauropterygians are placed in three distinct clusters (Figure 1A; but see also supplementary material: Table S7), mainly reflecting phylogenetic affinities (Mantel test:  $p$ -value= 0.003) as in Laboury et al. (2023). The first cluster comprises all pachypleurosauroids, the second comprises the nothosauroids + *Wangosaurus* [the nothosauroid-like pistosauroid (Ma et al. 2015; Laboury et al. 2023)] and finally, the third consists of all pistosauroids. The pachypleurosauroids plot with negative axis 1 values whereas the two other clusters plot with positive values. Furthermore, nothosauroids plot with axis 2 negative values while most pistosauroids plot with positive values. Within these latter, the rhomaleosaurid plesiosaurians also occupy a distinct region and appear more diversified than the other plesiosaurians. The temporal distribution of taxa highlights a drastic change and significant reduction in the eosauropterygian ecomorphospace occupation across the T/J transition (Figure 1C, but see also supplementary material: Table S9), as both nothosauroids and pachypleurosauroids are solely found in the Triassic. A similar pattern is also observed when analysing postcranial data (supplementary material: Figures S27–S30). Nevertheless, the Triassic pistosauroids *Augustasaurus hagdorni* and *Yunguisaurus liae* are nested within a region of high occupational density, along with basal plesiosaurians (Figures 1A and 1C). This representation of morphological traits indicates that the ‘typical’ plesiosaurian cranial morphology, not just body shape, already appeared in Middle Triassic pistosauroids.

The pattern of ichthyosaurian ecomorphospace contrasts with that of eosauropterygians (Figures 1B and 1D, but see also supplementary material: Table S8). A clear distribution of the phylogenetic structure (Mantel test:  $p$ -value = 0.48) or temporal groups is not recovered, as species from different groups are widely spread across ecomorphospace. Most notably, Early Jurassic species occupy a broad area of the ecomorphospace, in contrast to

the coeval plesiosaurians. Similarly, our statistical tests do not detect significant disparity shifts in ecomorphospace occupation between our time intervals (supplementary material: Table S9), including across the Triassic-Jurassic transition. Some phylogenetically and temporally distant ichthyosaurians occupy close positions in morphospace (Figures 1B and 1D), highlighting a recurrence of craniodental morphotypes throughout the Middle Triassic to Early Jurassic. Significant convergence is identified between the Triassic merriamosaurian *Qianichthyosaurus zhoui* and the small early Jurassic parvipelvian *Leptonectes moorei* no matter the number of axes or the methodology used (Ct measures or method Castiglione et al. [2019] method (supplementary material: Tables S11 and S12). The morphological resemblance between the large Triassic and Early Jurassic hypercarnivorous taxa (*Cymbospondylus youngorum* and *Temnodontosaurus eurycephalus*) is present but ambiguous, with only some metrics indicating convergence (supplementary material: Tables S11 and S12). Significant results between the Middle Triassic ichthyosaurian *Mixosaurus cornalianus* and the Early Jurassic thunnosaurian *Hauffiopteryx typicus* are recovered when considering the first two axes of variation but not when considering the first five and all axes of the PCoA or the Castiglione et al. (2019) method. Their proximity in the morphospace based on the first and second axes of the PCoA, along with the lack of significant statistical results when analysing convergence, rather reflects superficial similarities in their craniodental architecture than true morphological convergence. In ichthyosaurians, the pattern in postcranial morphological data contrast with that generated from the craniodental traits, and rather follow a similar trend to that of eosauroptrygians, with a clear distinction visible between Triassic and Jurassic taxa and no evident overlap in ecomorphospace occupation (supplementary material: Figures S39–S41).

## **B) TEMPORAL TRENDS OF DISPARITY**

Both eosauroptrygians and ichthyosaurians peaked in ecomorphological disparity during the Middle Triassic (Figures 2A and 2B). Our more precise time-sliced analyses indicate that ichthyosaurians maintained a high level of disparity into the Carnian (early Late Triassic) (Figure 2D). During this period, Middle Triassic ichthyosaurian faunas experienced the replacement of mixosaurid- and cymbospondylid-dominated assemblages by diversified early merriamosaurians. Time-sliced analyses also suggest a significant decline in disparity in both clades during the first half of the Late Triassic, and this drop looks to be even more severe for eosauroptrygians (Figure 2C). This eosauroptrygian decline is mainly due to the disappearance of most non-plesiosaurian eosauroptrygians; though this is likely exacerbated by the lack of well-articulated eosauroptrygian specimens from Carnian and Norian strata. Indeed, morphologically disparate eosauroptrygians, including pistosauroids (e.g., *Bobosaurus*), large nothosaurians ambush predators (e.g., *Nothosaurus giganteus*) but also durophages and supposed filter-feeders (the simosaurids *Simosaurus* and *Paludidraco* respectively), are known from coastal environments of the Carnian (Rieppel and Wild 1996; Dalla Vecchia 2006, 2008; Kear and Maxwell 2013; de Miguel Chaves et al. 2018; García-Ávila et al. 2021). However, these taxa are not complete enough to be included in our ecomorphological analyses here; their morphologies nevertheless suggest that the true disparity among the early Late Triassic eosauroptrygians certainly is likely higher than what is recovered in our analyses (e.g., Figure 2A). As highlighted by Benson et al. (2012), even though subsequent eosauroptrygian disparity gradually increases until the end of the Early Jurassic, early-branching plesiosaurians never achieved a level of morphological diversity comparable to Middle Triassic eosauroptrygians (Figures 2A and 2C). Ichthyosaurian disparity seems to progressively increase after the Norian, with the initial diversification of parvipelvians, and then reaches values comparable to those observed in the Carnian (Figure 2D). No dramatic disparity drop in disparity that could be labelled as a macroevolutionary bottleneck at or close to the T/J transition is observed, neither for eosauroptrygians nor for ichthyosaurians.

### C) EVOLUTION OF FIN SHAPE AND BODY SIZE

Rather than a stepwise evolutionary pattern, both the brachial and crural indexes (proxies for the degree of aquatic adaptation of the limbs) mapped across phylogeny reveal a drastic change in the relative size of zeugopods (radius/tibia) compared to stylopods (humerus/femur), during the first half of the Late Triassic, coinciding with the emergence of the ‘underwater-flying’ plesiosaurians and fusiform parvipelvians (Figures 3A–D, but see also supplementary material: Figures S58 and S61). Their much lower values on both indexes indicate a higher degree of adaptation to an open ocean lifestyle. Middle Triassic eosauropterygians are mostly clustered with high values for both the brachial and crural indexes (0.48– 0.66 for the brachial index and 0.45–0.61 for the crural index), regardless of their phylogenetic affinities (Figures 3A and 3C). The pistosauroid *Yungisaurus liae*, considered to be a close relative of plesiosaurians, has the highest crural index value (0.61) and thus cannot be considered a morphological intermediate between Middle Triassic species and plesiosaurians. Its relatively large tibia size seems to corroborate the inference of Gutarra et al. (2023) that the postcranial morphology of *Yungisaurus* is consistent with a rowing locomotion, similar to nothosauroids. The lowest values among the eosauropterygians we sampled are those of the Rhaetian juvenile plesiosauroid *Rhaeticosaurus mertensi* highlighting a profound modification of limb shapes during the Late Triassic, at least in the preserved taxa. This is similar to what is also observed in ichthyosaurians. Large to gigantic ichthyosaurian taxa such as *Cymbospondylus* and ‘shastasaurids’, have brachial and crural index values within the same range as those of early ichthyosaurians, which were restricted to coastal environments. However, these giant taxa are thought to have colonized the open ocean, considering their size and global distribution (Sander 1989; Sander et al. 2022). It is plausible that these giants might have retained an undulatory swimming mode as exemplified by their relatively high trunk proportion (Sander 1989; Nicholls and Manabe 2004; Bindellini et al. 2021). Among the merriamosaurians that diversified during the Late Triassic, only *Callawayia neoscapularis* has a brachial index value and limb proportions comparable to that of parvipelvians (0.45) making it the only ‘intermediate’ between typically Triassic and Jurassic forms. Early Jurassic thunnosaurians such *Ichthyosaurus* and *Stenopterygius* have the lowest brachial and crural indexes of all in our sample. Their limb morphology thus reflects a substantial shift towards extremely compact fins.

Temporal fluctuations in dorsal centrum height, used here as a proxy for body size, also tend to reveal a different pattern in ichthyosaurians and eosauropterygians during the Late Triassic and Early Jurassic (Figures 3E and 3F). With the available material up to date, it seems that the T/J transition is associated with quite marked reduction in the size range for ichthyosaurians. This drop in maximal centrum size among ichthyosaurians is primarily due to the disappearance of the gigantic ‘shastasaurids’ during the end of the Triassic (Fischer et al. 2014; Lomax et al. 2018, 2024; Sander et al. 2022), while small and medium-sized forms persisted. The size range of the dorsal vertebrae of ichthyosaurians does not vary considerably during the Early Jurassic even if some early parvipelvians such as *Temnodontosaurus* or *Eurhinosaurus* could have reached lengths greater than 5 m (McGowan and Motani 2003). Contrary to ichthyosaurians, centrum dimensions of eosauropterygians likely appear stable during the T/J transition even if more data in the latest Triassic would allow to better characterize their body size evolution. In the Early Jurassic, the co-occurrence of large rhomaleosaurids with small early-diverging plesiosaurians results in a greater range of body sizes than in ichthyosaurians in the same time interval.



## Discussion

### D) DISTINCT EVOLUTIONARY PATTERNS IN MARINE RAPTORIAL PREDATORS ACROSS THE TRIASSIC– JURASSIC TRANSITION

Our analyses highlight contrasting patterns in the morphological diversification of ichthyosaurians and eosauropterygians during the Middle Triassic to Early Jurassic interval. The craniodental diversification of eosauropterygians retains a significant underlying phylogenetic signal, as there is no overlap between the major clades (Pachypleurosauroidea, Nothosauroida and Pistosauroidea). Indeed, each group retained distinct morphotypes, functional specializations, and exhibited niche conservatism relative to one another (Rieppel 2002; Laboury et al. 2023). This pattern in eosauropterygians potentially indicates a stepwise colonization of novel ecological niches (e.g., small suction feeders in Pachypleurosauroidea, moderate durophagous and taxa using their dentition as a fish trap in Nothosauroida; see Rieppel [2002] and Laboury et al. [2023]) during the Triassic that were never re-explored after the extinction of Triassic taxa (Stubbs and Benton 2016; Reeves et al. 2021). Furthermore, our ecomorphospace analysis suggests that the development of the typical ‘pistosaur/plesiosaur’ cranial architecture would have remained relatively stable throughout the early evolutionary history of Pistosauria, with the exception of the peculiar rhomaleosaurids (Cruickshank 1994; Smith and Dyke 2008; Smith and Vincent 2010; Smith and Benson 2014). Early Jurassic ichthyosaurians not only diversified into new morphotypes, notably hyperlongirostrine forms (McGowan 1986; Dick and Maxwell 2015), but also, in contrast to eosauropterygians, resembled and broadly overlapped with Middle to Late Triassic taxa. This overlap in morphospace reflects the iterative evolution of similar craniodental morphotypes repeatedly within Ichthyosauria over the Triassic–Jurassic transition, a pattern that is rarely detected (but see Stubbs and Benton [2016]). This ‘back-and-forth’ pattern and the absence of a clear shift in craniodental anatomy between Triassic and Early Jurassic ichthyosaurians in our multivariate analyses markedly contrasts with the previous perception of a reduction in the range of skull phenotypes and a contraction in morphospace occupation after the Triassic (the ‘bottleneck’ hypothesis) (Thorne et al. 2011; Moon and Stubbs 2020; Reeves et al. 2021). However, this hypothesis stemmed from analyses based on cladistic characters or broad ecological categories in an ecospace modelling approach and may be oversimplified (Thorne et al. 2011; Dick and Maxwell 2015; Moon and Stubbs 2020; Reeves et al. 2021). Our results also challenge the ‘migration model’ proposed by Dick and Maxwell (2015) which states that ichthyosaurians continuously abandoned previously occupied regions of ecospace or morphospace before colonizing new adaptive peaks. This model mainly arose through the use of a temporal character which essentially force a dissimilarity in the ecospace occupation between species from different time intervals and may be considered partially artificial. Dick and Maxwell (2015) argue that following the Middle/ Late Triassic transition, ichthyosaurians ‘abandoned’ circalittoral ecological niches in favour of open-ocean ones. However, while our analyses reveal major stepwise shifts in postcranial anatomy between coastal and pelagic taxa, these shifts are better explained by selective extinction of specific ecological niches due to sea regressions rather than the complete ‘abandonment’ of a morphospace region in place of another. Furthermore, because no clear migration in the craniodental ecomorphospace is evidenced over time, this model should no longer be applicable to characterize the evolution of the cranium throughout T/J transition. Although some of the craniodental morphotypes re-appeared after the Triassic, ichthyosaurians never reached body sizes comparable to those of the colossal ‘shastasaurids’ after the Triassic (Moon and Stubbs 2020; Sander et al. 2021). Consequently, the Late Triassic extinction events still wiped out a unique aspect of Triassic disparity: whale-sized marine reptiles. Our different interpretation of the ichthyosaurian craniodental evolution from the ‘bottleneck hypothesis’ as well as the ‘migration model’ highlights that using of different type of data can produce contrasting macroevolutionary results (Anderson and Friedman 2012).

## **E) DID A MACROEVOLUTIONARY BOTTLENECK IN THE LATEST TRIASSIC INFLUENCE THE EVOLUTION OF PELAGIC TETRAPODS?**

The perception of a massive macroevolutionary bottleneck reshaping marine reptile assemblages at the end of the Triassic has been commonly accepted over the past decade (Thorne et al. 2011; Dick and Maxwell 2015; Stubbs and Benton 2016; Moon and Stubbs 2020; Reeves et al. 2021). Several studies identifying this significant reduction in disparity relied on different data types, such as cladistic matrices (Thorne et al. 2011; Moon and Stubbs 2020), morphofunctional discrete or continuous traits (Stubbs and Benton 2016) and general ecological characters designed for ecospace modelling (Dick and Maxwell 2015; Reeves et al. 2021). In these studies, data were binned at the stage-level (Thorne et al. 2011; Moon and Stubbs 2020; Reeves et al. 2021) or at even larger time intervals (Dick and Maxwell 2015) despite marked differences in stage durations during the Late Triassic (Sander et al. 2022). Our findings suggest a different interpretation of the effects of the end-Triassic extinction events, notably for the better sampled ichthyosaurians. Considering the data available for the latest Triassic, we propose here a two-phase extinction event for non-parvipelvians, rather than a single dramatic ‘bottleneck’ event at the end of the Triassic (Thorne et al. 2011). A similar scenario depicting two distinct extinction events affecting global marine diversity during the Late Triassic was previously proposed by Benton (1986). Based on the results of the present study and on previous work (Benson and Butler 2011; Kelley et al. 2014; Stubbs and Benton 2016), we clearly identify the first extinction phase that occurred near the Middle/Late Triassic boundary. This phase led to the disappearance of the large-sized pelagic forms, such as cymbospondylids along with nearly all coastal forms. Extinctions in shallow-water environments coincide with rapid sealevel fluctuations and major regression events which greatly reshaped the structure of marine ecosystems and resulted in the loss of a large proportion of coastal marine reptile species (Benson and Butler 2011; Kelley et al. 2014; Druckenmiller et al. 2020). This extinction event is indeed marked by both a reduction in disparity and slowing-down of rates of morphological evolution among ichthyosaurians (Stubbs and Benton 2016; Moon and Stubbs 2020), as only pelagic merriamosaurians are thought to have survived these events. Carnian and Norian assemblages, also referred as ‘transitional ichthyosaur faunas’, exhibit significant similarities and are characterized by the dominance of colossal ‘shastasaurids’ alongside smaller merriamosaurians and early-branching parvipelvians (Merriam 1908; McGowan 1997; McGowan and Motani 2003; Nicholls and Manabe 2004; Kelley et al. 2022; Zverkov et al. 2022). The emergence of parvipelvians in the Norian is associated with appearance of significant modifications in fin shapes (McGowan 1995, 1996). Although some remains of gigantic ‘shastasaurids’ have been found in the earliest Jurassic (Martin et al. 2015), suggesting a more complex scenario, the disappearance of the vast majority of these giants by the end the Rhaetian (Fischer et al. 2014; Sander et al. 2022; Lomax et al. 2024) would represent the second phase in the extinction of Triassic ichthyosaurians. As mentioned by Fischer et al. (2014), it remains uncertain whether these shastasaurids suffered from diffuse extinctions since the Norian or restricted to the end of the Rhaetian. Nevertheless, these extinctions resulted in a profound turnover that led to the dominance of parvipelvians in Europe (Motani 2009; Bardet et al. 2014). Considering that the divergence of the major parvipelvians lineages likely occurred during the Late Triassic (Fischer et al. 2013; Laboury et al. 2022) combined with their high diversity and disparity recorded at the base of the Jurassic, we speculate that pelagic parvipelvians diversified before (and therefore crossed) the T/J boundary. This again contrasts with a macroevolutionary ‘bottleneck’ proposed at the very end of the Triassic. However, the poor sampling of marine reptile fossils from the latest Triassic (Bardet et al. 2014; Fischer et al. 2014; Sander et al. 2022) obscures evidence of any substantial parvipelvic diversification before the Early Jurassic.

Despite the paucity of the Late Triassic eosauropterygian fossil record, evidence for a significant extinction event affecting their diversity several million years before the latest Triassic is consistently emerging. In contrary to ichthyosaurians, coastal taxa such as the last nothosauroids and basal pistosauroids are recorded during the Early Carnian (Julian), suggesting a more diffused tempo of extinctions and the presence of shallow-marine refugia

during the transgressions (Rieppel and Wild 1996; Dalla Vecchia 2006, 2008; de Miguel Chaves et al. 2018; García-Ávila et al. 2021). More advanced pistosauroids and/or plesiosaurians possibly emerged during the early to middle Norian (Sennikov and Arkhangelsky 2010) or at least during the Rhaetian (Wintrich et al. 2017). As appears to be the case for the ichthyosaurians, the morphological similarity of some latest Triassic remains with Jurassic taxa (Fischer et al. 2014) and the high diversity of plesiosaurians right at the start of the Jurassic also suggest an earlier diversification during the Late Triassic (Benson et al. 2012; Wintrich et al. 2017).

While it is clear that Carnian–Norian and earliest Jurassic marine reptile faunas are completely dissimilar (McGowan and Motani 2003; Nicholls and Manabe 2004; Benson et al. 2012; Benton et al. 2013; Zverkov et al. 2022), the widespread narrative of a catastrophic loss of taxic and morphological diversity among marine reptiles at the end of the Triassic (Thorne et al. 2011; Dick and Maxwell 2015; Moon and Stubbs 2020) is difficult to reconcile with our results and those of other studies (Benson et al. 2010, 2012; Wintrich et al. 2017). A shift in morphospace occupation and fin shape is observed earlier, during the first half of the Late Triassic and the limited fossil sampling from the Late Triassic–Early Jurassic interval rather suggests relative stability of ichthyosaurian and pistosauroid phenotypes. Most extinction events appears to predate and are thus supposedly distinct from the Triassic–Jurassic boundary volcanism and anoxia (Tanner et al. 2004). However, the end of the Triassic still unambiguously coincides with the extinction of the last known placodont sauropterygians (Pinna and Mazin 1993; Neenan and Scheyer 2014) and potentially saurosphargids (Scheyer et al. 2022) as well. Our study highlights diverse, clade-specific responses to multiple, previously conflated Late Triassic events. Nevertheless, caution is still needed in our interpretations, as the scarcity of the latest Triassic fossil record oversimplifies what were more complex events. Significant shifts in sedimentary regimes and environmental conditions during the Late Triassic have resulted in a marine fossil record that is temporally uneven (Benson and Butler 2011; Dunhill et al. 2014a; Kelley et al. 2014), obscuring our view of the precise tempo and magnitude of these events. As a result, interpreting signals from this period remains challenging, and the observed extinction patterns in the Late Triassic may therefore be somewhat influenced by the Signor-Lipps effect (Signor III and Lipps 1982). Nonetheless, our study sought to better characterise extinction events that affected pelagic tetrapods during the Late Triassic.

## CONCLUSIONS

We comprehensively present the disparity, fin shape and body size evolution of the main raptorial marine predators across the Middle Triassic–Early Jurassic time interval in order to reinvestigate the hypothesis of a dramatic macroevolutionary bottleneck during the latest Triassic. We reveal for the first time contrasting macroevolutionary patterns in the craniodental diversification of both Eosauropterygia and Ichthyosauria during this crucial time interval. The ecomorphospace of eosauropterygians retain a deep phylogenetic structure characterized by a clear clustering of pachypleurosauroids, nothosauroids and pistosauroids. This pattern suggests the earliest members rapidly diverged from one another and did not subsequently radiate into each other craniodental morphospace and presumably ecological niche. In contrast, ichthyosaurians lack any discernible evolutionary trajectory in their craniodental disparity. They continued to radiate into different areas of morphospace, seemingly regardless of phylogenetic affinity. Alongside exploration of new ecomorphospace regions, ichthyosaurian evolution in the aftermath of the T/J transition is marked by the reappearance of phenotypes already present in the Triassic. Late Triassic extinction events were previously conflated because of the coarser data, yielding the illusion of a single, abrupt ‘bottleneck’. While caution is needed to account for the various biases in the latest Triassic fossil record, our results support the existence of a major extinction event that likely decimated multiple coastal forms during the early Late Triassic, disconnected from the end-Triassic mass extinction.



## **Data availability**

The data and R scripts are deposited on Dryad at [DOI: 10.5061/dryad.f4qrfj74j](https://doi.org/10.5061/dryad.f4qrfj74j). All 3D models used to gather raw data are all available on online data repository MorphoSource in different projects: <https://www.morphosource.org/projects/000508432?locale=en> ; <https://www.morphosource.org/projects/000519988?locale=en> and <https://www.morphosource.org/projects/000614685?locale=en> (see details in Supplementary Material).

## **Author contributions**

A.L., V.F., T.L.S and T.M.S. conceived and designed the study. A.L., A.S.W., J.L. and M.E.H.J collected the data. A.L. performed the analyses, wrote the code with inputs from V.F. and T.L.S., prepared all figures and tables and wrote the draft of the manuscript, with contributions of all authors. All authors revised the final draft of the manuscript, gave final approval for publication and agreed to be held accountable for the work performed therein.

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## **Conflict of interest statement**

The authors declare no conflicts of interest.

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## Figure and corresponding captions

**Figure 1.** Eosauropterygian and ichthyosaurian phylo- and temporal craniodental ecomorphospace occupation based on the first two axes of PCoA analysis. Data points are coloured according to their taxonomic groups (A, B) or time bins (C, D) and their diameter is proportional to the skull size of the corresponding taxa. (A, B) Phylo-ecomorphospace occupation of (A) eosauropterygians and (B) ichthyosaurians, superimposed on the density of taxa visualized by the shades of grey (darker = higher density). (C, D) Temporal ecomorphospace occupation of (C) eosauropterygians and (D) ichthyosaurians. Polygons connect outlier taxa of each time bin.

**Figure 2.** Temporal pattern of eosauropterygians and ichthyosaurians morphological disparity. (A, B) Disparity distributions (sum of variances metric and 1000 bootstraps replications) based on all axes of the PCoA calculated with all ecomorphological traits for our sampled time intervals for (A) eosauropterygians and (B) ichthyosaurians. The four temporal bins chosen are Ani–Lad (= Anisian– Ladinian); Car–Nor (= Carnian– Norian); Rhae (= Rhaetian); Het–Sin (= Hettangian–Sinemurian) and Pli– Toa (= Pliensbachian–Toarcian). (C, D) Evolution of time-sliced disparity (sum of variances metric and 1,000 bootstraps replications) through the Middle Triassic–Early Jurassic time interval based on (C) phylomorphospace occupation for eosauropterygians and on (D) our phylogenetic tree for ichthyosaurians phylomorphospace occupation for eosauropterygians (see Material and Methods, section Ordination methods and temporal disparity analyses, for more details). Light blue and blue envelopes represent respectively 95% and 50% confidence intervals. All phylogenetic trees used to calculate disparity or to compute the phylomorphospace were timescaled with the Hedman algorithm. In all graphs, red line indicates the Triassic–Jurassic transition.

**Figure 3.** Pattern of fin shape and body size evolution. Data points are coloured according to their taxonomic groups. (A, B) Brachial index phenograms for (A) eosauropterygians and (B) ichthyosaurians. (C, D) Crural index phenograms for (C) eosauropterygians and (D) ichthyosaurians. All phenograms were created with Hedman-dated corresponding phylogenetic trees. (E, F) Distribution of dorsal vertebrae height through the Later Triassic–Early Jurassic time interval for (E) eosauropterygians and (F) ichthyosaurians. In all graphs, red line indicates the Triassic–Jurassic transition.

Figure 21

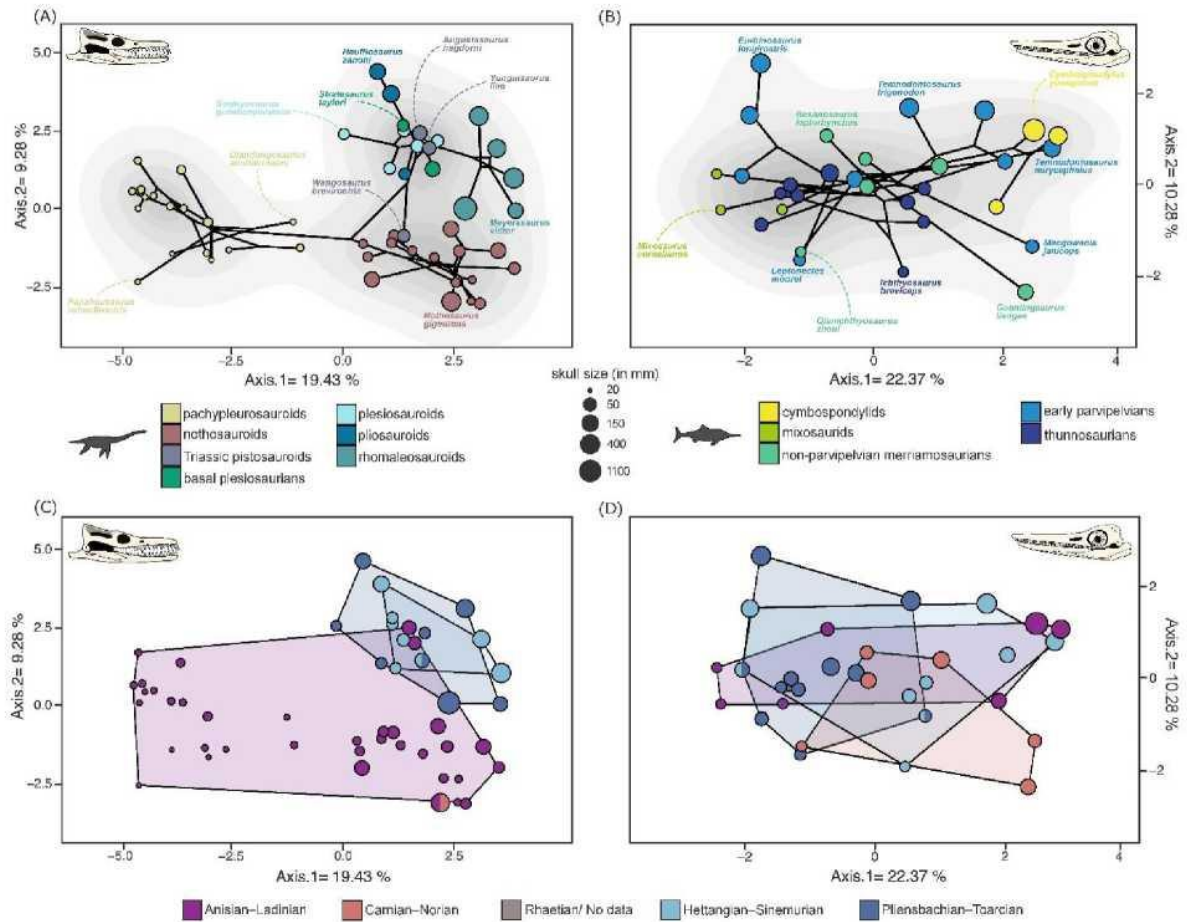


Figure 21

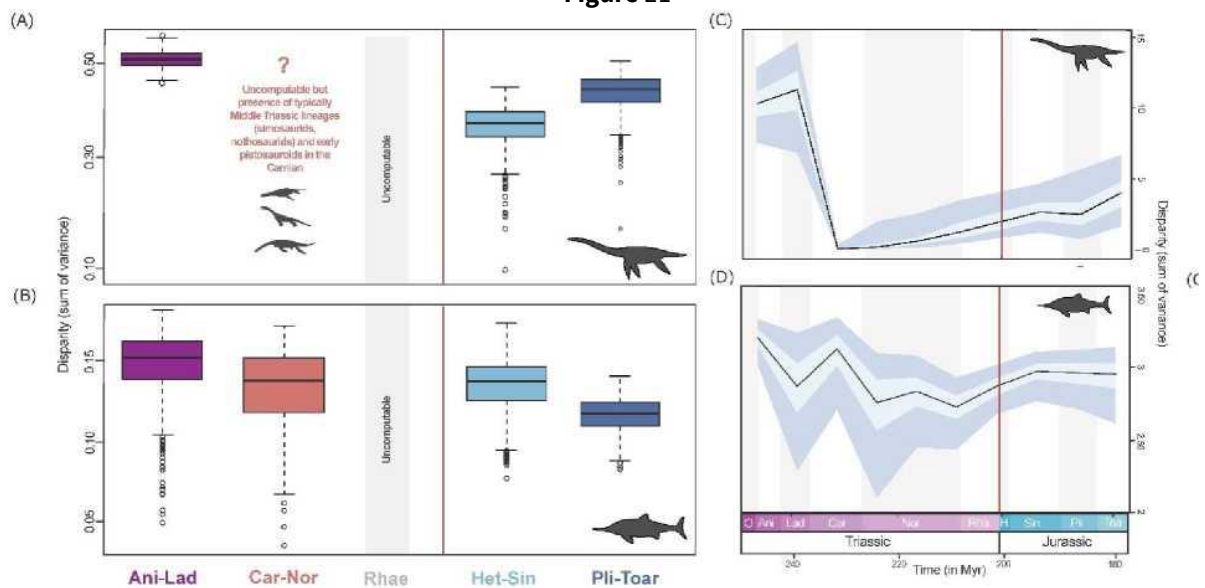


Figure 22

