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Paper:

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1   **EVOLUTIONARY PATHWAYS TOWARDS GIGANTISM IN SHARKS AND RAYS**
2
3   RH: How to be a giant shark
4
5   **Abstract**
6

7   Through elasmobranch (sharks and rays) evolutionary history, gigantism evolved multiple times
8   in phylogenetically distant species, some of which are now extinct. Interestingly, the world's
9   largest elasmobranchs display two specializations found never to overlap: filter-feeding and
10   mesothermy. The contrasting lifestyles of elasmobranch giants provide an ideal case study to
11   elucidate the evolutionary pathways leading to gigantism in the oceans. Here, we applied a
12   phylogenetic approach to a global dataset of 459 taxa to study the evolution of elasmobranch
13   gigantism. We found that filter feeders and mesotherms deviate from general relationships between
14   trophic level and body size, and exhibit significantly larger sizes than ectothermic-macropredators.
15   We confirm that filter-feeding arose multiple times during the Paleogene, and suggest the
16   possibility of a single origin of mesothermy in the Cretaceous. Together, our results elucidate two
17   main evolutionary pathways that enable gigantism: mesothermic and filter-feeding. These
18   pathways were followed by ancestrally large clades and facilitated extreme sizes through
19   specializations for enhancing prey intake. Although a negligible percentage of ectothermic-
20   macropredators reach gigantic sizes, these species lack such specializations and are
21   correspondingly constrained to the lower limits of gigantism. Importantly, the very adaptive
22   strategies that enabled the evolution of the largest sharks can also confer high extinction
23   susceptibility.
24
25   *Keywords.*—body size, elasmobranchs, evolution, filter-feeding, gigantism, mesothermy.
26
27   **INTRODUCTION**
28
29   Gigantism may confer animals with numerous ecological advantages, such as competitive
30   superiority and enhanced predation efficacy (Vermeij 2016). Despite these benefits, gigantism is
31   generally exhibited by only a small minority of taxa in most clades (Kozlowski and Gawelczyk
32   2002; Kingsolver and Pfennig 2004; Vermeij 2016). Because larger organisms require more
33   resources, gigantism might be predicted to be restricted to top-level consumers. Indeed, a strong,
34   positive relationship exists between body size and trophic level in certain clades, including some
35   fishes (Pauly et al. 1998; Romanuk et al. 2011). Nevertheless, the attainment of gigantism is
36   generally not limited by trophic level, but by the quality and abundance of an environment's
37   resources (McNab 1983; Kingsolver and Pfennig 2004; McNab 2009), and by a species' ability to
38   exploit them (e.g. maneuverability and thermoregulatory capabilities; Webb and De Buffrénil
39   1990; Domenici 2001). Hence, while some giants with relatively low metabolic demands and
40   sluggish habits may feed on vast amounts of small but abundant food items such as plankton,
41   others with higher metabolic demands may be active macropredators capable of efficiently hunting
42   large prey (Webb and De Buffrénil 1990; Domenici 2001; Vermeij 2016). Gigantism is therefore
43   associated with an enhanced capacity for environmental exploitation.
44
45   Most efforts to understand the evolutionary pathways underlying the acquisition of gigantism in
46   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 unravelling evolutionary pathways towards the origin of giant marine macropredators. This might be because even the largest macropredators 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 macropredatory 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 macropredators 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 macropredator 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

93 scale and/or throughout geological time, and local giants are defined as the largest species in a
94 particular major subclade, time interval or locality (Vermeij 2016). Following this definition, there
95 are two global giant elasmobranchs: megalodon (†*O. megalodon*) and the whale shark (*R. typus*),
96 which reach the maximum size ever attained by sharks, of ~18 m (McClain et al. 2015; Pimiento
97 and Balk 2015). Local giants include the basking shark (*Cetorhinus maximus*, the largest temperate
98 shark, ~12 m), the giant oceanic manta ray (*Manta birostris*, the largest batoid, ~9 m), the tiger
99 shark and white shark (*Galeocerdo cuvier* and *Carcharodon carcharias*, the largest
100 macropredators, ~7.5 and ~7 m, respectively) and the Greenland shark (*Somniosus microcephalus*,
101 the largest polar shark, ~6.4 m) (McClain et al. 2015). Because these elasmobranchs exhibit
102 maximum total body lengths exceeding 6 m, we defined the limit of elasmobranch gigantism as >
103 6 m for the purpose of this study, and consequently, also include the following species estimated
104 or known to reach or exceed this threshold: the fossil white shark and fossil basking shark
105 (†*Carcharodon hastalis* and †*Cetorhinus* spp., ~6.5 m), the goblin shark (*Mitsukurina owstoni*,
106 ~6.2 m), the great hammerhead shark, (*Sphyrna mokarran,* ~6.1 m), the megamouth sharks
107 (*Megachasma pelagios* and †*Megachasma applegatei,* both ~6 m) and the extinct snaggletooth
108 shark (†*Hemipristis serra,* ~6 m) (Uyeno et al. 1990; Kent 1994; Shimada et al. 2014; Welton
109 2014; McClain et al. 2015; Welton 2015; Froese and Pauly 2017).
110
111 **Tree and calibration**
112 We used the originally undated elasmobranch phylogeny produced by Naylor et al. (2012). We
113 chose this phylogeny among others available for the following reasons: 1) it is based on 595 species
114 and brackets the phylogenetic breadth of elasmobranch crown group diversity (including batoids);
115 2) it is a densely taxon-sampled phylogenetic hypothesis based on analysis of NADH2 (a
116 mitochondrial, protein-coding gene) using sequences generated *de novo* from samples collected
117 and identified by the authors (therefore avoids using barcode sequences derived from GenBank,
118 which can potentially include misidentified specimens or sequences of questionable provenance;
119 for a discussion on these issues see Naylor et al. 2012); 3) given that is sequence-based, it is
120 independent of the morphology-related variables we examine in this work; 4) it includes all 15
121 extant lamniform species. We time-scaled this phylogeny using the Penalized Likelihood
122 algorithm implemented in the software treePL (Smith and O'Meara 2012) and applied cross-
123 validation to empirically determine the optimal smoothing factor using the default settings in
124 treePL. To do so, we used the ages of 11 fossil calibrations representing the oldest total-clade
125 records of the following elasmobranch orders: 164.7–167.7 Ma for Carcharhiniformes; 145.5–
126 150.8 Ma for Lamniformes; 175.6–183 Ma for Orectolobiformes; 175.6–183 Ma for
127 Heterodontiformes; 125–130 Ma for Squaliformes; 155.7–161.2 Ma for Squantiniformes; 99.6–
128 112 Ma for Pristiophoriformes; 189.6–196.5 Ma for Hexanchiformes; 33.9–56 for Rajiformes;
129 61.7–65.5 Ma for Torpediniformes; and 130–136.4 Ma for Myliobatiformes. These dates are
130 derived from the fossil record (Table S1) and are based mostly on the work of Cappetta (2012).
131 Details on our use of fossil calibrations and additional references are provided in the electronic
132 supplementary material.
133
134 **Traits**
135 We downloaded maximum total size of all extant elasmobranch species from FishBase (Froese
136 and Pauly 2017; www.fishbase.org) using the *R* package *rfishbase* (Boettiger et al. 2012). In
137 sharks, body sizes are expressed as total length (TL), estimated as the distance from the tip of the
138 snout to the posterior end of the dorsal caudal lobe. In batoids (except sawfishes; see below), the

139 width of the disc (WD) is estimated as the distance between the wing tips (accordingly, the tail
140 and rostrum lengths of batoids are not considered). Maximum body size was expressed as the
141 largest TL or WD values recorded for each species. We checked each of these and adjusted when
142 necessary based on the most recent literature (e.g. McClain et al. 2015). Body sizes of sawfishes
143 (which are batoids, Pristidae) and sawsharks (which are sharks, Pristiophoriformes) were treated
144 differently given their unusually elongate rostra, to avoid biased body size estimates (for the
145 purposes of this study, 'rostrum' specifically refers to the structure bearing rostral spines, whereas
146 'snout' refers to an elongation of the head without a spinous rostrum). Given that correlations
147 between body size and TL or WD do not accommodate the greatly elongated rostra of sawfishes
148 and sawsharks, we ran our analyses excluding rostra for these taxa. In so doing, we subtracted one
149 quarter of the TL, which roughly corresponds to the proportional length of their rostra (see Bigelow
150 1953; Bigelow and Schroeder 1953; Carpenter and Niem 1999; McEachran et al. 2002).

152 We downloaded data on the mean trophic level for all elasmobranchs from FishBase (Froese and
153 Pauly 2017). Trophic level defines the position of organisms within a food web while considering
154 both their diet composition and the trophic levels of their food items. FishBase estimates this value
155 from the mean trophic level of prey, plus one (Boettiger et al. 2012; Froese and Pauly 2017).
156 Within FishBase, prey information is gathered from stomach contents of fish species at a given
157 locality and season (Boettiger et al. 2012; Froese and Pauly 2017). We also assigned data on
158 thermoregulation and feeding strategy to each species. Thermoregulatory strategies in
159 elasmobranchs can take two forms: ectothermy (animals incapable of self-regulating their body
160 temperatures) and mesothermy (animals that can control the temperature of some of their most
161 important organs, also called regional endothermy). Ectothermy is the most common physiological
162 strategy among fishes, whereas mesothermy is restricted to certain taxa, such as lamnid sharks and
163 two species of *Alopias* (*A. superciliosus* and *A. vulpinus*) (Carey and Teal 1969; Block and Carey
164 1985; Bernal et al. 2003, 2005, 2012; Bernal and Sepulveda 2005; Sepulveda et al. 2005; Grady et
165 al. 2014). Similarly, elasmobranchs can be roughly divided into two groups with regard to their
166 feeding strategies: macropredators (i.e. macrophagous) and filter feeders (i.e. microphagous or
167 planktivorous). While the macropredatory lifestyle is the most common form in elasmobranchs,
168 filter-feeding is exhibited by 14 extant species: *C. maximus, M. pelagios, R. typus, Manta alfredi,*
169 *M. birostris, Mobula eregoodootenekee, Mobula hypostoma, Mobula japonica, Mobula kuhlii,*
170 *Mobula mobular, Mobula munkiana, Mobula rochebrunei, Mobula tarapacana* and *Mobula*
171 *thurstoni* (Paig-Tran and Summers 2014). In total, 449 of the 595 species across the phylogeny
172 examined by Naylor et al. (2012) were associated with trait data (~75%; Table S2).

174 **Fossil taxa**
175 We included fossils in our statistical analyses (see below) in instances where both phylogenetic
176 position and trait inferences were reasonably supported. Accordingly, we conducted an exhaustive
177 search for appropriate fossils of crown group elasmobranchs to be included in our analyses. Based
178 on this search, 10 fossil taxa exhibiting clear taxonomic identifications and adequately resolved
179 phylogenetic relationships were included: †*C. hastalis,* †*C. hubbelli,* †*Cetorhinus* (non-*C.*
180 *maximus* spp.), †*Cretalamna* sp., †*H. serra,* †*Keasius,* †*Megachasma alisonae,* †*M. applegatei,*
181 †*Megalolamna paradoxodon* and †*Otodus.* Giant fossil taxa of uncertain phylogenetic position
182 were excluded (Shimada 2008; Frederickson et al. 2015; Shimada et al. 2015; Amalfitano et al.
183 2017). First and last appearance dates for fossil taxa were gathered from the literature (see Table
184 S3 and Supplementary References). For †*Otodus*, we considered the entire megatoothed lineage

185   as a single clade consisting of chronospecies from †*O. obliquus* to †*O. megalodon* (Ward and
186   Bonavia 2001). In order to place this lineage in the tree, we considered alternative phylogenetic
187   hypotheses recently proposed for Lamnidae (Applegate and Espinosa-Arrubarrena 1996; Gottfried
188   et al. 1996; Purdy 1996; Purdy et al. 2001; Ward and Bonavia 2001; Nyberg et al. 2006; Cappetta
189   2012; Shimada et al. 2017), and followed the hypothesis supporting the megatoothed lineage as a
190   distinct family (†Otodontidae), derived from the extinct genus †*Cretalamna* (Applegate and
191   Espinosa-Arrubarrena 1996; Nyberg et al. 2006; Shimada et al. 2017). However, given that the
192   interrelationships of otodontids and other lamniforms remain questionable, we ran our analyses
193   using three possible strategic placements for Otodontidae (Fig. S1) in which we consider the
194   following: a) otodontid teeth exhibit more derived characteristics than those of Mitsukurinidae; b)
195   Mitsukurinidae is regarded as the basal-most lamniform clade (see Cappetta 2012; Naylor et al.
196   2012); and c) the otodontid clade lies outside Lamnidae. Our results were consistent in light of
197   these alternative phylogenetic positions. We adjusted these placements based on the most likely
198   origination and extinction times of the clade (Table S3; Applegate and Espinosa-Arrubarrena
199   1996; Pimiento et al. 2013; Pimiento and Clements 2014; Pimiento et al. 2016). Finally, we
200   assigned trait values for maximum total length, trophic level, thermoregulatory mode and feeding
201   strategy for fossil species based on estimates from the literature (Table S2). Details on trait
202   reconstructions and ages for fossil species can be found in the electronic supplementary material
203   along with all references used. Because the number of fossil taxa in our analyses was limited, all
204   statistical analyses were re-run excluding fossils to evaluate their influence on our reconstructions
205   and both sets of results are reported.
206
207   **Statistical analyses**
208   All our statistical analyses were carried out in the *R* computing environment (R Core Team 2017).
209   To assess the relationship between trophic level and body size we applied a phylogenetic
210   regression (PGLS), and deviations from this regression were quantified using phylogenetic
211   analysis of covariance ('pANCOVA'; Smaers and Rohlf 2016) as implemented in the *evomap R*
212   package. To test the relationship between the three thermoregulatory-dietary strategies associated
213   with elasmobranch gigantism (i.e. ectothermic macropredation, mesothermic macropredation and
214   ectothermic filter-feeding) and body size (Table 1), we ran a multi-state PGLS using the library
215   *caper* (Orme et al. 2015) in which the three strategies were combined into a three-state independent
216   variable (Gates et al. 2016). We ran additional PGLS using two binary state combinations (filter
217   feeders *vs*. macropredators and mesotherms *vs*. ectotherms). The structure of phylogenetic signal
218   was controlled by estimating lambda using maximum likelihood. We further estimated ancestral
219   states using maximum likelihood. This was achieved using a multiple variance Brownian motion
220   approach allowing for variable rates among lineages (Smaers et al. 2016). We compared ancestral
221   size estimates for clades exhibiting filter-feeding and mesothermic specializations with those that
222   do not using a Welch two-sample t-test. Major shifts in body size evolution were quantified using
223   a Bayesian reversible-jump multi-regime Ornstein-Uhlenbeck approach (Uyeda and Harmon
224   2014) as implemented in the *bayou R* package. Five MCMC chains of five million iterations (with
225   30% burn-in) were run for each analysis. We allowed only one shift per branch and the total
226   number of shifts was constrained by means of a conditional Poisson prior with a mean equal to
227   2.5% of the total number of branches in the tree and a maximum number of shifts equal to 5%.
228   Starting points for MCMC chains were set randomly by drawing a number of shifts from the prior
229   distribution and assigning these shifts to branches randomly drawn from the phylogeny with a

230 probability proportional to the size of the clade descended from that branch. This procedure
231 ensured convergence of parameter estimates across chains.
232
233 **RESULTS**

234 **Gigantism across elasmobranch phylogeny**
235 Throughout the elasmobranch tree, gigantism (>6 m of total length) arose several times
236 independently (Albert and Johnson 2012) in clades exhibiting an array of feeding (macropredation
237 *vs.* filter-feeding) and thermoregulatory (ectothermy *vs.* mesothermy) strategies (Table 2).
238 Specifically, 14 species in our tree are considered giants (see numbers 1–14 in figures 1A, E),
239 representing the 97th percentile and above in terms of elasmobranch body size (Table 1). Notably,
240 gigantic forms comprise a substantial proportion of filter feeders and mesotherms (50% and 25%,
241 respectively), whereas only 1% of ectothermic-macropredators reach gigantic sizes (Table 1). It is
242 worth noting that additional gigantic fossils are known that were excluded from our analyses given
243 their uncertain phylogenetic positions (see methods), including an indeterminate lamniform from
244 the Albian (6.3 m; 113–100 Ma; Shimada 1997; Frederickson et al. 2015), multiple macropredators
245 from the late Cretaceous such as *Cretoxyrhina* (6.9 m; Shimada 2008) and *Cretodus* (6.5 m;
246 Amalfitano et al. 2017), and an enigmatic Cretaceous durophagous shark *Ptychodus* (10+ m;
247 Shimada et al. 2010). Accordingly, although our analyses only incorporate fossil giants from the
248 Cenozoic (Fig. 1E), we can trace the origin of gigantism back to the early Cretaceous in the order
249 Lamniformes (Fig. 1D).
250
251 **The relationship between body size and species' traits**
252 To identify the biological traits associated with the attainment of gigantism in elasmobranchs, we
253 tested for relationships between size and trophic level, feeding mechanism, and thermoregulatory
254 strategy. We found that body size and trophic level are positively correlated (PGLS; t=4.55,
255 λ=0.95, P<0.001, df=459; Fig. 1A). This relationship holds even when excluding filter feeders
256 (t=5.54, λ=0.92, P<0.001, df=447) or mesotherms (t=4.42, λ=0.94, P<0.001, df=447) and when
257 removing fossil species (t=4.43, λ=0.94, P<0.001, df=449; Fig. S2A). We further found that both
258 filter feeders and mesotherms significantly deviate from this relationship (pANCOVA; filter
259 feeders: F=57.99, P<0.001; mesotherms: F=14.25, P<0.001). This deviation is upheld even when
260 excluding fossil species (filter feeders: F=42.11, P<0.001; mesotherms: F=4.64, P<0.05; Fig.
261 S2A). Additionally, we found that both filter feeders and mesotherms are significantly larger than
262 their ectothermic-macropredatory counterparts (F=7.792; P<0.001; Fig. 1B). However, additional
263 analyses using two binary states and excluding fossils failed to recover mesotherms as significantly
264 larger than ectotherms (Table S4; Fig. S2B). Filter feeders were, however, still recovered as
265 significantly larger than macropredators (Table S4; Fig. S2B).
266
267 **The evolution of filter-feeding and mesothermy**
268 Because we found that mesothermy and filter-feeding are both associated with large body size in
269 elasmobranchs, we next assessed the origin of these two specializations. Consistent with previous
270 studies (Friedman et al. 2010; Friedman 2012; Paig-Tran and Summers 2014), we found filter-
271 feeding to have evolved independently in four elasmobranch clades. Age estimates for most of
272 these transitions, except one, are largely constrained the Paleocene and Eocene: between 56.6 and
273 50.5 Ma in Mobulidae; between 68 and 38 Ma in Megachasmidae; between 90.5 and 41.2 Ma in
274 Cetorhinidae; and between 68.1 and 33.9 Ma in Rhincodontidae (purple squares [nodes] and dots
275 [tips] in Fig. 1E). These results are upheld when excluding fossils (Fig. S2C). It is worth noting

276 that a putative filter-feeding lamniform, *Pseudomegachasma*, is known from the earliest late
277 Cretaceous (Shimada et al. 2015). However, given that its exact phylogenetic position (placement
278 in paraphyletic 'Odontaspididae') and body size are uncertain, we did not include it in our analyses.
279 Nevertheless, the timing of the evolution of this geologically short-lived taxon suggests the
280 possibility of elasmobranch filter-feeding appearing as early as around 100 Ma.
281
282 In contrast to the widespread assumption of mesothermy arising convergently across the
283 elasmobranch tree (Block and Finnerty 1994; Sepulveda et al. 2005), our analyses including fossils
284 suggest that mesothermy arose only once within Lamniformes during the early Cretaceous
285 (between 145.5 and 113.5 Ma; see red square [node] and dots [tips] in Fig. 1E) in a clade sister to
286 Mitsukurinidae (Fig. 1E: clade marked with red square, *Mitsukurina owstoni,* also giant #6 [see
287 caption]). However, our additional analyses excluding fossils (and their inferred traits) suggest that
288 mesothermy appeared three times independently during the Cenozoic (specifically in Lamnidae,
289 *A. superciliosus* and *A. vulpinus*; Fig. S2C). Resolving this uncertainty regarding the number of
290 independent origins of mesothermy across elasmobranchs should be a priority for future work once
291 more fossils with strongly supported phylogenetic positions and trait inferences become available.
292
293 **The evolution of gigantic body size in elasmobranchs**
294 To reconstruct evolutionary pathways towards elasmobranch gigantism, we estimated the ancestral
295 states for clades that include giants. We found that gigantism (>6 m) is not the ancestral condition
296 for any elasmobranch lineage (Table 2). However, ancestrally filter-feeding and ancestrally
297 mesothermic clades exhibit significantly (*t=4.09; P=0.01*) larger ancestral sizes relative to
298 ancestral ectothermic-macropredatory clades. Significantly different estimates for the tempo and
299 mode of body size evolution were obtained for Lamniformes with respect to all other elasmobranch
300 clades. Lamniformes is the only order within which mesothermy has evolved, and contains the
301 majority of giant species as well as the earliest known giant (Fig. 1E). The unique body size
302 dynamics of Lamniformes include an early shift in body size evolution along the lamniform stem
303 lineage between 200 and 150 Ma (posterior probability = 0.97; Fig. 1D–E), and an ancestral body
304 size increase towards a crown lamniform macroevolutionary optimum of 4.9 m (magnitude of theta
305 = 6.2) ~145 Ma (Fig. 1D). Although this optimum falls below the limits of gigantism as defined
306 here, it is much larger than the estimated size optimum for the rest of elasmobranchs (root optimum
307 = 1 m).
308
309 **DISCUSSION**
310
311 Our results show that, although trophic level is positively correlated with body size in
312 elasmobranchs (as has previously been reported for other fishes; Pauly et al. 1998; Romanuk et al.
313 2011), filter feeders and mesotherms significantly deviate from this relationship. Indeed, the
314 largest elasmobranch giants occupy diametrically opposed ends of the trophic spectrum (shown by
315 the highest red and purple values in Fig. 1A). This suggests that species exhibiting these mutually
316 exclusive feeding strategies have followed different evolutionary pathways with respect to the rest
317 of elasmobranchs. This interpretation is corroborated by 1) our ancestral state estimates, which
318 indicate significantly larger ancestral sizes for clades including filter feeders or mesotherms (2–6
319 m, Table 2; Fig. 1C); and 2) by the tendency of mesotherms, and especially filter feeders, to be
320 significantly larger than their ectothermic-macropredatory counterparts (Fig. 1B, S2B). Our results

321 allow us to identify two main evolutionary pathways underlying the evolution of gigantism in
322 elasmobranchs: the ancestral mesothermic pathway and the filter-feeding pathway.
323
324 **The ancestral mesothermic pathway**
325 Our results point to a single origin of mesothermy in the late Cretaceous, within Lamniformes (Fig.
326 1E). However, alternative analyses excluding fossils support multiple independent Cenozoic
327 acquisitions of mesothermy within this clade (Fig. S2). Given that thermoregulatory mode can
328 only be inferred in the fossil record (as opposed to directly observed), we cannot rule out the
329 possibility of independent origins of mesothermy. Nonetheless, the mesothermic conditions
330 estimated for our fossil dataset are well supported by different lines of evidence (see supplementary
331 material; also see Ferrón 2017; Ferrón et al. 2017). Because fossils possess unique and important
332 trait information from early-diverging lineages, we consider our analyses including fossils to be
333 more robust and accurate despite the limitations of an incomplete fossil record (Doyle and
334 Donoghue 1987; Donoghue et al. 1989; Finarelli and Flynn 2006; Albert et al. 2009; Slater et al.
335 2012; Hsiang et al. 2015; Field and Hsiang 2018).
336
337 Based on our results incorporating fossils, we hypothesize that the first elasmobranch giants arose
338 from a relatively large (3.54 m; Fig. 1C; Table 2) mesothermic ancestor. This pathway originated
339 with a shift in elasmobranch body size evolution during the Jurassic (Figs. 1D-E), followed by the
340 origin of crown Lamniformes. By the earliest Cretaceous (~145 Ma), ancestral lamniforms had
341 attained a body size optimum of 4.1 m. Mesothermy may have evolved afterwards (between 145
342 and 113 Ma), just before the rise of the first elasmobranch giant (during the Albian, between 113.0
343 and 100, Fig. 1D). In the late Cretaceous, a subsequent diversification event witnessed the rise of
344 multiple gigantic lineages (Maisey et al. 2004).
345
346 The mesothermic pathway to gigantism ultimately resulted in the evolution of the largest marine
347 macropredator to have ever lived, the ~18 m †*O. megalodon* (Ferrón 2017; Ferrón et al. 2017),
348 which is known from the Miocene to the Pliocene (Pimiento and Clements 2014; Pimiento et al.
349 2016). Given the high metabolic demands that it imposes (McNab 2009), mesothermy is associated
350 with high extinction risk among large bodied species when large prey become scarce (Pimiento et
351 al. 2017). This may have been the case in the late Pliocene, when coastal areas were reduced due
352 to large sea level oscillations (Pimiento et al. 2017). Therefore, the mesothermic pathway appears
353 to have promoted the acquisition of extremely large size (e.g. 18 m) until the Pliocene, during
354 periods where coastal habitats were large enough to provide the ecological infrastructure for
355 metabolically demanding, extreme-sized predators. The only gigantic mesothermic shark that
356 persisted beyond the Pliocene is the modern white shark (*C. carcharias*, max TL = ~7 m) which
357 is significantly smaller than the extreme-sized †*O. megalodon*. The disproportionate extinction of
358 mesotherms during the Pliocene (Pimiento et al. 2017) can partially explain why filter feeders
359 emerge as significantly larger than mesotherms in extant-only analyses (Fig. S2B).
360
361 Empirical evidence suggests that the origin of mesothermy in Lamniformes likely facilitated
362 predation efficiency by increasing tolerance to colder waters (niche expansion) and by increasing
363 cruising speeds (Bernal et al. 2003, 2005, 2012; Dickson and Graham 2004; Bernal and Sepulveda
364 2005; Sepulveda et al. 2005; Watanabe et al. 2015). The subsequent origin of gigantism among
365 mesothermic macropredators was likely related to achieving competitive superiority (Vermeij
366 2016). Although further studies are needed to confirm the timing and number of origins of

367 mesothermy in sharks, based on our best estimates of the timing of its appearance we hypothesize
368 that the ancestral mesothermic pathway to gigantism evolved as a means to enhance the intake of
369 large prey in the face of low sea temperatures (Dickson and Graham 2004) in the late Jurassic and
370 early Cretaceous (Price 1999; Puceat et al. 2003; Steuber et al. 2005; Amiot et al. 2011), while
371 avoiding competition with contemporaneous, gigantic, planktivorous bony fishes (Liston 2008;
372 Friedman et al. 2010; Liston et al. 2013). In addition, the subsequent diversification of gigantic
373 macropredatory lamniforms during the late Cretaceous could have been a response to persistent
374 predatory pressure from the large marine reptiles that dominated Mesozoic seas (Massare 1987)
375 as well as to the need of continued niche partitioning with gigantic planktivorous bony fishes
376 (Friedman et al. 2013; Schumacher et al. 2016).
377
378 **The filter-feeding pathway**
379 Our results show that filter-feeding evolved independently in four elasmobranch clades:
380 Mobulidae, Megachasmidae, Rhincodontidae and Cetorhinidae (Fig. 1E). Most of these
381 appearances took place around the Paleocene–Eocene Thermal Maximum (PETM), a period of
382 increased productivity in the world's oceans (Zachos et al. 2001). Nevertheless, the range of
383 appearance of filter-feeding in the clade Cetorhinidae extends back to the late Cretaceous. This
384 timing, compatible with the late Cretaceous occurrence of †*Pseudomegachasma* (Shimada et al.
385 2015), a putative filter feeder not included in our analyses given uncertainties related to its
386 phylogenetic position and trait attributes, suggest the possibility of elasmobranch filter-feeding
387 appearing much earlier than the Paleogene (Fig. 1D), during a period also known for elevated
388 primary productivity (Price 1999; Puceat et al. 2003; Steuber et al. 2005). Although tantalizing, a
389 late Cretaceous origin of filter-feeding in elasmobranchs cannot be adequately tested with the
390 information at hand. Accordingly, in agreement with previous studies (Friedman et al. 2010;
391 Friedman 2012; Paig-Tran and Summers 2014), the most conservative interpretation is that filter-
392 feeding as a major elasmobranch feeding strategy originated in the Paleogene (Fig. 1E).
393
394 Parallel to the pathway followed by other filter-feeding giants (e.g. Friedman 2012; but see
395 Fordyce and Marx 2018), gigantism among filter-feeding elasmobranchs appeared after ancestrally
396 macropredatory species had already shifted to planktivory (Friedman 2012). Nonetheless, the
397 filter-feeding pathway to elasmobranch gigantism differs from that of other planktivorous gigantic
398 fishes in that it arose within both benthic (*M. birostris* and *R. typus*) and pelagic (*Cetorhinus* and
399 *Megachasma*) clades. If the origin of mesothermy in Lamniformes can be ascribed to a single
400 evolutionary transition (Fig. 1E), then the gigantic filter feeders that are ancestrally pelagic were
401 also ancestrally mesothermic. Therefore, the extant filter feeders *Cetorhinus* and *Megachasma*
402 may have transitioned to an ectothermic physiology secondarily, from a mesothermic,
403 macropredatory ancestor. This hypothesis needs to be addressed once the timing and number of
404 origins of mesothermy in sharks is confirmed.
405
406 Based on our results, we propose that the filter-feeding pathway to gigantism arose in clades with
407 relatively large ancestors (2–6 m, Fig. 1C; Table 2) as a response to the increased productivity and
408 consequent enhancement of the ecological infrastructure of the Paleogene's oceans (Vermeij
409 2016). This process may have been influenced or facilitated by the planktonic turnover of the
410 Cretaceous–Paleogene (K–Pg; Tajika et al. 2018). Similarly, the ultimate attainment of filter-
411 feeding gigantism could have been a response to the vacant niches left by the extinction of gigantic

412 planktivorous bony fishes at the K–Pg boundary (Friedman et al. 2010), and persistent pressure
413 from large predators through the Cenozoic (Lambert et al. 2010; Pimiento et al. 2016).
414
415 The filter-feeding pathway to gigantism in elasmobranchs resembles that followed by marine
416 mammals later in the Cenozoic, which has been proposed to be the result of increased primary
417 productivity and predatory release during the Plio-Pleistocene (Lambert et al. 2010; Pimiento and
418 Clements 2014; Slater et al. 2017). Accordingly, the oceanographic dynamics of the Plio-
419 Pleistocene caused the extinction of extreme-sized macropredatory mesothermic sharks, e.g. †*O.*
420 *megalodon,* due to habitat loss, while promoting the evolution of extremely large endothermic
421 filter-feeding whales through an increase in primary productivity. The occurrence and persistence
422 of extremely large filter feeders in the world's oceans (i.e. bony fishes [10 m], sharks [18 m] and
423 mammals [24 m] (Friedman et al. 2010; Friedman 2012; Liston et al. 2013; McClain et al. 2015;
424 Pimiento and Balk 2015; Pyenson and Vermeij 2016; Slater et al. 2017) and their larger size
425 relative to non-filter-feeding ectotherms (Fig. S2B, Table S4) suggest that this pathway has been
426 sustained throughout geologic time, at least since the mid-Jurassic. However, given that high levels
427 of microplastic toxins are increasingly threatening filter-feeding organisms in today's oceans
428 (Germanov et al. 2018), the future persistence of giant filter feeders may be now at risk.
429
430 **Ectothermic-macropredatory giants and further considerations**
431 Despite the fact that macropredatory ectotherms do not reach the lengths of the largest
432 elasmobranchs (e.g. 18 m), five species (i.e. *G. cuvier, S. microcephalus, M. owstoni, S. mokarran*
433 and †*H. serra*) were able to surpass our defined limits of gigantism, reaching sizes between 6 and
434 7.5 m (Fig. 1A). Unlike mesothermic or filter-feeding clades, giant macropredatory ectotherms
435 originated from significantly smaller ancestors (Table 2, Fig. S3) and, as a group, are significantly
436 smaller than mesotherms and filter feeders (Figs. 1B, S2B). We propose that because giant
437 ectothermic macropredators lack the specializations for enhancing prey intake and environmental
438 exploitation, they are: a) correspondingly constrained to the lower limits of gigantism; b) unable
439 to reach the extreme sizes of the largest mesotherms and filter feeders (i.e. ~18 m; McClain et al.
440 2015; Pimiento and Balk 2015); and c) represent outliers in the body size evolution of their clades.
441 Consequently, ectothermic-macropredation cannot be considered an evolutionary pathway
442 towards elasmobranch gigantism.
443
444 It is worth noting that the origin of the two main evolutionary pathways towards elasmobranch
445 gigantism we propose here (mesothermic and filter-feeding) are limited to fossil taxa with
446 reasonably well resolved phylogenies and with inferable physiological traits. For instance,
447 Mesozoic species that have shown gigantic traits [e.g., *Cretoxyrhina* (Shimada 2008), *Cretodus*
448 (Amalfitano et al. 2017), and *Ptychodus* (Shimada et al. 2010)], and putative filter feeders [e.g.,
449 †*Pseudomegachasma* (Shimada et al. 2015)] or mesotherms [e.g., ctenacanthiforms (Maisey et al.
450 2017)] could not be included in our analyses. This particularly affects our results regarding the
451 mesothermic pathway, which are sensitive to the inclusion of fossils (Fig. S2). Indeed, the
452 exclusion of fossils leads to an alternative hypothesis in which mesothermy evolves multiple times.
453 This suggests that despite the inherent problems associated with the incompleteness of the fossil
454 record, fossil taxa add critical trait information at, or near the base of different clades, which is
455 fundamental to estimate ancestral states and to elucidate the time and origin of evolutionary
456 pathways. While our study marks the first attempt to assess the evolutionary pathways that led to
457 gigantism in elasmobranchs (a group that displays an array of feeding and thermoregulatory

458 adaptations) based on available paleontological data, future studies should seek to resolve the
459 phylogenetic relationships of fossil lamniforms, and to gather empirical evidence on the presence
460 of mesothermy and filter-feeding traits in ancient fossil species to further confirm the time of origin
461 of the evolutionary pathways towards elasmobranch gigantism.
462
463 **Concluding remarks**
464 Taken together, our results suggest that there are two main evolutionary mechanisms that have
465 given rise to gigantism among elasmobranchs: the mesothermic and filter-feeding pathways. These
466 pathways were followed by clades with relatively large ancestral sizes and involved the initial
467 acquisition of specialized adaptations to enhance prey intake in the face of environmental change.
468 Although giant sizes can be reached by ectothermic-macropredators, these species evolved from
469 smaller ancestors and did not acquire thermoregulatory or dietary specializations. The final
470 attainment of giant sizes following the main evolutionary pathways towards gigantism appears to
471 be, at least in part, a response to biotic factors, namely predation avoidance and niche availability
472 (see Vermeij 2016). The lack of specializations among ectothermic macropredators has restricted
473 their gigantic representatives to the lower limits of elasmobranch gigantism (6–7.5 m). By contrast,
474 the mesothermic (in combination with macropredation) and filter-feeding (or diet specialization)
475 pathways have facilitated the evolution of the largest elasmobranchs in Earth history (~18 m).
476
477 In general, large elasmobranchs are particularly susceptible to extinction in today's oceans (Dulvy
478 et al. 2014). Our results suggest that mesotherms and filter feeders followed different evolutionary
479 pathways that allowed them to reach larger sizes than the rest of elasmobranchs. Because such
480 evolutionary pathways involve transitions to specializations that essentially depend on the quality
481 and abundance of food items in the oceans (McNab 2009; Vermeij 2016), mesothermic and filter-
482 feeding species face particular constraints that further affect their extinction susceptibility.
483 Mesotherms rely on the availability of large prey to maintain their high metabolic demands
484 (McNab 1983; Block and Finnerty 1994; McNab 2009; Vermeij 2016; Ferrón et al. 2017). Because
485 the persistence and availability of large prey mainly depend on the area available (Wright 1983),
486 the mesothermic pathway can promote extreme sizes as long as habitats are large enough to
487 provide the ecological infrastructure for metabolically demanding giant predators. Therefore,
488 when large vertebrate prey became scarce in the Pliocene due to a significant loss of habitable
489 area, the largest mesothermic sharks (e.g. †*O. megalodon*) became extinct (Pimiento et al. 2017).
490 The filter-feeding pathway, on the other hand, is the mechanism that has given rise to the largest
491 extant elasmobranch, the whale shark (McClain et al. 2015). Because plankton is consistently more
492 abundant than large prey (McNab 2009; Vermeij 2016), especially during periods of rapid
493 environmental change (e.g. when habitat is lost), filter-feeding may confer giant species with more
494 resilience than mesothermy in the face of environmental challenges. However, given that filter
495 feeders are particularly susceptible to high levels of microplastic toxins in today's oceans
496 (Germanov et al. 2018), this strategy, which has persisted since at least the Paleogene, may be at
497 risk in modern oceans.
498

TABLES

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

Group	N	Min	Max	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 endothermic condition may have evolved secondarily, as a derived character, along with filter-feeding (see text).

Fig. caption

Fig. 1. Body size evolution in elasmobranchs. (*A*) Relationship between body size and trophic level (both 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 Log-scaled body size evolutionary 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 Myr intervals.

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