

Evolutionary pathways toward gigantism in sharks and rays

Catalina Pimiento,^{1,2,3,4}  Juan L. Cantalapiedra,^{2,5}  Kenshu Shimada,⁶ Daniel J. Field,⁷ 
 and Jeroen B. Smaers⁸

¹*Department of Biosciences, Swansea University, Swansea SA28PP, United Kingdom*

²*Museum für Naturkunde, Leibniz Institute for Evolution and Biodiversity Science, Berlin 10115, Germany*

³*Smithsonian Tropical Research Institute, Balboa, Panama*

⁴*E-mail: c.pimiento@swansea.ac.uk*

⁵*Departamento Ciencias de la Vida, Universidad de Alcalá, Madrid, Spain*

⁶*Department of Environmental Science and Studies and Department of Biological Sciences, DePaul University, Chicago IL 60614*

⁷*Department of Earth Sciences, University of Cambridge, Cambridge, Cambridgeshire CB2 3EQ, UK*

⁸*Department of Anthropology, Stony Brook University, New York NY 11794*

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Through elasmobranch (sharks and rays) evolutionary history, gigantism evolved multiple times in phylogenetically distant species, some of which are now extinct. Interestingly, the world's largest elasmobranchs display two specializations found never to overlap: filter feeding and mesothermy. The contrasting lifestyles of elasmobranch giants provide an ideal case study to elucidate the evolutionary pathways leading to gigantism in the oceans. Here, we applied a phylogenetic approach to a global dataset of 459 taxa to study the evolution of elasmobranch gigantism. We found that filter feeders and mesotherms deviate from general relationships between trophic level and body size, and exhibit significantly larger sizes than ectothermic-macropredators. We confirm that filter feeding arose multiple times during the Paleogene, and suggest the possibility of a single origin of mesothermy in the Cretaceous. Together, our results elucidate two main evolutionary pathways that enable gigantism: mesothermic and filter feeding. These pathways were followed by ancestrally large clades and facilitated extreme sizes through specializations for enhancing prey intake. Although a negligible percentage of ectothermic-macropredators reach gigantic sizes, these species lack such specializations and are correspondingly constrained to the lower limits of gigantism. Importantly, the very adaptive strategies that enabled the evolution of the largest sharks can also confer high extinction susceptibility.

KEY WORDS: Body size, elasmobranchs, evolution, filter feeding, gigantism, mesothermy.

Gigantism may confer animals with numerous ecological advantages, such as competitive superiority and enhanced predation efficacy (Vermeij 2016). Despite these benefits, gigantism is generally exhibited by only a small minority of taxa in most clades (Kozłowski and Gawelczyk 2002; Kingsolver and Pfennig 2004; Vermeij 2016). Because larger organisms require more resources, gigantism might be predicted to be restricted to top-level consumers. Indeed, a strong, positive relationship exists between body size and trophic level in certain clades, including some

fishes (Pauly et al. 1998; Romanuk et al. 2011). Nevertheless, the attainment of gigantism is generally not limited by trophic level, but by the quality and abundance of an environment's resources (McNab 1983; Kingsolver and Pfennig 2004; McNab 2009), and by a species' ability to exploit them (e.g., maneuverability and thermoregulatory capabilities; Webb and De Buffrénil 1990; Domenici 2001). Hence, while some giants with relatively low metabolic demands and sluggish habits may feed on vast amounts of small but abundant food items such as plankton,

others with higher metabolic demands may be active macro-predators capable of efficiently hunting large prey (Webb and De Buffrénil 1990; Domenici 2001; Vermeij 2016). Gigantism is therefore associated with an enhanced capacity for environmental exploitation.

Most efforts to understand the evolutionary pathways underlying the acquisition of gigantism in the oceans have focused on planktivorous giants. Accordingly, filter feeding has emerged as the key adaptive strategy facilitating the evolutionary origin of giant bony fishes in the Mesozoic (Liston, 2008, 2013; Friedman et al. 2010; Friedman 2012; Liston et al. 2013). Similarly, the evolution of gigantic marine mammals in the Cenozoic has been linked to the ability of filter-feeding whales to exploit abundant plankton during episodes of elevated primary productivity (Clauset and Erwin 2008; Field et al. 2010; Smith and Lyons 2011; Clauset 2013; Pyenson and Vermeij 2016; Slater et al. 2017). By contrast, fewer efforts have been devoted to unraveling evolutionary pathways toward the origin of giant marine macro-predators. This might be because even the largest macro-predators tend to be smaller than their filter feeder counterparts, as a result of an inevitable lower abundance of large prey items relative to plankton (McNab, 1983, 2009; Vermeij 2016; Ferrón et al. 2017). However, recent studies on extinct macro-predatory sharks have suggested that the attainment of gigantic size in these active predators was linked to the retention of body heat by aerobic swimming muscles, hereafter referred to as mesothermy (Ferrón 2017; Ferrón et al. 2017). Mesothermy facilitates enhanced hunting efficiency among marine predators, as it allows greater distances to be covered (latitudinal and vertical niche expansion) and enables faster cruising speeds (Dickson and Graham 2004; Watanabe et al. 2015). Although links between both planktivory and mesothermy and body size have been previously investigated, a synthetic view of the array of evolutionary pathways underlying the origin of marine gigantism in both filter feeders and macro-predators is still lacking.

Modern sharks and rays (crown Elasmobranchii) offer an ideal system to study the evolutionary trajectories underlying gigantism in the oceans. Crown group elasmobranchs have an evolutionary history of at least 250 million years (Cappetta 2012), and extremely large body sizes have arisen in phylogenetically distant and ecologically disparate species. For instance, the largest sharks ever recorded (both ~18 m in length) are the ectothermic, filter-feeding whale shark (*Rhincodon typus*), and the extinct megalodon (†*Otodus megalodon*), a presumed mesotherm and the largest marine macro-predator to ever live (McClain et al. 2015; Pimiento and Balk 2015; Ferrón 2017; Ferrón et al. 2017). Patterns of body size evolution, and the preadaptive underpinnings of convergent gigantism, have never previously been evaluated across elasmobranchs within a phylogenetic framework. Here, we quantitatively investigate the evolutionary pathways that have

resulted in elasmobranch gigantism by applying a trait-based, phylogenetic approach to an extensive database of extant and extinct elasmobranch species. We assess the relationship between body size and species traits (i.e., trophic level, feeding strategy, and thermoregulatory mode), and investigate the origins of filter feeding and mesothermy in relation to the evolution of gigantic body size across elasmobranch phylogeny. Our results elucidate alternative pathways to elasmobranch gigantism, as well as associations among size-related biological parameters and extinction risk.

Methods

DEFINITION OF GIGANTISM

To investigate the pathways that have led to the evolution of gigantic size in elasmobranchs, it is necessary to define the limits of gigantism. Accordingly, we have set a biologically informed size limit for elasmobranchs, following previous studies on other marine organisms (e.g., >8 m in bony fishes (Friedman 2012; Liston et al. 2013), >10 m in marine mammals (Slater et al. 2017; but also see Fordyce and Marx 2018)). In so doing, we have followed the most recent, comprehensive work on biological gigantism (Vermeij 2016), which defines a giant as the largest species of its clade or ecological category. In this context, global giants are defined as the largest species at the global scale and/or throughout geological time, and local giants are defined as the largest species in a particular major subclade, time interval, or locality (Vermeij 2016). Following this definition, there are two global giant elasmobranchs: megalodon (†*O. megalodon*) and the whale shark (*R. typus*), which reach the maximum size ever attained by sharks, of ~18 m (McClain et al. 2015; Pimiento and Balk 2015). Local giants include the basking shark (*Cetorhinus maximus*, the largest temperate shark, ~12 m), the giant oceanic manta ray (*Manta birostris*, the largest batoid, ~9 m), the tiger shark and white shark (*Galeocerdo cuvier* and *Carcharodon carcharias*, the largest macro-predators, ~7.5 and ~7 m, respectively) and the Greenland shark (*Somniosus microcephalus*, the largest polar shark, ~6.4 m) (McClain et al. 2015). Because these elasmobranchs exhibit maximum total body lengths exceeding 6 m, we defined the limit of elasmobranch gigantism as >6 m for the purpose of this study, and consequently, also include the following species estimated or known to reach or exceed this threshold: the fossil white shark and fossil basking shark (†*Carcharodon hastalis* and †*Cetorhinus* spp., ~6.5 m), the goblin shark (*Mitsukurina owstoni*, ~6.2 m), the great hammerhead shark (*Sphyrna mokarran*, ~6.1 m), the megamouth sharks (*Megachasma pelagios* and †*Megachasma applegatei*, both ~6 m) and the extinct snaggle-tooth shark (†*Hemipristis serra*, ~6 m) (Uyeno et al. 1990; Kent 1994; Shimada et al. 2014; Welton 2014; McClain et al. 2015; Welton 2015; Froese and Pauly 2017).

TREE AND CALIBRATION

We used the originally undated elasmobranch phylogeny produced by Naylor et al. (2012). We chose this phylogeny among others available for the following reasons: (1) it is based on 595 species and brackets the phylogenetic breadth of elasmobranch crown group diversity (including batoids); (2) it is a densely taxon-sampled phylogenetic hypothesis based on analysis of NADH₂ (a mitochondrial, protein-coding gene) using sequences generated *de novo* from samples collected and identified by the authors (therefore avoids using barcode sequences derived from GenBank, which can potentially include misidentified specimens or sequences of questionable provenance; for a discussion on these issues see Naylor et al. 2012); (3) given that it is sequence-based, it is independent of the morphology-related variables we examine in this work; and (4) it includes all 15 extant lamniform species. We time-scaled this phylogeny using the Penalized Likelihood algorithm implemented in the software treePL (Smith and O'Meara 2012) and applied cross-validation to empirically determine the optimal smoothing factor using the default settings in treePL. To do so, we used the ages of 11 fossil calibrations representing the oldest total-clade records of the following elasmobranch orders: 164.7–167.7 million years ago for *Carcharhiniformes*; 145.5–150.8 million years ago for *Lamniformes*; 175.6–183 million years ago for *Orectolobiformes*; 175.6–183 million years ago for *Heterodontiformes*; 125–130 million years ago for *Squaliformes*; 155.7–161.2 million years ago for *Squatiniformes*; 99.6–112 million years ago for *Pristiophoriformes*; 189.6–196.5 million years ago for *Hexanchiformes*; 33.9–56 million years ago for *Rajiformes*; 61.7–65.5 million years ago for *Torpediniformes*; and 130–136.4 million years ago for *Myliobatiformes*. These dates are derived from the fossil record (Table S1) and are based mostly on the work of Cappetta (2012). Details on our use of fossil calibrations and additional references are provided in the Supporting Information.

TRAITS

We downloaded maximum total size of all extant elasmobranch species from FishBase (Froese and Pauly 2017; www.fishbase.org) using the *R* package *rfishbase* (Boettiger et al. 2012). In sharks, body sizes are expressed as total length (TL), estimated as the distance from the tip of the snout to the posterior end of the dorsal caudal lobe. In batoids (except sawfishes; see below), the width of the disc (WD) is estimated as the distance between the wing tips (accordingly, the tail and rostrum lengths of batoids are not considered). Maximum body size was expressed as the largest TL or WD values recorded for each species. We checked each of these and adjusted when necessary based on the most recent literature (e.g., McClain et al. 2015). Body sizes of sawfishes (which are batoids, Pristidae) and sawsharks (which are sharks, Pristiophoriformes) were treated differently given their unusually

elongate rostra, to avoid biased body size estimates (for the purposes of this study, “rostrum” specifically refers to the structure bearing rostral spines, whereas “snout” refers to an elongation of the head without a spinous rostrum). Given that correlations between body size and TL or WD do not accommodate the greatly elongated rostra of sawfishes and sawsharks, we ran our analyses excluding rostra for these taxa. In so doing, we subtracted one quarter of the TL, which roughly corresponds to the proportional length of their rostra (see Bigelow 1953; Bigelow and Schroeder 1953; Carpenter and Niem 1999; McEachran et al. 2002).

We downloaded data on the mean trophic level for all elasmobranchs from FishBase (Froese and Pauly 2017). Trophic level defines the position of organisms within a food web while considering both their diet composition and the trophic levels of their food items. FishBase estimates this value from the mean trophic level of prey, plus one (Boettiger et al. 2012; Froese and Pauly 2017). Within FishBase, prey information is gathered from stomach contents of fish species at a given locality and season (Boettiger et al. 2012; Froese and Pauly 2017). We also assigned data on thermoregulation and feeding strategy to each species. Thermoregulatory strategies in elasmobranchs can take two forms: ectothermy (animals incapable of self-regulating their body temperatures) and mesothermy (animals that can control the temperature of some of their most important organs, also called regional endothermy). Ectothermy is the most common physiological strategy among fishes, whereas mesothermy is restricted to certain taxa, such as lamnid sharks and two species of *Alopias* (*A. superciliosus* and *A. vulpinus*) (Carey and Teal 1969; Block and Carey 1985; Bernal et al., 2003, 2005, 2012; Bernal and Sepulveda 2005; Sepulveda et al. 2005; Grady et al. 2014). Similarly, elasmobranchs can be roughly divided into two groups with regard to their feeding strategies: macropredators (i.e., macrophagous) and filter feeders (i.e., microphagous or planktivorous). While the macropredatory lifestyle is the most common form in elasmobranchs, filter feeding is exhibited by 14 extant species: *C. maximus*, *M. pelagios*, *R. typus*, *Manta alfredi*, *M. birostris*, *Mobula eregoodootenkee*, *Mobula hypostoma*, *Mobula japonica*, *Mobula kuhlii*, *Mobula mobular*, *Mobula munkiana*, *Mobula rochebrunei*, *Mobula tarapacana*, and *Mobula thurstoni* (Paig-Tran and Summers 2014). In total, 449 of the 595 species across the phylogeny examined by Naylor et al. (2012) were associated with trait data (~75%; Table S2).

FOSSIL TAXA

We included fossils in our statistical analyses (see below) in instances where both phylogenetic position and trait inferences were reasonably supported. Accordingly, we conducted an exhaustive search for appropriate fossils of crown group elasmobranchs to be included in our analyses. Based on this search, 10 fossil taxa exhibiting clear taxonomic identifications and adequately

resolved phylogenetic relationships were included: †*C. hastalis*, †*C. hubbelli*, †*Cetorhinus* (non-*C. maximus* spp.), †*Cretalamna* sp., †*H. serra*, †*Keasius*, †*Megachasma alisonae*, †*M. applegatei*, †*Megalolamna paradoxodon*, and †*Otodus*. Giant fossil taxa of uncertain phylogenetic position were excluded (Shimada 2008; Frederickson et al. 2015; Shimada et al. 2015; Amalfitano et al. 2017). First and last appearance dates for fossil taxa were gathered from the literature (see Table S3 and Supporting Information References). For †*Otodus*, we considered the entire megatoothed lineage as a single clade consisting of chronospecies from †*O. obliquus* to †*O. megalodon* (Ward and Bonavia 2001). In order to place this lineage in the tree, we considered alternative phylogenetic hypotheses recently proposed for Lamnidae (Applegate and Espinosa-Arrubarrena 1996; Gottfried et al. 1996; Purdy 1996; Purdy et al. 2001; Ward and Bonavia 2001; Nyberg et al. 2006; Cappetta 2012; Shimada et al. 2017), and followed the hypothesis supporting the megatoothed lineage as a distinct family (†Otodontidae), derived from the extinct genus †*Cretalamna* (Applegate and Espinosa-Arrubarrena 1996; Nyberg et al. 2006; Shimada et al. 2017). However, given that the interrelationships of otodontids and other lamniforms remain questionable, we ran our analyses using three possible strategic placements for †Otodontidae (Fig. S1) in which we consider the following: (a) otodontid teeth exhibit more derived characteristics than those of Mitsukurinidae; (b) Mitsukurinidae is regarded as the basal-most lamniform clade (see Cappetta 2012; Naylor et al. 2012); and (c) the otodontid clade lies outside Lamnidae. Our results were consistent in light of these alternative phylogenetic positions. We adjusted these placements based on the most likely origination and extinction times of the clade (Table S3; Applegate and Espinosa-Arrubarrena 1996; Pimiento et al. 2013; Pimiento and Clements 2014; Pimiento et al. 2016). Finally, we assigned trait values for maximum total length, trophic level, thermoregulatory mode, and feeding strategy for fossil species based on estimates from the literature (Table S2). Details on trait reconstructions and ages for fossil species can be found in the Supporting Information along with all references used. Because the number of fossil taxa in our analyses was limited, all statistical analyses were re-run excluding fossils to evaluate their influence on our reconstructions and both sets of results are reported.

STATISTICAL ANALYSES

All our statistical analyses were carried out in the R computing environment (R Core Team 2017). To assess the relationship between trophic level and body size, we applied a phylogenetic regression (PGLS), and deviations from this regression were quantified using phylogenetic analysis of covariance (“pANCOVA”; Smaers and Rohlf 2016) as implemented in the *evomap R* package. To test the relationship between the three thermoregulatory-dietary strategies associated with elasmobranch gigantism (i.e.,

ectothermic macropredation, mesothermic macropredation, and ectothermic filter feeding) and body size (Table 1), we ran a multistate PGLS using the library *caper* (Orme et al. 2013) in which the three strategies were combined into a three-state independent variable (Gates et al. 2016). We ran additional PGLS using two binary state combinations (filter feeders vs. macropredators and mesotherms vs. ectotherms). The structure of phylogenetic signal was controlled by estimating lambda using maximum likelihood. We further estimated ancestral states using maximum likelihood. This was achieved using a multiple variance Brownian motion approach allowing for variable rates among lineages (Smaers et al. 2016). We compared ancestral size estimates for clades exhibiting filter feeding and mesothermic specializations with those that do not using a Welch two-sample *t*-test. Major shifts in body size evolution were quantified using a Bayesian reversible-jump multi-regime Ornstein–Uhlenbeck approach (Uyeda and Harmon 2014) as implemented in the *bayou R* package. Five MCMC chains of five million iterations (with 30% burn-in) were run for each analysis. We allowed only one shift per branch and the total number of shifts was constrained by means of a conditional Poisson prior with a mean equal to 2.5% of the total number of branches in the tree and a maximum number of shifts equal to 5%. Starting points for MCMC chains were set randomly by drawing a number of shifts from the prior distribution and assigning these shifts to branches randomly drawn from the phylogeny with a probability proportional to the size of the clade descended from that branch. This procedure ensured convergence of parameter estimates across chains.

Results

GIGANTISM ACROSS ELASMOBRANCH PHYLOGENY

Throughout the elasmobranch tree, gigantism (>6 m of total length) arose several times independently (Albert and Johnson 2012) in clades exhibiting an array of feeding (macropredation vs. filter feeding) and thermoregulatory (ectothermy vs. mesothermy) strategies (Table 2). Specifically, 14 species in our tree are considered giants (see numbers 1–14 in Fig. 1A, E), representing the 97th percentile and above in terms of elasmobranch body size (Table 1). Notably, gigantic forms comprise a substantial proportion of filter feeders and mesotherms (50% and 25%, respectively), whereas only 1% of ectothermic-macropredators reach gigantic sizes (Table 1). It is worth noting that additional gigantic fossils are known that were excluded from our analyses given their uncertain phylogenetic positions (see Methods), including an indeterminate lamniform from the Albian (6.3 m; 113–100 million years ago; Shimada 1997; Frederickson et al. 2015), multiple macropredators from the late Cretaceous such as *Cretoxyrhina* (6.9 m; Shimada 2008) and *Cretodus* (6.5 m; Amalfitano et al. 2017), and an enigmatic Cretaceous durophagous shark *Ptychodus*

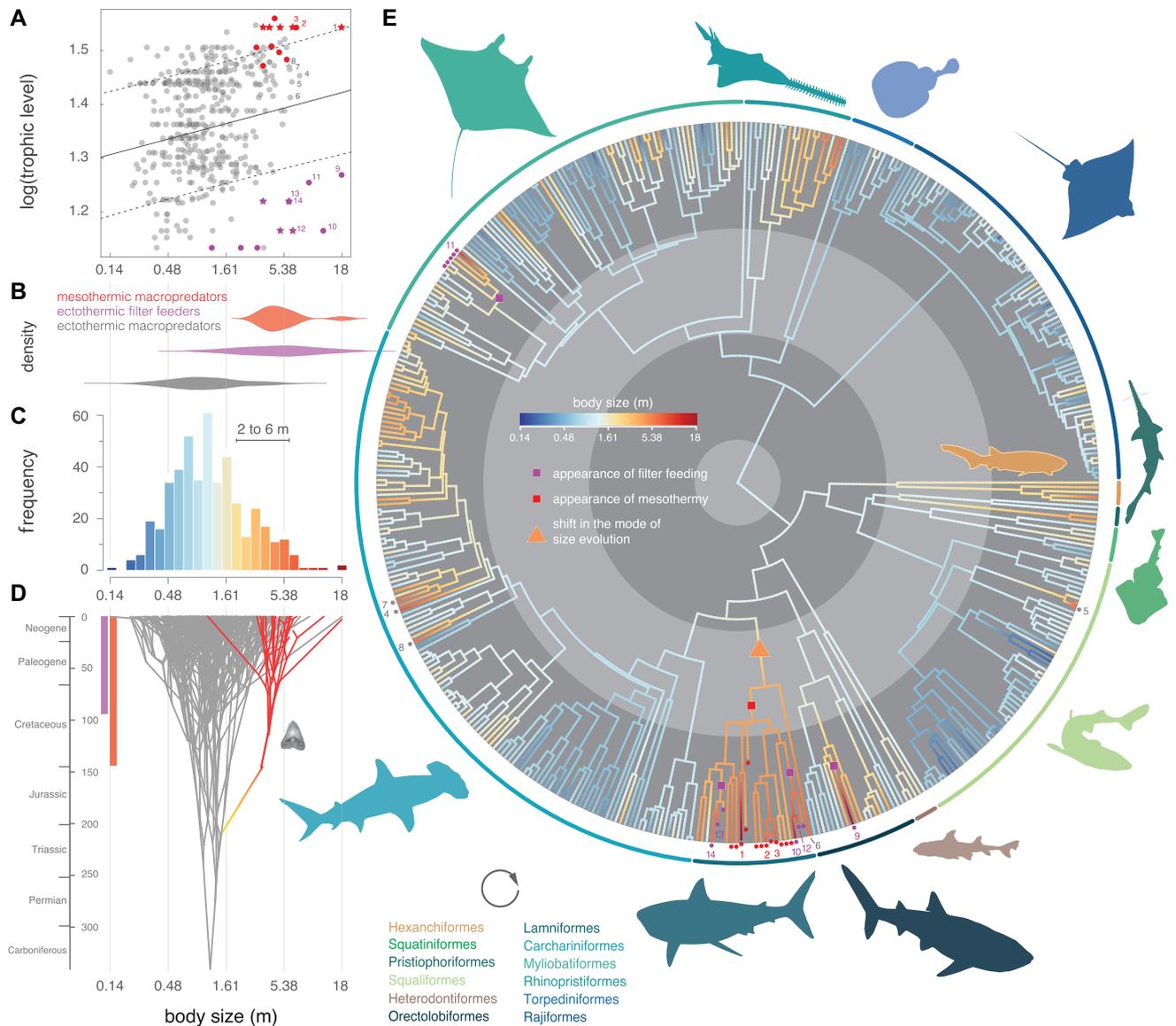


Figure 1. Body size evolution in elasmobranchs. (A) Relationship between body size and trophic level (log-transformed) after controlling for phylogeny (PGLS). Mesothermic macropredators and filter feeders are highlighted in red and purple, respectively. Fossil species are represented by stars, and giant elasmobranchs are numbered as follows: (1) †*Otodus* (maximum total length [max TL] = 18 m, first appearance date [FAD] = early Palaeocene); (2) *Carcharodon carcharias* (max TL = 7 m, FAD = early Pliocene); (3) †*Carcharodon (Cosmopolitodus) hastalis* (max TL = 7 m, FAD = early Miocene); (4) *Galeocerdo cuvier* (max TL = 8 m, FAD = early Pliocene); (5) *Somniosus microcephalus* (max TL = 6 m, FAD = early Pliocene); (6) *Mitsukurina owstoni* (max TL = 7 m, FAD = Pliocene); (7) *Sphyrna mokarran* (max TL = 6 m, FAD = early Pliocene); (8) †*Hemipristis serra* (max TL = 6 m, FAD = Miocene); (9) *Rhincodon typus* (max TL = 18 m, FAD = late Oligocene); (10) *Cetorhinus maximus* (max TL = 12 m, FAD = late Miocene); (11) *Manta birostris* (max TL = 9 m, FAD = Pliocene); (12) †*Cetorhinus* (non-*maximus*; max TL = 6 m, FAD = early Miocene); (13) †*Megachasma applegatei* (max TL = 6 m, FAD = late Oligocene); and (14) *Megachasma pelagios* (max TL = 6 m, FAD = late Miocene). (B) Relative density of body sizes across the three strategies considered. (C) Histogram of elasmobranch body size. Horizontal line shows the range of ancestral sizes for filter feeder and mesothermic giants. (D) Phenogram showing patterns of body size evolution through time. Lamniformes, the only clade with a significant macroevolutionary shift, is highlighted. Vertical bars on the left represent reconstructed temporal spans in which filter feeding and mesothermic strategies have existed. Tooth represents the fossil occurrence of the first known giant shark (Albian). (E) Patterns of body size evolution across elasmobranch phylogeny. Triangle shows a significant shift in estimated size optimum at the base of Lamniformes (also see D), and is colored according to the estimated optimal size. Mesothermic macropredators, filter feeders, and giant elasmobranchs are highlighted as in (A). Names of major elasmobranch subclades are detailed at the bottom and are color-coded along with their silhouettes. Ancestral sizes in (D) and (E) were estimated using a multiple variance Brownian Motion model (see Methods). Concentric grey bands represent 100 million year intervals. Body size is log-scaled in all figures.

Table 1. Elasmobranch body size (in meters) across different feeding and thermoregulatory strategies.

Group	<i>N</i>	Minimum	Maximum	Mean	Mode	Giants (%)
Ectothermic macropredators	435	1.40	7.50	1.39	1.00	1%
Mesothermic macropredators	12	3.05	18.00	5.82	3.50	25%
Ectothermic filter feeders	12	1.00	18.00	5.35	6.00	50%
All	459	1.40	18.00	1.56	1.00	3%

Table 2. Ancestral state estimates for elasmobranch clades. Clades that include giants are in uppercase.

Clade	Feeding mechanism	Thermoregulatory adaptation	Ancestral state (m)
CARCHARHINIFORMES	macropredator	ectothermic	1.20
LAMNIFORMES*	macropredator	mesothermic	3.54
MEGACHASMIDAE	filter feeder	ectothermic	3.87
CETORHINIDAE	filter feeder	ectothermic	5.83
RHINCODONTIDAE	filter feeder	ectothermic	3.13
SOMNIOSIDAE	macropredator	ectothermic	1.05
MOBULIDAE	filter feeder	ectothermic	2.05
Heterodontiformes	macropredator	ectothermic	1.45
Squaliformes and relatives	macropredator	ectothermic	1.48
Torpediniformes + Rhinopristiformes	macropredator	ectothermic	0.97
Rajiformes	macropredator	ectothermic	0.68
Root	macropredator	ectothermic	1.24

* Clade where mesothermy originated, but ectothermic condition may have evolved secondarily, as a derived character, along with filter feeding (see text).

(10+ m; Shimada et al. 2010). Accordingly, although our analyses only incorporate fossil giants from the Cenozoic (Fig. 1E), we can trace the origin of gigantism back to the early Cretaceous in the order Lamniformes (Fig. 1D).

THE RELATIONSHIP BETWEEN BODY SIZE AND SPECIES' TRAITS

To identify the biological traits associated with the attainment of gigantism in elasmobranchs, we tested for relationships between size and trophic level, feeding mechanism, and thermoregulatory strategy. We found that body size and trophic level are positively correlated (PGLS; $t = 4.55$, $\lambda = 0.95$, $P < 0.001$, $df = 459$; Fig. 1A). This relationship holds even when excluding filter feeders ($t = 5.54$, $\lambda = 0.92$, $P < 0.001$, $df = 447$) or mesotherms ($t = 4.42$, $\lambda = 0.94$, $P < 0.001$, $df = 447$) and when removing fossil species ($t = 4.43$, $\lambda = 0.94$, $P < 0.001$, $df = 449$; Fig. S2A). We further found that both filter feeders and mesotherms significantly deviate from this relationship (pANCOVA; filter feeders: $F = 57.99$, $P < 0.001$; mesotherms: $F = 14.25$, $P < 0.001$). This deviation is upheld even when excluding fossil species (filter feeders: $F = 42.11$, $P < 0.001$; mesotherms: $F = 4.64$, $P < 0.05$; Fig. S2A). Additionally, we found that both filter feeders and mesotherms are significantly larger than their ectothermic-macropredatory coun-

terparts ($F = 7.792$; $P < 0.001$; Fig. 1B). However, additional analyses using two binary states and excluding fossils failed to recover mesotherms as significantly larger than ectotherms (Table S4; Fig. S2B). Filter feeders were, however, still recovered as significantly larger than macropredators (Table S4; Fig. S2B).

THE EVOLUTION OF FILTER FEEDING AND MESOTHERMY

Because we found that mesothermy and filter feeding are both associated with large body size in elasmobranchs, we next assessed the origin of these two specializations. Consistent with previous studies (Friedman et al. 2010; Friedman 2012; Paig-Tran and Summers 2014), we found filter feeding to have evolved independently in four elasmobranch clades. Age estimates for most of these transitions, except one, are largely constrained the Paleocene and Eocene: between 56.6 and 50.5 million years ago in Mobulidae; between 68 and 38 million years ago in Megachasmidae; between 90.5 and 41.2 million years ago in Cetorhinidae; and between 68.1 and 33.9 million years ago in Rhincodontidae (purple squares [nodes] and dots [tips] in Fig. 1E). These results are upheld when excluding fossils (Fig. S2C). It is worth noting that a putative filter-feeding lamniform, *Pseudomegachasma*, is known from the earliest late Cretaceous (Shimada et al. 2015).

However, given that its exact phylogenetic position (placement in paraphyletic ‘Odontaspidae’) and body size are uncertain, we did not include it in our analyses. Nevertheless, the timing of the evolution of this geologically short-lived taxon suggests the possibility of elasmobranch filter feeding appearing as early as around 100 million years ago.

In contrast to the widespread assumption of mesothermy arising convergently across the elasmobranch tree (Block and Finnerty 1994; Sepulveda et al. 2005), our analyses including fossils suggest that mesothermy arose only once within Lamniformes during the early Cretaceous (between 145.5 and 113.5 million years ago; see red square [node] and dots [tips] in Fig. 1E) in a clade sister to Mitsukurinidae (Fig. 1E: clade marked with red square, *Mitsukurina owstoni* is giant #6 [see caption]). However, our additional analyses excluding fossils (and their inferred traits) suggest that mesothermy appeared three times independently during the Cenozoic (specifically in Lamnidae, *A. superciliosus* and *A. vulpinus*; Fig. S2C). Resolving this uncertainty regarding the number of independent origins of mesothermy across elasmobranchs should be a priority for future work once more fossils with strongly supported phylogenetic positions and trait inferences become available.

THE EVOLUTION OF GIGANTIC BODY SIZE IN ELASMOBRANCHS

To reconstruct evolutionary pathways toward elasmobranch gigantism, we estimated the ancestral states for clades that include giants. We found that gigantism (>6 m) is not the ancestral condition for any elasmobranch lineage (Table 2). However, ancestrally filter feeding and ancestrally mesothermic clades exhibit significantly ($t = 4.09$; $P = 0.01$) larger ancestral sizes relative to ancestral ectothermic-macropredatory clades. Significantly different estimates for the tempo and mode of body size evolution were obtained for Lamniformes with respect to all other elasmobranch clades. Lamniformes is the only order within which mesothermy has evolved, and contains the majority of giant species as well as the earliest known giant (Fig. 1E). The unique body size dynamics of Lamniformes include an early shift in body size evolution along the lamniform stem lineage between 200 and 150 million years ago (posterior probability = 0.97; Fig. 1D and E), and an ancestral body size increase toward a crown lamniform macroevolutionary optimum of 4.9 m (magnitude of $\theta = 6.2$) ~145 million years ago (Fig. 1D). Although this optimum falls below the limits of gigantism as defined here, it is much larger than the estimated size optimum for the rest of elasmobranchs (root optimum = 1 m).

Discussion

Our results show that, although trophic level is positively correlated with body size in elasmobranchs (as has previously been

reported for other fishes; Pauly et al. 1998; Romanuk et al. 2011), filter feeders and mesotherms significantly deviate from this relationship. Indeed, the largest elasmobranch giants occupy diametrically opposed ends of the trophic spectrum (shown by the highest red and purple values in Fig. 1A). This suggests that species exhibiting these mutually exclusive feeding strategies have followed different evolutionary pathways with respect to the rest of elasmobranchs. This interpretation is corroborated by (1) our ancestral state estimates, which indicate significantly larger ancestral sizes for clades including filter feeders or mesotherms (2–6 m, Table 2; Fig. 1C); and (2) by the tendency of mesotherms, and especially filter feeders, to be significantly larger than their ectothermic-macropredatory counterparts (Fig. 1B; Fig. S2B). Our results allow us to identify two main evolutionary pathways underlying the evolution of gigantism in elasmobranchs: the ancestral mesothermic pathway and the filter-feeding pathway.

THE ANCESTRAL MESOTHERMIC PATHWAY

Our results point to a single origin of mesothermy in the late Cretaceous, within Lamniformes (Fig. 1E). However, alternative analyses excluding fossils support multiple independent Cenozoic acquisitions of mesothermy within this clade (Fig. S2). Given that thermoregulatory mode can only be inferred in the fossil record (as opposed to directly observed), we cannot rule out the possibility of independent origins of mesothermy. Nonetheless, the mesothermic conditions estimated for our fossil dataset are well supported by different lines of evidence (see Supporting Information; also see Ferrón 2017; Ferrón et al. 2017). Because fossils possess unique and important trait information from early-diverging lineages, we consider our analyses including fossils to be more robust and accurate despite the limitations of an incomplete fossil record (Doyle and Donoghue 1987; Donoghue et al. 1989; Finarelli and Flynn 2006; Albert et al. 2009; Slater et al. 2012; Hsiang et al. 2015; Field and Hsiang 2018).

Based on our results incorporating fossils, we hypothesize that the first elasmobranch giants arose from a relatively large (3.54 m; Fig. 1C; Table 2) mesothermic ancestor. This pathway originated with a shift in elasmobranch body size evolution during the Jurassic (Figs. 1D and E), followed by the origin of crown Lamniformes. By the earliest Cretaceous (~145 million years ago), ancestral lamniforms had attained a body size optimum of 4.1 m. Mesothermy may have evolved afterward (between 145 and 113 million years ago), just before the rise of the first elasmobranch giant (during the Albian, between 113.0 and 100, Fig. 1D). In the late Cretaceous, a subsequent diversification event witnessed the rise of multiple gigantic lineages (Maisey et al. 2004).

The mesothermic pathway to gigantism ultimately resulted in the evolution of the largest marine macropredator to have ever lived, the ~18 m †*O. megalodon* (Ferrón 2017; Ferrón et al. 2017),

which is known from the Miocene to the Pliocene (Pimiento and Clements 2014; Pimiento et al. 2016). Given the high metabolic demands that it imposes (McNab 2009), mesothermy is associated with high extinction risk among large bodied species when large prey become scarce (Pimiento et al. 2017). This may have been the case in the late Pliocene, when coastal areas were reduced due to large sea level oscillations (Pimiento et al. 2017). Therefore, the mesothermic pathway appears to have promoted the acquisition of extremely large size (e.g., 18 m) until the Pliocene, during periods where coastal habitats were large enough to provide the ecological infrastructure for metabolically demanding, extreme-sized predators. The only gigantic mesothermic shark that persisted beyond the Pliocene is the modern white shark (*C. carcharias*, max TL = ~7 m), which is significantly smaller than the extreme-sized †*O. megalodon*. The disproportionate extinction of mesotherms during the Pliocene (Pimiento et al. 2017) can partially explain why filter feeders emerge as significantly larger than mesotherms in extant-only analyses (Fig. S2B).

Empirical evidence suggests that the origin of mesothermy in Lamniformes likely facilitated predation efficiency by increasing tolerance to colder waters (niche expansion) and by increasing cruising speeds (Bernal et al., 2003, 2005, 2012; Dickson and Graham 2004; Bernal and Sepulveda 2005; Sepulveda et al. 2005; Watanabe et al. 2015). The subsequent origin of gigantism among mesothermic macropredators was likely related to achieving competitive superiority (Vermeij 2016). Although further studies are needed to confirm the timing and number of origins of mesothermy in sharks, based on our best estimates of the timing of its appearance, we hypothesize that the ancestral mesothermic pathway to gigantism evolved as a means to enhance the intake of large prey in the face of low sea temperatures (Dickson and Graham 2004) in the late Jurassic and early Cretaceous (Price 1999; Puceat et al. 2003; Steuber et al. 2005; Amiot et al. 2011), while avoiding competition with contemporaneous, gigantic, planktivorous bony fishes (Liston 2008; Friedman et al. 2010; Liston et al. 2013). In addition, the subsequent diversification of gigantic macropredatory lamniforms during the late Cretaceous could have been a response to persistent predatory pressure from the large marine reptiles that dominated Mesozoic seas (Massare 1987) as well as to the need of continued niche partitioning with gigantic planktivorous bony fishes (Friedman et al. 2013; Schumacher et al. 2016).

THE FILTER-FEEDING PATHWAY

Our results show that filter feeding evolved independently in four elasmobranch clades: Mobulidae, Megachasmidae, Rhincodontidae, and Cetorhinidae (Fig. 1E). Most of these appearances took place around the Paleocene–Eocene Thermal Maximum (PETM), a period of increased productivity in the world's oceans (Zachos et al. 2001). Nevertheless, the range of appearance of

filter feeding in the clade Cetorhinidae extends back to the late Cretaceous. This timing, compatible with the late Cretaceous occurrence of †*Pseudomegachasma* (Shimada et al. 2015), a putative filter feeder not included in our analyses given uncertainties related to its phylogenetic position and trait attributes, suggest the possibility of elasmobranch filter feeding appearing much earlier than the Paleogene (Fig. 1D), during a period also known for elevated primary productivity (Price 1999; Puceat et al. 2003; Steuber et al. 2005). Although tantalizing, a late Cretaceous origin of filter feeding in elasmobranchs cannot be adequately tested with the information at hand. Accordingly, in agreement with previous studies (Friedman et al. 2010; Friedman 2012; Paig-Tran and Summers 2014), the most conservative interpretation is that filter feeding as a major elasmobranch feeding strategy originated in the Paleogene (Fig. 1E).

Parallel to the pathway followed by other filter-feeding giants (e.g., Friedman 2012; but see Fordyce and Marx 2018), gigantism among filter-feeding elasmobranchs appeared after ancestrally macropredatory species had already shifted to planktivory (Friedman 2012). Nonetheless, the filter-feeding pathway to elasmobranch gigantism differs from that of other planktivorous gigantic fishes in that it arose within both primitively benthic (*M. birostris* and *R. typus*) and pelagic (*Cetorhinus* and *Megachasma*) clades (Friedman 2012). If the origin of mesothermy in Lamniformes can be ascribed to a single evolutionary transition (Fig. 1E), then the gigantic filter feeders that are ancestrally pelagic were also ancestrally mesothermic. Therefore, the extant filter feeders *Cetorhinus* and *Megachasma* may have transitioned to an ectothermic physiology secondarily, from a mesothermic, macropredatory ancestor. This hypothesis needs to be addressed once the timing and number of origins of mesothermy in sharks is confirmed.

Based on our results, we propose that the filter-feeding pathway to gigantism arose in clades with relatively large ancestors (2–6 m, Fig. 1C; Table 2) as a response to the increased productivity and consequent enhancement of the ecological infrastructure of the Paleogene's oceans (Vermeij 2016). This process may have been influenced or facilitated by the planktonic turnover of the Cretaceous–Paleogene (K–Pg; Tajika et al. 2018). Similarly, the ultimate attainment of filter-feeding gigantism could have been a response to the vacant niches left by the extinction of gigantic planktivorous bony fishes at the K–Pg boundary (Friedman et al. 2010), and persistent pressure from large predators through the Cenozoic (Lambert et al. 2010; Pimiento et al. 2016).

The filter-feeding pathway to gigantism in elasmobranchs resembles that followed by marine mammals later in the Cenozoic, which has been proposed to be the result of increased primary productivity and predatory release during the Plio-Pleistocene (Lambert et al. 2010; Pimiento and Clements 2014; Slater et al. 2017). Accordingly, the oceanographic dynamics of the Plio-Pleistocene caused the extinction of extreme-sized

macropredatory mesothermic sharks, for example, †*O. megalodon*, due to habitat loss, while promoting the evolution of extremely large endothermic filter-feeding whales through an increase in primary productivity. The occurrence and persistence of extremely large filter feeders in the world's oceans (i.e., bony fishes [10 m], sharks [18 m], and mammals [24 m]; Friedman et al. 2010; Friedman 2012; Liston et al. 2013; McClain et al. 2015; Pyenson and Vermeij 2016; Slater et al. 2017) and their larger size relative to non-filter-feeding ectotherms (Fig. S2B, Table S4) suggest that this pathway has been sustained throughout geologic time, at least since the mid-Jurassic. However, given that high levels of microplastic toxins are increasingly threatening filter-feeding organisms in today's oceans (Germanov et al. 2018), the future persistence of giant filter feeders may be now at risk.

ECTOTHERMIC-MACROPREDATORY GIANTS AND FURTHER CONSIDERATIONS

Despite the fact that macropredatory ectotherms do not reach the lengths of the largest elasmobranchs (e.g., 18 m), five species (i.e., *G. cuvier*, *S. microcephalus*, *M. owstoni*, *S. mokarran*, and †*H. serra*) were able to surpass our defined limits of gigantism, reaching sizes between 6 and 7.5 m (Fig. 1A). Unlike mesothermic or filter-feeding clades, giant macropredatory ectotherms originated from significantly smaller ancestors (Table 2; Fig. S3) and, as a group, are significantly smaller than mesotherms and filter feeders (Figs. 1B; Fig. S2B). We propose that because giant ectothermic macropredators lack the specializations for enhancing prey intake and environmental exploitation, they are: (a) correspondingly constrained to the lower limits of gigantism; (b) unable to reach the extreme sizes of the largest mesotherms and filter feeders (i.e., ~18 m; McClain et al. 2015; Pimiento and Balk 2015); and (c) represent outliers in the body size evolution of their clades. Consequently, ectothermic-macropredation cannot be considered an evolutionary pathway toward elasmobranch gigantism.

It is worth noting that the origin of the two main evolutionary pathways toward elasmobranch gigantism we propose here (mesothermic and filter feeding) are limited to fossil taxa with reasonably well resolved phylogenies and with inferable physiological traits. For instance, Mesozoic species that have shown gigantic traits (e.g., *Cretoxyrhina* [Shimada 2008], *Cretodus* [Amalfitano et al. 2017], and *Ptychodus* [Shimada et al. 2010]), and putative filter feeders (e.g., †*Pseudomegachasma* [Shimada et al. 2015]) or mesotherms (e.g., ctenacanthiforms [Maisey et al. 2017]) could not be included in our analyses. This particularly affects our results regarding the mesothermic pathway, which are sensitive to the inclusion of fossils (Fig. S2). Indeed, the exclusion of fossils leads to an alternative hypothesis in which mesothermy evolves multiple times. This suggests that despite the inherent problems associated with the incompleteness of the fossil record, fossil taxa add critical trait information at, or near the base of different

clades, which is fundamental to estimate ancestral states and to elucidate the time and origin of evolutionary pathways. While our study marks the first attempt to assess the evolutionary pathways that led to gigantism in elasmobranchs (a group that displays an array of feeding and thermoregulatory adaptations) based on available paleontological data, future studies should seek to resolve the phylogenetic relationships of fossil lamniforms, and to gather empirical evidence on the presence of mesothermy and filter-feeding traits in ancient fossil species to further confirm the time of origin of the evolutionary pathways toward elasmobranch gigantism.

Concluding Remarks

Taken together, our results suggest that there are two main evolutionary mechanisms that have given rise to gigantism among elasmobranchs: the mesothermic and filter-feeding pathways. These pathways were followed by clades with relatively large ancestral sizes and involved the initial acquisition of specialized adaptations to enhance prey intake in the face of environmental change. Although giant sizes can be reached by ectothermic-macropredators, these species evolved from smaller ancestors and did not acquire thermoregulatory or dietary specializations. The final attainment of giant sizes following the main evolutionary pathways toward gigantism appears to be, at least in part, a response to biotic factors, namely predation avoidance and niche availability (see Vermeij 2016). The lack of specializations among ectothermic macropredators has restricted their gigantic representatives to the lower limits of elasmobranch gigantism (6–7.5 m). By contrast, the mesothermic (in combination with macropredation) and filter feeding (or diet specialization) pathways have facilitated the evolution of the largest elasmobranchs in Earth history (~18 m).

In general, large elasmobranchs are particularly susceptible to extinction in today's oceans (Dulvy et al. 2014). Our results suggest that mesotherms and filter feeders followed different evolutionary pathways that allowed them to reach larger sizes than the rest of elasmobranchs. Because such evolutionary pathways involve transitions to specializations that essentially depend on the quality and abundance of food items in the oceans (McNab 2009; Vermeij 2016), mesothermic and filter-feeding species face particular constraints that further affect their extinction susceptibility. Mesotherms rely on the availability of large prey to maintain their high metabolic demands (McNab 1983; Block and Finnerty 1994; McNab 2009; Vermeij 2016; Ferrón et al. 2017). Because the persistence and availability of large prey mainly depend on the area available (Wright 1983), the mesothermic pathway can promote extreme sizes as long as habitats are large enough to provide the ecological infrastructure for metabolically demanding giant predators. Therefore, when large vertebrate prey became scarce in the Pliocene due to a significant loss of habitable area, the

largest mesothermic sharks (e.g., †*O. megalodon*) became extinct (Pimiento et al. 2017). The filter-feeding pathway, on the other hand, is the mechanism that has given rise to the largest extant elasmobranch, the whale shark (McClain et al. 2015). Because plankton is consistently more abundant than large prey (McNab 2009; Vermeij 2016), especially during periods of rapid environmental change (e.g., when habitat is lost), filter feeding may confer giant species with more resilience than mesothermy in the face of environmental challenges. However, given that filter feeders are particularly susceptible to high levels of microplastic toxins in today's oceans (Germanov et al. 2018), this strategy, which has persisted since at least the Paleogene, may be at risk in modern oceans.

AUTHOR CONTRIBUTIONS

C.P. conceived the project. C.P. and J.B.S. designed the research. C.P. and K.S. collected the data. C.P., J.L.C., and J.B.S. analyzed the data. J.L.C., K.S., D.J.F., and J.B.S. contributed to manuscript preparation. C.P. wrote the paper.

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CONFLICT OF INTEREST

The authors declare no competing interests.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Eleven fossil calibration dates used to scale our tree to time.

Table S2. Elasmobranch trait data.

Table S3. Fossil taxa added to the phylogeny.

Table S4. Additional PGLS.

Figure S1. Graphical representation of the different (pink, blue and green) placements of the family †Otodontidae, all considered in the analyses (see Methods).

Figure S2. Body size evolution in Elasmobranchs excluding fossil species.

Figure S3. Distribution of ancestral state estimation of main elasmobranch clades.