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Recognising and quantifying the evolution of skeletal paedomorphosis in Plesiosauria

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https://zoobank.org/1128975D-7A2B-4624-870E-926469C943C1

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Abstract

Plesiosaurs are one of the longest-ranging tetrapod groups in the Mesozoic and underwent a major adaptive radiation in the Late Triassic/Early Jurassic, so they are an ideal clade to study the long-term implications and deep-time evolution of specific developmental patterns. We compiled a database of all published plesiosaur specimens and recorded their skeletal maturity status. We use statistical modelling to demonstrate that the abundance of allegedly 'juvenile' specimens increases through time, which contradicts the null hypothesis that the relative proportion of juvenile to adult specimens should remain constant throughout evolution. These results indicate that many 'juvenile' specimens are really adults exhibiting heterochronic traits, particularly paedomorphism. Heterochrony is a developmental pattern particularly widespread in secondarily adapted organisms such as plesiosaurs. However, heterochronic patterns are typically only studied in individual genera/species or restricted clades. We demonstrate that the pervasiveness of paedomorphism in plesiosaurs increased gradually throughout the evolution of the clade, rather than being a specialization of specific clades.

Key Words

Introduction

Plesiosaurs (=Plesiosauria) are a globally distributed group of extinct predatory aquatic reptiles that formed an important component of Jurassic and Cretaceous marine ecosystems. All plesiosaurs have a short torso, a short tail, and four large flippers, but their skull and neck proportions vary greatly. Plesiosaur morphotypes range between two extremes: plesiosauromorphs with a long neck and small head, and pliosauromorphs with a short neck and large head (O'Keefe 2002). The first studies of plesiosaur ontogeny were conducted by Andrews (1895, 1910) on *Cryptoclidus* from the Middle Jurassic (Callovian) Oxford Clay Formation of the UK. Brown (1981) followed up on this work and set the modern standard for determining ontogenetic growth stages within Plesiosauria, herein referred to as the 'Brown model'. Brown (1981) analysed ontogenetic sequences

of two cryptoclidids, *Cryptoclidus* and *Muraenosaurus*, both from the Oxford Clay Formation of the UK. This foundational work established intraspecific ontogenetic variability patterns among plesiosaurs. *Cryptoclidus* provides an especially good case study because it is known from abundant and substantially complete material representing different growth stages. The Brown model *sensu stricto* uses osteological maturity, specifically the degree of fusion between the vertebral centra and neural arch, as a proxy for sexual maturity. Under this model there are three categories: in 'juveniles' the neural arches and centra are unfused, in 'adults' the neural arches and centra are fused but a neurocentral suture is still visible, and in 'old adults' the neural arches and centra are fused and the neurocentral suture is obliterated (Brown 1981). Caldwell (1997a) expanded on this work by investigating ossification patterns in the limbs of *Cryptoclidus*. The Brown model has been adopted by all subsequent

workers and the patterns observed for *Cryptoclidus* have been generalized to all other plesiosaurs, including pliosauroids and elasmosaurids, to determine their sexual maturity. The problems with applying the Brown model in this way are three-fold: (1) sexual maturity does not necessitate osteological maturity, so assuming the two correlate omits the possible ontogenetic effects of paedomorphism; (2) different parts of the skeleton may ossify at different stages of maturity; (3) ontogenetic patterns observed in *Cryptoclidus* and *Muraenosaurus* may not be applicable to all plesiosaurs. In summary, the Brown model conflates osteological maturity with ontogenetic or sexual maturity.

The possible importance of paedomorphism within plesiosaurs and the potential implications of paedomorphic characters for plesiosaur paleobiology, paleoecology, evolution, and systematics, has received little research attention to date (Buchy et al. 2005; Araújo et al. 2015; Wintrich et al. 2017). Paedomorphic traits have been identified in various secondarily-adapted tetrapods (Delfino and Sánchez-Villagra 2010). However, the long-term evolution of paedomorphism has not been investigated in plesiosaurs, or any other clade. The Plesiosauria is a long-lived clade that survived for 135 Ma, witnessing the breakup of Pangea, various major oceanic anoxic events (AOEs), dramatic changes in thermohaline oceanic circulation, and the rise and fall of various other Mesozoic marine reptiles such as thalattosuchians, ichthyosaurs and mosasaurs (Polcyn et al. 2014; Ősi et al. 2018; Moon 2019). This unique clade is therefore an ideal candidate to study the long-term, large-scale evolutionary persistence of heterochronic mechanisms affecting skeletal morphology.

Heterochrony is the dissociation of the relative timing of developmental events during the ontogeny of ancestral and descendant organisms (Raff 1996). Gould (1977) partitions heterochrony into two fundamental divisions: paedomorphism denotes an underdevelopment in descendants relative to the ancestor, while peramorphosis denotes an overdevelopment of ontogenetic traits. These concepts can be further subdivided into distinct processes. There are three types of paedomorphism: progenesis (early finishing/offset), neoteny (slower growth rate), and postdisplacement (delayed starting/onset). But to extricate which of these processes affects a given ontogenetic trait requires underlying knowledge of the rates of development. Smith (2001) proposed an alternative, sequence heterochrony, to avoid the need to calculate these rates and to make it feasible to apply a conceptual framework of heterochrony to museum or paleontological specimens. Sequence heterochrony simply denotes changes in the offset or onset of a given phenotypic trait. So, even without accurate information on the developmental rates it is possible to recognise and understand underdeveloped or overdeveloped morphological traits relative to the ancestor condition in fossils.

Speciation events may undergo a mosaic of heterochronic processes, with different traits being affected by peramorphosis and paedomorphosis concomitantly. For example, peramorphic processes result in convergent evolution of polydactyly and hyperphalangy in multiple Mesozoic marine reptile lineages (Caldwell 1997b). However, paedomorphism is observed more often in secondarily-adapted amniotes, probably due to the staggering degree of convergence between distantly related clades, ranging from porpoises to thalattosuchians. Inspired by the work of Piveteau and Dechaseaux (1955) and Lehman (1955), de Ricqlès (1975) coined the term "aquatic neoteny" referring to the juvenilized morphology of tetrapods as an adaptation to the aquatic environment. However, neoteny refers to a specific paedomorphic process referring to slower growth rate (Gould 1977; Raff 1996; McNamara 1997), and other paedomorphic processes, such as progenesis, can be related to adaptations to the aquatic environment (Galatius 2010). The term 'skeletal paedomorphosis' (Rieppel 1989a) is more appropriate because it refers to the heterochronic process more generally but can be applied to the specific anatomical loci affected by it.

Miniaturized taxa are often, but not always, paedomorphic. Some authors have proposed that some aristonectines may be miniaturized paedomorphic plesiosaurs (Araújo et al. 2015; Otero et al. 2015). Clades with dramatic minimum size limits also tend to be more diverse (Angielczyk and Feldman 2013) and, coincidently, the Aristonectinae is the most diverse plesiosaur clade by the Campanian-Maastrichtian. Miniaturization is a pathway for evolutionary novelty and diversification because dwarfed forms can partition resources and occupy ecological niches that are otherwise inaccessible to larger forms (Miller 1996; Angielczyk and Feldman 2013). However, most paedomorphic traits in Mesozoic marine reptiles do not seem to be related to body size, as they are mostly reflected in the axial and appendicular skeleton (Rieppel 1989a). Paedomorphism produces sexually mature organisms that otherwise retain a juvenile morphology by promoting the developmental truncation, deceleration or deletion of some traits (Britz et al. 2009; Angielczyk and Feldman 2013). The meristic deletion of mesopodial elements in sauropterygians (Rieppel 1989b) is a typical example of aquatic skeletal paedomorphosis. Although several paedomorphic traits were attained in the early radiation of Sauropterygia, it is unclear how these traits evolved in plesiosaurs. Brown (1981) standardized the way to assess plesiosaur ontogeny but did not take into account the confounding effects of heterochrony.

A clear extrication of juvenile and paedomorphic characters in relation to the ancestral state, as well as complementary evidence from histology, is crucial for understanding plesiosaur evolution. This paper presents the results of an analysis of osteological maturity in hundreds of plesiosaur specimens across all clades, spanning the entire stratigraphic history of the group, to help elucidate the presence of juvenile vs. paedomorphic characters, to test the Brown model, and to avoid a biased view of plesiosaur ontogeny.

Methods

Data collection

We compiled an extensive database of hundreds of published records of plesiosaur specimens to assess their osteological maturity. The database contains 712 plesiosaur specimens representing different individuals. The database contains all plesiosaur publications known to us up until December 2022, excluding descriptions of isolated teeth or other material for which the osteological maturity could not be determined. The number of specimens that have been published since then are negligible and should not change the results significantly. Each entry corresponds to one specimen, to which we provide the most recent consensus concerning its systematic classification, following (in most cases) the higher-ranking taxonomy of Benson and Druckenmiller (2014). We have classified each specimen based on a bipartite scheme of classification (Plesiosauroidea and Pliosauroidea). Plesiosauroidea comprises Microcleididae, Polycotylidae, Leptocleididae, Cryptoclididae and Elasmosauridae. Pliosauroidea comprises Rhomaleosauridae and Pliosauridae. 34 specimens were taxonomically ascribed to Plesiosauria indet. and those without a firm systematic placement (13) were excluded from the clade-by-clade analysis. These are 'Plesiosaurus' cliduchus, Eoplesiosaurus antiquior, Sthenarosaurus dawkinsi, Bobosaurus forojuliensis, Raptocleidus blakei, Raptocleidus bondi, Macroplata tenuiceps, Plesiopterys wildii, 'Plesiosaurus' macrocephalus, 'Plesiosaurus' costatus, 'Plesiosaurus' rugosus (BRSMG Cb2458), 'Thaumatosaurus' indicus and 'Plesiosaurus hesternus'.

For each specimen we recorded the following information: specimen number; its Superfamily (Plesiosauroidea or Pliosauroidea); its Family; the operational taxonomic unit (i.e. lowest possible taxonomy, genus and species when possible); its ontogenetic stage under the Brown model in a binary system ('mature' or 'partially mature or immature)', its ontogenetic stage under the Brown model in a tripartite system ('mature', 'partially mature', or 'immature'); its ontogenetic traits; its geological range in Stages; its average age in Ma; and references.

The specimens' ontogenetic maturity was classified based upon anatomical descriptions and figures found in the literature and/or personal observations. Table 1 lists the criteria we used to determine the osteological maturity of each specimen. We used a bipartite scheme (mature vs. immature), which is a modification of the tripartite scheme (mature vs. partially mature vs. immature), by including mature and *partially mature* specimens under the term 'mature'. The tripartite classification scheme is inspired by Brown (1981), where: a mature specimen has the neural arch and vertebral centrum completely fused leaving no neurocentral suture visible, a partially mature specimen has the neural arch and the vertebral centrum partly co-ossified but has the neurocentral suture visible, and an immature specimen has separate neural arch and

Table 1. Criteria used to determine the osteological maturity of each specimen.

Osteological maturity	Vertebrae	Limbs	Girdles
Immature	Neural arch unfused to centrum	Rounded edges, no trochanter or tuberosity	Rounded edges, girdle elements unfused
Partially mature	Neural arch fused to centrum but neuro-central suture visible	Angular edges, Trochanter or tuberosity partially separated from propodial head	Angular edges, Girdle elements partially fused
Mature	Neural arch completely fused to centrum, no neuro-central suture visible	Angular edges, trochanter or tuberosity completely separated from propodial head	Angular edges, girdle elements completely fused

vertebral centra. Based on the geological and stratigraphic data provided in the literature for each specimen we convert it into an approximate absolute age of occurrence based on Ogg et al. (2016).

Terminology

It is important to clarify terminology, especially because the meaning of 'maturity' can be applied in several ways. Specifically, we must consider the differences and areas of overlap between 'osteological maturity', 'sexual maturity', and 'ontogenetic maturity'. The term 'sexual maturity' as a proxy for maturity in a given specimen is unsatisfactory in practice because it cannot be assessed in the fossil record and does not untangle heterochronic issues. Therefore, an alternative terminology for assessing maturity is required.

Osteological maturity: immature, partially mature, and mature

The abundant Callovian plesiosaur record amassed from the Oxford Clay Formation of the UK consists mainly of different cryptoclidid and pliosaurid taxa. In addition to the Brown (1981) criterium *sensu stricto*, Brown identified other characters that change through ontogeny that should therefore be excluded from taxonomic purposes (Brown 1981). Among these, two characters have been widely cited for all major plesiosaur clades as representing a juvenile state (Table 1): (1) a humeral tuberosity or femoral trochanter unseparated by a condylar isthmus from the capitulum; and (2) an unfaceted distal propodial epiphysis. However, there are few records of pliosaurs (except for *P. funkei*, see Knutsen et al. 2012, *P. irgisensis*, see Storrs 2000 and some specimens of *Peloneustes*, Tarlo 1960) and few rhomaleosaurids (with the exception of *R. zetlandicus* and *R. thorntoni*) with faceted distal epiphyses (e.g., Sollas 1881; Tarlo 1959; Hampe 2005; Smith 2007; Vincent 2010; Ketchum and Benson 2011a, 2011b; Benson et al. 2013). Also, to date no rhomaleosaurids

have been found possessing an isthmus separating the humeral or femoral head (Smith 2007). Moreover, in several plesiosaur clades all individuals have visible neurocentral sutures or separated neural arches and centra (Rhomaleosauridae, Pliosauridae, Leptocleididae, except *Gronausaurus wegneri* see Hampe 2013; fig. 12). This apparent contradiction can be explained by the retention of the plesiomorphic condition of Pistosauria, which themselves exhibit paedomorphism (Rieppel 2000). So, in *Cryptoclidus* and *Muraenosaurus*, faceted propodials and separated humeral and femoral tubercles/trochanters are apomorphic traits (Druckenmiller and Russell 2008).

Sexual maturity: juveniles, adults, and old adults

This issue requires a careful definition of different sexual stages, namely the contrast between 'juveniles' and 'adults'. The 'adult' condition usually refers to an individual that has reached sexual maturity. This definition of adulthood is exclusively biological (e.g., legal adulthood in humans is a different issue). However, sexual maturity can rarely be confidently determined in the paleontological record, with one exception in the plesiosaur fossil record represented by a pregnant individual (O'Keefe and Chiappe 2011). By looking at the degree of fusion between the centra and neural arches, Brown (1981) refers instead to the degree of osteological maturity. For example, an osteologically immature specimen has unfused neural arches. A modern analogue exemplifying sexual maturity before osteological maturity as a result of paedomorphism is the harbour porpoise, *Phocoena phocoena* (fig. 10; Galatius and Kinze 2003; Galatius et al. 2006, 2011; Galatius 2010). Hereinafter we use the terms 'juvenile', 'adult', and 'old adult' (in inverted commas) according to Brown 1981; so when single quotes are not used we refer to true juveniles, excluding paedomorphism.

Ontogenetic maturity

This term simply refers to the actual age (i.e., time since birth) of the animal. This concept differs from sexual maturity as it does not make any suppositions about reproducibility of the organism.

Rationale and caveats

To assess the evolution of paedomorphism in plesiosaurs we used a ratio of the frequency of osteologically immature specimens (I) to the frequency of the sum between partially osteologically mature specimens (P) and fully osteologically mature specimens (M), the I/(P+M) ratio, through time bins representing the evolutionary history of plesiosaurs. The null hypothesis is that this ratio should remain constant through time. There is no reason to think that fertility ratios should vary through time given the available

evidence that plesiosaurs are K-selectors (O'Keefe and Chiappe 2011), nor should there be any variation or taphonomic biases towards osteologically immature (or osteologically mature) specimens through time (Benson et al. 2010). There are some intrinsic collection, temporal and geographical biases in the fossil record, but correction protocols are always dependent on the existing face-value paleontological record (Benson et al. 2021). In other words, it may be spurious to 'correct' the record if the attempted correction is not known to be true itself.

The alternative hypothesis we propose is that variations of I/(P+M) ratio through geological time reflect variations of heterochronic processes, namely paedomorphism, through the evolutionary history of plesiosaurs. It is important to note that our results could be overly conservative because we lump partially mature specimens together with fully mature specimens in the denominator. However, this is intentional. If we can observe a pattern of variation of the I/(P+M) ratio through time then, it would only be more conspicuous if partially mature specimens were lumped with immature specimens.

Statistical modelling of plesiosaur paedomorphism evolution

We divided geologic time from 234.55 Ma (Early Carnian) up to 66 Ma (Late Maastrichtian) into equally sized time-bins of 4.5 Ma each. 4.5 Ma was the minimum age range, required to provide a meaningful assessment of our hypothesis given the abundance of plesiosaurs in the fossil record. In other words, 4.5 Ma is the minimum spread of time required to avoid having various time periods without any plesiosaur specimens, which would give the impression of an interrupted record. Figure 1 shows the specimen frequency based on tripartite division of osteological maturity into different time bins of 2, 4.5, 6 and 10 Ma. The time bins, therefore, do not correspond directly to stratigraphic stages.

We calculated the ratio of the frequency of osteologically immature versus osteologically mature specimens (and osteologically immature versus osteologically mature + partially osteologically mature specimens) in each time bin. The time bin refers to the average between the maximum and minimum age.

We optimised the dataset according to different types of equations to model the evolution of paedomorphism, using the ratio of immature versus mature + partially mature specimens per time bin as a proxy, hereinafter I/(P+M) ratio. The I/(P+M) ratio may be over-conservative towards reducing the real effects of paedomorphism because it lumps partially osteologically mature specimens together with osteologically mature specimens. Partially osteologically mature specimens may also be affected by paedomorphism. On the other hand, osteologically immature specimens through time should be retrieved in fossil collections at a constant rate.

Each equation was limited to a maximum of four estimated parameters to ensure optimization using the
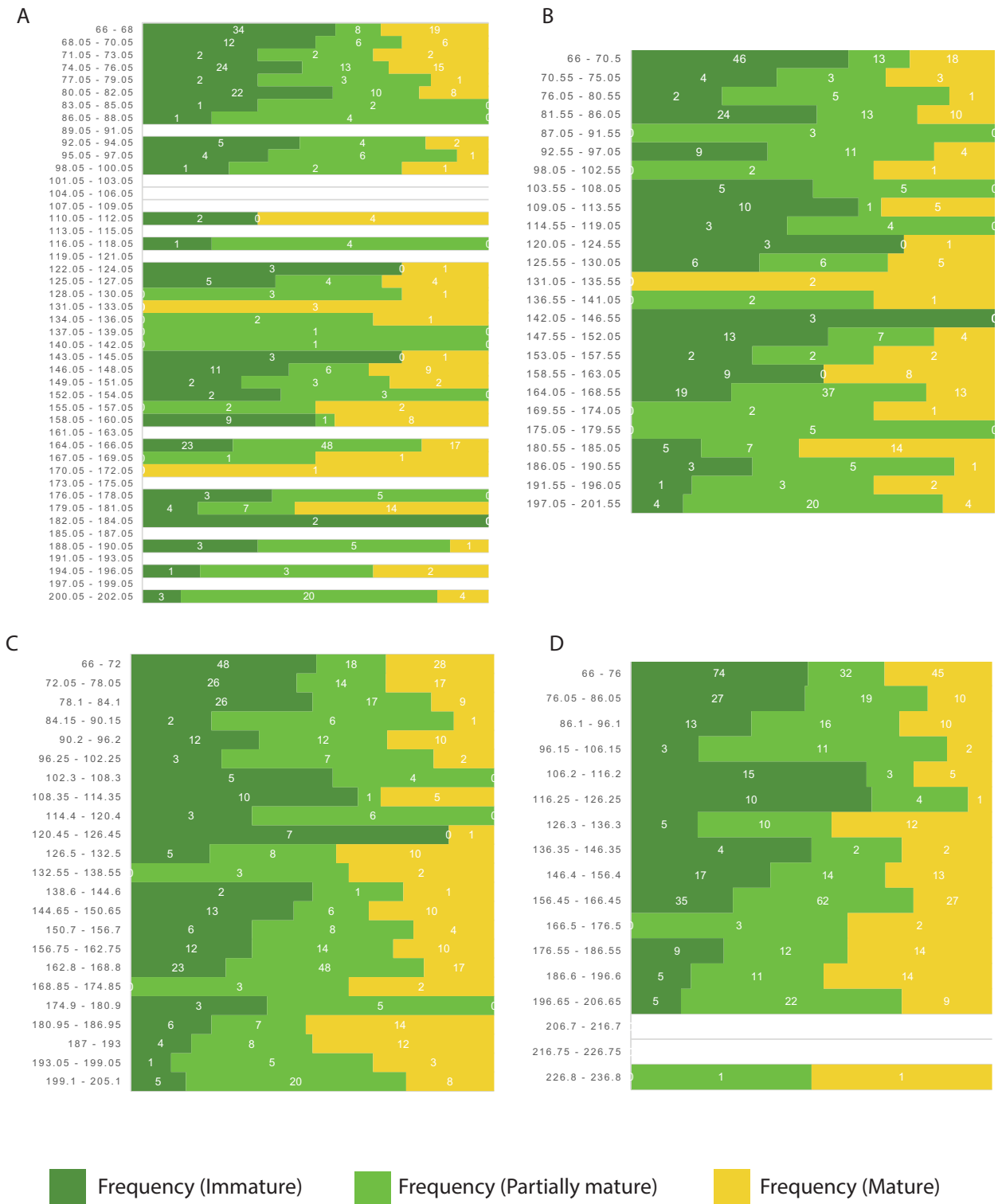
Figure 1. Frequencies of immature (dark green), partially mature (light green) and mature (yellow) specimens through time. **A.** 2 Ma time bin. **B.** 4.5 Ma bin. **C.** 6 Ma bin. **D.** 10 Ma bin. Note that the frequency of immature specimens increases through time independent to the time bin scheme used.

simplest, thus more parsimonious, models possible. The parametric models include linear, exponential, and other equations types (see Tables 2, 3). To ensure that the models were not being affected by outliers we ran a Grubbs tests and calculated Z scores. Statistical outliers are here identified when there is an anomalously high I/(P+M) ratio.

The ratio is null or incalculable when there are simply no plesiosaur records for a given time bin. We optimized a linear model, without the outlier, for which we calculated the confidence intervals based on a significance level of 5%, the Cook's distances, the mean of the squares of the errors (MSE) and the square root mean square of the

Table 2. Statistical assumption tests for each time bin for linear models. Marginally non-significant regressions are in bold.

		2 Ma	4.5 Ma	6 Ma	10 Ma
Correlation coefficient	Spearman	-0.537	-0.415	-0.613	-0.637
Analysis of variance model	p-value	0.010	**0.095**	0.015	**0.065**
Statistical tests for linear regression assumptions					
Outliers	Grubbs	Yes	Yes	Yes	Yes
Removed outliers	Z-score	Berriasian + Aptian	Aptian	Aptian	Aptian/Albian
Multicolinearity	VIF (<5)	1.339	1.184	1.400	1.383
Homoscedasticity	White test p-value (>0.05)	0.274	0.115	0.175	0.279
Autocorrelation	Durbin-Watson p-value (>0.05)	0.929	0.656	0.393	0.157

errors (RMSE), and various other statistics (Suppl. material 1). Optimal models have lower MSE, AIC and AICc values because these statistics essentially account for the amount of deviation from the linear or nonlinear model. All models were calculated using XLSTAT2014.3.
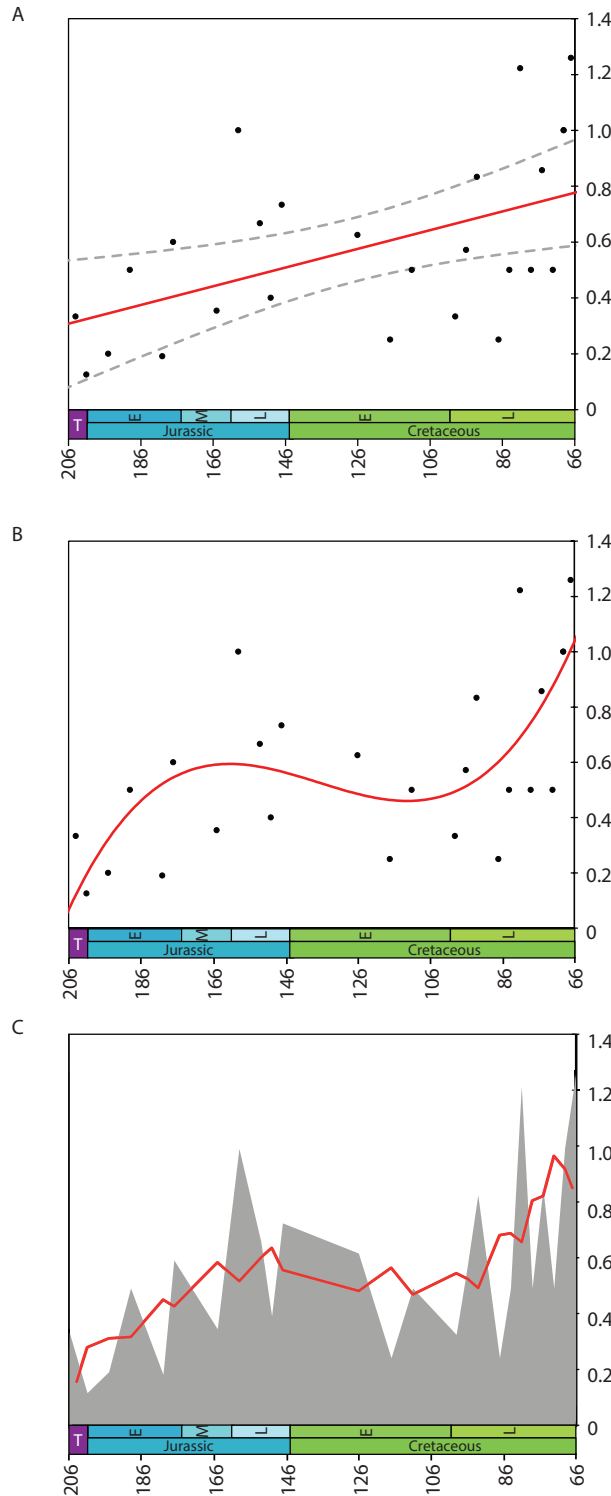
Non-parametric regression

We performed a non-parametric regression that relaxes the assumptions made by the linear regression model (Fig. 2C, Table 4). We performed a LOWESS regression and a robust LOWESS regression (Cleveland 1979) for all time bin partitions, which are locally weighted scatter-plot smoothing techniques performed in XLSTAT2014.3.
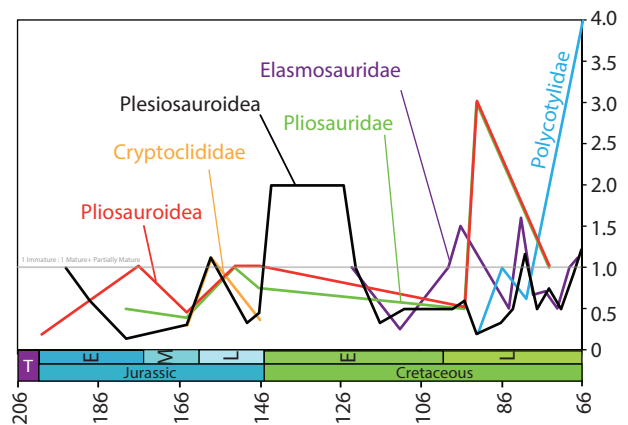
Clade-by-clade analyses

We partitioned and analysed the plesiosaur dataset into various clades to assess the weight of phylogeny on the global evolution of paedomorphism in Plesiosauria, and to understand if there was any particular trend through time in individual plesiosaur clades (Figs 3, 4). We reproduced the same methodology as outlined above, but with subsets of the database and we only plotted the I/(P+M) ratio through time. We drew simple frequency graphs in instances where very few entries exist for each clade per time bin (Microcleididae,

Table 3. The type of function, the general tendency demonstrated by the function fitted to the data, relative likelihood and the mean square errors (MSE), for each model and time bin. Green model, relative likelihood RL > 0.05 for all time bins Green, RL > 0.05. Red, model with RL < 0.05 for every time bin. BM, best model.

Model	2 Ma time bin			4.5 Ma time bin			6 Ma time bin			10 Ma time bin			Tendency through time
	MSE	RLAIC	RLAICc	MSE	RLAIC	RLAICc	MSE	RLAIC	RLAICc	MSE	RLAIC	RLAICc	
Linear	0.077	BM	-	0.237	BM	-	0.127	BM	-	0.205	BM	-	Increase
Beta Growth	0.080	0.135	0.064	0.252	0.135	0.186	0.127	0.236	0.594	0.219	0.164	0.132	Increase
Exponential Growth	0.076	0.402	0.315	0.237	0.367	0.832	0.133	0.241	BM	0.214	0.277	BM	Increase
Boltzman Sigmoidal	0.075	0.215	0.062	0.256	0.079	0.040	0.174	0.007	0.007	0.228	0.092	0.016	Uniform, burst increase
One phase decay	0.071	0.587	0.278	0.252	0.136	0.186	0.135	0.135	0.339	0.226	0.135	0.109	Increase
Two phases decay	0.071	0.248	0.043	0.258	0.052	0.006	0.153	0.018	0.006	0.283	0.018	0.000	Increase, step increase
One phase association	0.103	0.010	0.007	0.280	0.074	0.168	0.178	0.013	0.053	0.284	0.045	0.161	Uniform
Two phases association	0.084	0.050	0.014	0.268	0.050	0.025	0.136	0.085	0.079	0.243	0.061	0.011	Increase
Second order polynomial	0.080	0.140	0.066	0.252	0.135	0.186	0.127	0.242	0.608	0.219	0.163	0.131	Increase
Third order polynomial	0.064	1.366	0.393	0.258	0.073	0.037	0.134	0.096	0.089	0.242	0.063	0.011	Increase, plateau, increase
Fourth order polynomial	0.064	0.943	0.165	0.272	0.031	0.003	0.137	0.056	0.019	0.255	0.035	0.000	Increase, plateau, increase
Quadratic one variable	0.282	0.000	0.000	0.432	0.002	0.007	0.381	0.000	0.000	0.466	0.003	0.016	Decrease
One parameter exponential	0.289	0.000	0.000	0.469	0.001	0.003	0.325	0.000	0.000	0.457	0.003	0.018	Uniform
Asymptotic regression	0.071	0.587	0.278	0.252	0.136	0.186	0.135	0.135	0.339	0.226	0.135	0.109	Increase
Michaelis-Menten	0.069	1.279	BM	0.232	0.441	BM	0.146	0.094	0.388	0.237	0.145	0.523	Increase then burst increase
Gompertz	0.164	0.000	0.000	0.598	0.000	0.000	0.633	0.000	0.000	0.740	0.000	0.000	Decrease
Substrate inhibition	0.072	0.470	0.223	0.247	0.162	0.223	0.144	0.068	0.171	0.244	0.081	0.065	Increase, burst increase
One site competition	0.093	0.020	0.009	0.240	0.214	0.294	0.173	0.011	0.027	0.279	0.034	0.027	Increase, step increase
Two site competition	0.180	0.000	0.000	0.271	0.032	0.004	0.153	0.018	0.006	0.314	0.009	0.000	Double step increase
Gaussian	0.080	0.146	0.069	0.252	0.135	0.185	0.129	0.202	0.507	0.216	0.179	0.144	Increase
Lerentzian	0.079	0.163	0.077	0.251	0.136	0.187	0.133	0.152	0.382	0.221	0.157	0.126	Increase
Allometric 2	0.087	0.051	0.024	0.272	0.064	0.087	0.161	0.023	0.058	0.280	0.033	0.027	Increase
Power	0.289	0.000	0.000	0.469	0.001	0.003	0.325	0.000	0.000	0.457	0.003	0.018	Uniform

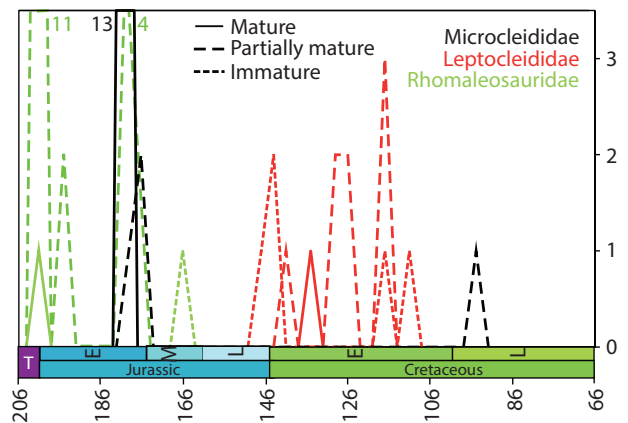**Table 4.** The mean square errors for non-parametric regressions, for each time bin. The best model is in bold.

Type of regression	2 Ma MSE	4.5 Ma MSE	6 Ma MSE	10 Ma MSE
LOWESS	**0.075**	0.354	0.172	0.446
Robust LOWESS	0.078	0.339	0.149	0.285

Figure 3. Evolution of paedomorphism through time in selected plesiosaurian clades for 2 Ma time bins. Geological time in Ma is represented in the x-axis and I/(M+P) in the y-axis. Higher I/(M+P) values indicate higher proportion of osteological immature specimens.

Figure 4. Evolution of paedomorphism as expressed by the I/(M+P) in families with few specimens. Frequencies of osteologically immature, partially mature, and mature specimens of leptocleidids, microcleidids and rhomaleosaurids through time. Geological time in Ma is represented in the abscissa and frequency (number) of specimens in the ordinate for each of the categories (mature, partially mature and immature).

Leptocleididae and Rhomaleosauridae) (Fig. 4). Data was partitioned into high level clades Plesiosauroidea and Pliosauroidea, and then into various subsets equivalent to the families Microcleididae, Polycotylidae, Leptocleididae, Cryptoclididae, Elasmosauridae, Pliosauridae and Rhomaleosauridae. Two time bins were used with durations of 2 and 4.5 Ma respectively, to evaluate if the patterns are affected by different time bin partitions.

Results

We found a statistically significant increase in the relative abundance of osteologically immature specimens through time. This finding is at odds with what should be expected from a taphonomic standpoint: the ratio of juvenile to adult specimens should have remained uniform through geological time. Figure 2 shows an average 50% of 'immature' specimens (i.e., specimens previously reported

Figure 2. Evolution of paedomorphism through geological time in Plesiosauria, as expressed by the I/(M+P) ratio. Geological time in Ma is represented in the abscissa and I/(M+P) in the ordinate. **A.** Best linear model. **B.** Best nonlinear model. **C.** Best nonparametric model.

as 'juveniles' or 'subadults') during the latest Cretaceous (82–66 Ma). This average might be an overestimation because several specimens considered as 'immature' may, in fact, be adult species of taxa displaying paedomorphosis. Steadily increasing rates of paedomorphism would explain this trend, and this data suggests that paedomorphism was widespread throughout plesiosaur clades, notably present in Rhomaleosauridae, Elasmosauridae, Pliosauridae, and Polycotylidae (Figs 3, 4).

Outliers. We found that the time bin for (approximately) the Early Aptian (120.05–124.55 Ma) was an outlier (Suppl. material 1). There is an evident peak of the ratio I/(P+M) at the Early Aptian that contrasts with the general gradual increase tendency through plesiosaur history. Before the Early Aptian the average I/(P+M) ratio is 0.40, and after it is 0.83, for the 4.5 Ma time bin partition. At the Early Aptian the I/(P+M) ratio is 3.0. For understanding this issue, please refer to the discussion.

Parametric regressions assumption tests

All of the linear regression tests that we conducted verify the assumptions to draw the parametric regression models. The Grubbs test and Z-scores find the Aptian time bin as an outlier independent of the time bin partition used, except for the Grubbs test for the 4.5 and 10 Ma partition (Table 2). There is no evidence for autocorrelation; the Durbin-Watson p-value is at least 0.157 for any time bin partition. The residuals are homoscedastic because the White's test p-value is at least 0.115, and we found no evidence for multicollinearity as the variance inflation factor is smaller than 5 for all time bin partitions. It is important to note that we only aim to find a tendency through time with these models, not necessarily to use the model parameters for estimation of I/(P+M) ratios.

Linear regression statistical modelling

The linear models are statistically significant ($p < 0.02$), except for the 4.5 and 10 Ma time bin partition ($p = 0.095$ and $p = 0.065$, see Discussion). The most significant time bin partition is for 2 Ma ($p = 0.001$), followed by the 6 Ma time bin partition ($p = 0.015$), Fig. 2A. The 10 Ma time bin partition shows the highest Spearman's correlation coefficient of -0.637, with the 4.5 Ma time bin partition showing the lowest (-0.415).

Nonlinear regression statistical modelling

The best fitting parametric models to the dataset show an increase of the I/(P+M) ratio – increased osteological immaturity – through time independent of the time bin partition used (Table 2, Fig. 2B). Overall, there is an increase of the MSE values with larger time bin partitions (see Table 2). The third order polynomial model performs best (i.e., lowest mean squares of errors, here abbreviated as MSE). However, Exponential Growth and Michaelis-Menten models could be selected irrespective of the time bin partition scheme used (relative likelihood > 0.05). Overall, the lowest MSE values are for the Exponential Growth for 10 Ma time bin partition, Beta Growth and second order polynomial for 6 Ma partition, and Michaelis-Menten for the 4.5 Ma time bin partition. Notably, all these models show a marked increase of the I/(P+M) ratio through time. Linear regressions are also among the best performing models in our analysis. Also importantly, the worst performing models show a decreasing or uniform tendency through time (e.g., Power function, Gompertz function, One Parameter exponential).

The best parametric model, the third order polynomial, shows a sharp increase of the I/(P+M) ratio until the end of the Jurassic, stabilizing during the Early Cretaceous, and subsequently increasing markedly up to ~1.0 (Fig. 2B).

Non-parametric LOWESS regression statistical modelling

The non-parametric regression models showed a consistent increase of the I/(P+M) ratio through time (Fig. 2C). There are no significant differences between the LOWESS and the robust LOWESS plots. However, the MSE scores are lower for the robust LOWESS model than for the LOWESS model, except for the 2 Ma time bin partition. The LOWESS model for the 2 Ma time bin partition draws a curve similar to the third order polynomial (see Fig. 2C and Discussion). All other models simply show a gradual increase of the I/(P+M) ratio through time.

Results by clade

Plesiosauroidea

In this superfamily as a whole there is only a sharp increase in the I/(M+P) ratio in the Early Cretaceous (Fig. 3). Otherwise, the ratio is relatively constant, but high, through time. It peaks at 2 in the Early Cretaceous, and dips to 0.2 in the Early Jurassic.

Pliosauroidea

There is a slight increase in I/(M+P) ratio through time, independent of the time bin partition used. In the Early Jurassic the I/(M+P) ratio is around 0.2 but by the Middle Jurassic and Early Cretaceous it is about 1 (Fig. 3).

Polycotylidae

The temporal range of polycotylids spans from the Aptian (Kear 2005) to the Maastrichtian (Welles and Gregg 1971; Fig. 3). Osteologically immature (~38%) and partially osteologically mature specimens account for 75% of the

specimens. The I/(M+P) ratio increases through time independently from the time bin partition used. By the end of the Cretaceous there are four more osteologically immature specimens than partially osteologically mature and osteologically mature polycotylid specimens combined, and the I/(M+P) ratio is ~4, whereas by the beginning of the Late Cretaceous the I/(M+P) ratio is ~0.2.

Various specimens of indeterminate polycotylids create an outlier in the latest Aptian (Vavrek et al. 2014), which was removed from the final results for this clade because of their uncertain taxonomic position (they could be leptocleidids). In fact, there are no published records of polycotylids by this time (109–113 Ma), and those reported by Vavrek et al. (2014) are all osteologically immature, except NUFV 1996 which is partially osteologically mature.

Elasmosauridae

Among elasmosaurids there is typically a ratio of one osteologically immature specimen per partially osteologically mature and osteologically mature specimen throughout the clade's longevity (Fig. 3). There is no statistically significant trend towards increasing or decreasing the I/(P+M) ratio through time.

Pliosauridae

Pliosauridae is a clade with a long temporal range, with records from the Early Jurassic (Hettangian) with taxa such as *Thalassiodracon*, to the Late Cretaceous (Late Campanian), such as indeterminate pliosaurid specimens recovered from New Zealand (Wiffen and Moisley 1986). Our database accounts for 72 specimens, of which ~34% are osteologically immature and only ~14% are fully osteologically mature (Fig. 3). There is a trend for increased I/(P+M) ratio through time, but this tendency seems to be affected by the patchy record of pliosaurids through time. Several osteologically immature specimens of *Kronosaurus queenslandicus* have been reported from the Aptian-Albian of Australia (McHenry 2009), thus creating a sudden increase around this time.

Cryptoclididae

Cryptoclidids are a clade with a temporal range from the Callovian to the Tithonian and are represented by 88 specimens in our database. There is a trend for increased I/(P+M) ratio through time; by the Callovian the ratio is ~0.4 and by the Tithonian it is 3 for the 6 Ma partition and 0.75 for the 4.5 Ma-partition (Fig. 3). Only ~27% of the specimens are fully osteologically mature and 25% of the specimens are osteologically immature.

Rhomaleosauridae

The rhomaleosaurid fossil record consists of very few published specimens (n = 22) and it is a clade with a short temporal range (Early to Middle Jurassic). Therefore, it is hard to obtain broad patterns on the evolution of paedomorphism in this clade (Fig. 4). However, most of the specimens are osteologically immature or partially osteologically mature (95.2%), suggesting paedomorphism in this clade.

Microcleididae

Microcleidids are a clade of plesiosauroids with a short temporal range at the end of the Early Jurassic and records of this group amount to only 17 published specimens (Fig. 4). The vast majority of the specimens are osteologically mature (76%), and the remaining (n = 4) are partially osteologically mature.

Leptocleididae

Leptocleidids have a temporal range within the Cretaceous from the Berriasian to the Albian and are represented in our database by 18 published specimens (Fig. 4). Only two specimens are osteologically mature: *Leptocleidus capensis* (SAM-K5822) and *Gronausaurus wegneri* (GMM-A3B.2). These represent only ~11% of the dataset. The counts of osteologically immature specimens (n = 8) equal those of partially osteologically mature specimens (n = 8).

Discussion

Several authors have considered ontogeny in plesiosaurs. For example, Andrews (1895) investigated ontogeny of the shoulder girdle of *Cryptoclidus*, Carpenter (1999) discussed the ontogenetic series for *Styxosaurus snowii* (p. 162), Carpenter (1996, p. 266) discussed the ontogenetic series for *Dolichorhynchops*, Caldwell (1997a) discussed ossification patterns in *Cryptoclidus*, Cruickshank and Long (1997) discussed sexual maturity in specimens of *Leptocleidus* (p. 273), Hiller et al. (2005, p. 269) discussed ontogeny in *Mauisaurus*, Wiffen and Moisley (1986) illustrated a growth series of elasmosaurid girdles, Wiffen et al. (1995) investigated ontogeny of bone structure in plesiosaurs, Talevi and Fernandez (2015) investigated microstructure of plesiosaur bone as an ontogenetic indicator, O'Keefe et al. (2019) studied polycotylid long bone ontogeny, Miller et al. (2020) considered ontogenetic variability in the plesiosaur pelvis, and Otero et al. (2014, 2018) and O'Gorman et al. 2014, O'Gorman and Coria 2017) discussed ontogeny in elasmosaurids. However, paedomorphism in plesiosaurs has not been considered as much.

Paedomorphism in Plesiosauria

Paedomorphism is a common trait among secondarily aquatically-adapted organisms (Fordyce and Barnes 1994; Galatius 2010). It has also been reported in stem-group sauropterygians (Carroll and Gaskill 1985;

Rieppel 1989a, 1989b; Klein 2010), and is suspected to occur also in Plesiosauria (Caldwell 1997a; Wintrich et al. 2017). The incongruent external morphology versus the histology of the propodials of Angolan specimens (Araújo et al. 2015) and *Abyssosaurus* (Berezin 2019) supports the idea of paedomorphism in Plesiosauria. Furthermore, as Galatius (2010) noted for some cetaceans, in the Angolan specimens the juvenile morphology and the smaller absolute size of the adults (as compared to other limb elements, for example) agrees with the idea of paedomorphism. However, this statement should be considered with caution because it is anchored on the small sample of data derived from Wiffen et al. (1995). Araújo et al. (2015) and Liebe and Hurum (2012) underscore that the histology of plesiosaurs is poorly known and needs to be systematically surveyed across both taxa and ontogeny. For example, the presence of pachyosteoslerotic and osteoporotic histology in sections that are a few centimeters apart in the same bone complicates the interpretation and indicates the need for more comprehensive histological analyses. Paedomorphism in whale lineages seems to only arise in derived forms (Fordyce and Barnes 1994). Analogous evidence for this heterochronic condition is most obvious in Late Cretaceous taxa (this paper). Thus, ontogenetic assessments should be a critical basis for taxonomic ascriptions in derived plesiosaur lineages. Pending histological analysis, plesiosaur specimens previously considered to be juveniles may simply be paedomorphic adults, unless osteologically mature specimens of the same species also exist to show this is not the case (e.g., Andrews 1910; Brown 1981; Bardet et al. 2008). External morphology is not always sufficient to determine the ontogenetic status of the specimens.

Implications for plesiosaur systematics

Following Brown (1981), many plesiosaur species were considered *nomina dubia* due to their 'juvenile' condition (e.g., *Tuarangisaurus? cabazai*, Gasparini et al. 2007; *Leurospondylus ultimus*, Sato and Wu 2006). However, paedomorphism is an equally parsimonious hypothesis to explain the osteologically immature external morphology seen in many plesiosaur specimens. Brown (1981) did not critically assess the confounding heterochronic effects and their potential taxonomic implications because he was working on a clade with a typical ontogenetic pattern with (comparatively) reduced heterochrony and complete fossilized ontogenetic sequences. An analysis of external morphological characters is necessary, but not sufficient, to assess a specimen's ontogenetic stage, particularly in plesiosaurs and other secondarily aquatically-adapted organisms. In order to avoid a circular argument, additional lines of evidence are ultimately required to test paedomorphism as an alternative hypothesis.

Our data suggests that not all plesiosaur clades co-ossify neural arches and centra at the same rate and extent. Thus, in certain clades these differences will bear a

phylogenetic signal. In other words, the apomorphic condition is a paedomorphic trait. For example, neural arches remain separated throughout ontogeny in every taxon of the rhomaleosaurid clade.

Implications for plesiosaur paleoecology - Paedomorphism or nurseries?

The presumption that osteologically immature external morphological traits imply a 'juvenile' condition led several authors to propose breeding ground and nursery hypotheses for certain plesiosaur assemblages (Wiffen et al. 1995; Kear 2006). For example, Kear (2006) suggested that the relatively high number of 'juvenile' elasmosaurids (and other marine amniotes) in the Bulldog Shale, Australia, was a result of favorable ecological conditions for 'safe calving grounds' and refuges for young animals prior to their entering the open sea as adults. Welles and Gregg (1971, p. 171) suggested that "infant mortality must have been high among the plesiosaurs" when looking at the late Campanian-early Maastrichtian elasmosaurid fauna of New Zealand. Conversely, other marine reptiles from the same assemblage (mosasaurs and turtles) do not exhibit the same pattern.

The perception of relative 'juvenile' abundance is dependent upon the assemblages and taxa under study (e.g., "juvenile plesiosaurs are relatively rare in the fossil record", Storrs 1995, p. 75; "complete juvenile plesiosaurs are indeed relatively rare in the fossil record …", Vincent 2010, p. 45).

The interpretation of these assemblages as plesiosaur nurseries rests on the assumption that the osteological immature specimens represent sexually immature and ontogenetically immature individuals. The hypothesis that coastal environments served as nurseries for plesiosaurs remains speculative pending histological studies except for one outlier: the Aptian-Albian. Kear (2006) proposed that an explanation for the high proportion of immature specimens in the Bulldog Shale (Early Aptian-Early Albian) could be explained by nutrient-rich cold-water coastal habitats serving as both 'safe calving grounds' and refuges for young animals prior to their entering the open sea as adults. This hypothesis was first proposed by Wiffen et al. (1995) when analysing the unique pattern of the osteohistology of Late Cretaceous elasmosaurids from New Zealand. Similarly, Sachs (2004) reports various specimens with "[neural arches] not fused with the centra" from the Late Aptian. In fact, in all our analyses, the Aptian time bin was found to be a statistically significant outlier. A close look at the dataset reveals that the vast majority of specimens are ascribed to the elasmosaurid taxon *Woolungasaurus glendowerensis* which is mostly composed of immature specimens (Sachs 2004). However, the use of the I/(P+M) ratio is insensitive to the sampling quality. Specimen sampling for the Aptian-Albian is poor, and although the nursery hypothesis cannot be rejected based upon presented evidence, we acknowledge that

more findings from this time bin might either eliminate this outlier or emphasize and verify the nursery hypothesis. At this point, the Aptian-Albian outlier represents a major decrease of fossil record quality. Converse to the Aptian-Albian pattern, other better sampled time bins show a gradual increase of paedomorphism through time.

The contribution of paleohistology to understanding paedomorphism

Paleohistology provides an alternative line of evidence for determining paedomorphism in plesiosaurs (Houssaye 2009). The available literature on plesiosaur histology is scarce (see Liebe and Hurum 2012 for a review), although there has been some expansion of knowledge on non-plesiosaurian sauropterygians (e.g., Klein 2010; Hugi et al. 2011). Wiffen et al. (1995) presented a thorough analysis of plesiosaur histology by analyzing several bones of different ontogenetic stages from Late Cretaceous specimens from New Zealand. The histology of isolated elasmosaurid propodials allowed the contrasting of two different ontogenetic stages: the 'juvenile' humerus is pachyostotic; i.e., has a thick layer of cortical bone and the medullary zone is pierced by some erosional lacunae; whereas the 'adult' specimen is cancellous and has intense Haversian remodeling, although it bears a relatively compact cortex locally. The 'Wiffen et al. (1995) juvenile' histological traits correlate with the 'Brown juvenile' (Brown 1981) external morphological traits; i.e., unfaceted propodials, relatively small dimensions, undeveloped tuberosity/trochanter, and overall propodial proportions. Nevertheless, new evidence seems to question the view that this material represents different ontogenetic stages and it may represent different taxa instead (Talevi and Fernández 2015), but data from more specimens needs to be gathered. For example, Fostowicz-Frelik and Gaździcki (2001) also compared the histology and external morphology of an elasmosaurid (cf. *Mauisaurus*) from the Campanian-Maastrichtian of Antarctica. They concluded that the Antarctic specimen was a sub-adult based on the presence of the humeral trochanter and bone dimensions, which were in accordance with the presence of bone remodeling, the proportion of cortical versus medullar bone in the humerus, and the concentration of secondary osteons.

In Angolan aristonectine specimens the humeri have an osteosclerotic histology, there are secondary osteons nearly all the way to the outermost regions of the sectioned bones, and there is a presence of three lines of arrested growth (Araújo et al. 2015). This set of traits points to a 'Wiffen et al. (1995) adult' condition. In addition, the muscle scars are formed by deeply grooved and reworked periosteum which is indicative of late ontogenetic stages as observed in other vertebrates (e.g., Tumarkin-Deratzian et al. 2006). In contrast, the external morphology, in particular the small size, the unfaceted distal propodials, the flat articular facets of the vertebrae, the non-fusion of the neural arches with the centra, the near absence of the posterior cornua of the coracoids, and the absence of the pectoral bar, implies a 'Brown juvenile' condition. The combination of these ontogenetically incongruent characters indicates: (1) paedomorphism; or (2) that Wiffen et al.'s (1995) ontogenetic classes are not fully and appropriately defined. On the other hand, Liebe and Hurum (2012) described the internal structure and microstructure of various cryptoclidids at different ontogenetic states. This is significant for the present study as a null hypothesis based on a phylogenetically significant outgroup. Liebe and Hurum (2012) detected the presence of secondary osteons in 'adult' specimens and an absence in 'juvenile' specimens. Also, the external morphology exhibits typically 'juvenile' traits, such as unfaceted propodials, which contrasts with the condition in the Angolan specimens. Synchrotron tomography techniques offer a modern, non-destructive, and scalable approach to assess the histologically maturity of specimens. This could be adopted to test the observed patterns of the plesiosaur fossil record as has been done for other taxa (e.g., Sanchez et al. 2012).

Early Cretaceous: changing seas, acquisition of new life history strategies, or poor specimen sampling?

The Early Cretaceous is characterized by elevated climatic volatility and major tectonic changes due to the accelerated breakup of Pangea (Fischer et al 2016; Föllmi 2012). The pre-Aptian Early Cretaceous witnessed a cold greenhouse climate with ephemeral ice sheets (Hay and Floegel 2012; Hu et al. 2012; Föllmi 2012), followed by one of the hottest period of the Mesozoic starting from the Aptian (Kidder and Worsley 2010). There were also major reversals of thermohaline ocean circulation and a major Oceanic Anoxic Event had occurred by the Early Aptian (Kidder and Worsley 2010; Sames et al. 2016). These major global oceanic transformations oceans could have led plesiosaurs to important radiation events and/or the acquisition of new life history strategies. During this time some of the most important and diverse plesiosaur clades originated: Polycotylidae and Elasmosauridae. Indeed, residual diversity for plesiosaurs, alongside chelonioids and derived ichthyosaurs, was high yet unaffected by Lagerstätten effects (Benson and Butler 2011). Elasmosaurids are already a paedomorphic clade when they originate in the Early Cretaceous. The origin of these important Late Cretaceous plesiosaur clades coincides with a common pattern detected from our models where there were significant changes in the $I/(P+M)$ ratio during the Early Cretaceous (see nonlinear regression results). However, the Early Cretaceous is also the poorest sampled epoch of plesiosaur existence. The Early Cretaceous represents ~33% of plesiosaur longevity, but only ~11% of the specimens in this analysis are from this interval. Conversely, the Late Cretaceous contains ~37% of the published specimens for ~25% of plesiosaur longevity, and the Middle Jurassic specimens are also

overrepresented (11% of the published specimens for 8% of plesiosaur longevity). The Early Cretaceous seems to be inadequately sampled for various Mesozoic marine reptiles (Benson et al. 2010, 2013; Fischer et al. 2016). Likewise, the "fish" fossil record, which is less prone to sampling effort/success biases, shows elevated percentage of ghost lineages by the pre-Aptian Early Cretaceous, which is a proxy for sampling quality (Guinot and Cavin 2015, 2016). Therefore, the sudden increase of the I/(P+M) ratio during the Early Cretaceous found by our best models, may be an artefact of poor sampling during this period.

The rate of paedomorphic evolution in Plesiosauria

By using alternative methods to linear regression modelling, the nonparametric LOWESS regression of the I/(P+M) ratio through time indicates a linear tendency. Furthermore, the linear model was retrieved consistently among the best statistical modelling techniques. This linear tendency implies a steady increase of I/(P+M) through geological time, allowing us to speculate about a possible rate of paedomorphism. The rate of paedomorphic evolution in Plesiosauria as whole is 0.6%/Ma with 95% confidence bounds oscillating between 0.3 to 0.9%/Ma. Whereas plesiosaurs seem to have a slow rate and gradual evolution of paedomorphic traits, a contrasting pattern is present in the odontocete phocoenids. Widespread paedomorphism seems to have been attained at a relatively accelerated rate in phocoenids, whose entire body plan has become paedomorphic in less than ~11 Ma (Barnes 1985) with heterochronic modifications on the brain (Racicot and Colbert 2013), postcranial skeleton (Galatius 2010) and skull (Barnes 1985). However, the plesiomorphic condition in non-plesiosaurian sauropterygians already shows a significant degree of aquatic skeletal paedomorphism (Rieppel 2000). The absence of a calcified sternum, the reduced number of carpal and tarsal elements, or the absence of the neurocentral fusion are some of the external morphological traits indicative of paedomorphism (Rieppel 2000). Paedomorphism in plesiosaurs is an aggregation of the basal sauropterygian condition.

However, some aristonectines represent extreme examples of paedomorphism by the Campanian-Maastrichtian (Araújo et al. 2015; Otero et al. 2015). The extremely 'juvenilized' external morphology of the skeleton, contrasts with the histologically maturity of the long bones (Araújo et al. 2015). The typical plesiosaur pattern is not as extreme, affecting only skeleton morphology to a lesser degree or in a combination of traits. Nevertheless, there are some consistent pleiotropic effects of paedomorphosis among Mesozoic marine reptiles. In plesiosaurs (see dataset), and also in other Mesozoic marine reptiles, paedomorphism not only affects vertebral closure, but also rib co-ossification, epicondyle morphology, and meristic reduction of mesopodial ossification concomitantly (Seeley 1908; Carroll 1997; Caldwell 2002; Herrera et al. 2013). Further study and refinement of the data collected

here may shed light on the evolutionary patterns of pleiotropic effects resulting from heterochronic modifications.

Paedomorphism and secondarily-adapted tetrapods

Paedomorphic traits are widespread among tetrapods, with salamanders and newts being a quintessential example where paedomorphic traits are viewed as adaptations to their complex life cycle (e.g., Oromi et al. 2016). However, paedomorphic characters have been linked to various major adaptive events such as flight in avian dinosaurs (Bhullar et al. 2012), adaptations to insularity in elephants (Larramendi and Palombo 2015), or even the human condition (Godfrey and Sutherland 1996; Mitteroecker et al. 2004).

While gravity is a primary constraint for tetrapod architecture (e.g., Clack 2012), buoyancy and water viscosity play a major controlling role in aquatic organisms (Fish 2000). Paedomorphism, as manifested in reduced ossification, is among the most common convergent trends among secondarily-adapted tetrapods at the level of bone histology and external morphology (de Ricqlès 1975; Rieppel 1989a; Houssaye et al. 2016). Aquatic skeletal paedomorphism is a passively selected modular trait caused by the hydrostatic balance provided by the aquatic medium. In contrast to their terrestrially-adapted counterparts, the formation of additional surface area for muscular and tendinous attachment via additional osseous processes is ineffectual in aquatic tetrapods. Aquatic paedomorphism is manifested in several ways, ranging from decreased degree of skeletal ossification in non-plesiosaurian sauropterygians (Rieppel 2000), to osteologically immature bone histology in ichthyosaurs and mosasauroids (De Buffrénil and Mazin 1990; Sheldon and Bell 1998), delayed neurocentral fusion in thalattosuchian crocodyliforms and ichthyosaurs (Seeley 1908; Herrera et al. 2013), overall skull morphology in baleen whales (neobalaenines) (Tsai and Fordyce 2014), reduction of the carapace ossification in sea turtles (Kordikova 2000, 2002), and the reduction of pectoral musculature in the Galápagos cormorants (Livezey 1992). Such disparate patterns result from different aquatic locomotory styles and clade-specific developmental constraints. Among the most thoroughly studied cases of skeletal paedomorphism are the phocoenids (Galatius and Kinze 2003; Galatius et al. 2006; Galatius 2010). These odontocete cetaceans show a retardation of the fusion of the vertebral epiphysis, pectoral girdle elements, and propodial epiphyses (Galatius and Kinze 2003). However, even in porpoises the neurocentral suture is always fused, which is the general condition in mammals. This shows that heterochronic shifts are deeply constrained by the phylogenetic patterns and developmental programmes of the group in question. For instance, not all pelagic secondarily-adapted tetrapods are selected towards increasing paedomorphism through their evolutionary history. Most mysticete whales are notable examples that do not show any particular trend

towards increasing paedomorphism (Tsai and Fordyce 2014). These disparate trends among secondarily-adapted amniotes can be related to phylogenetic incumbency, different life-history patterns, habitual biomechanical demands, or degree of terrestrial dependency. For instance, the degree of cranial sutural closure may vary significantly within pinnipeds with walruses showing nearly complete closure whereas elephant seals show almost no co-ossification (Goswami et al. 2013). Nevertheless, it is clear that sauropterygians, and plesiosaurs in particular, show an overall pattern towards increasing paedomorphism. The proportion of osteologically immature specimens increases significantly through time and this can only be explained by a long-term trend towards delayed or truncated growth. Despite the relatively small size compared to other contemporaneous plesiosaurs, microcleidids seem to be an exception, with most specimens being osteologically mature (Großmann 2006, 2007). The purported 'juvenile' specimens (Großmann 2006, 2007) seem to be true ontogenetically immature individuals. Microcleidids can be viewed as an example where dwarfism is not attained by heterochronic processes, but rather constrained by phylogenetic and ecological factors.

Conclusions

Paedomorphism is a major confounding factor in determining the ontogenetic stage in plesiosaur skeletons, with subsequent taxonomic implications. As a consequence, many ontogenetic stage determinations for different plesiosaur taxa may be mistaken. Although our results suggest that the ontogenetic stage in early plesiosaurs (Early to Middle Jurassic) may be identifiable based on external morphological features, external morphology alone renders interpretation more difficult in later plesiosaurs, because a high proportion of osteologically immature specimens prevail. Nevertheless, even in basal and early plesiosaur clades, such as rhomaleosaurids, morphological features indicative of osteological immaturity are pervasive, such as unfaceted propodials and lightly co-ossified vertebrae and neural arches. To help tackle these issues we propose:

1. To replace the sexual maturity terminology by Brown (1981) used in ontogenetic assessments, with terms that denote external morphology and osteological maturity instead: osteologically immature, partially osteologically mature, and osteologically mature.
2. Ontogenetic assessments remain hypothetical until backed up with paleohistological data.

Acknowledgements

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Supplementary material 1

Raw data and analyses

Authors: Ricardo Araújo, Adam S. Smith

Data type: Excel files (in ZIP. archive)

Explanation note: Plesiosaur occurrences, osteological maturity assessment, references and statistical analyses.

Link: https://doi.org/10.3897/fr.26.97686.suppl1