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1 **New scale analyses reveal centenarian coelacanths *Latimeria chalumnae***

2

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14 **Summary**

15 **The extant coelacanth was discovered in 1938<sup>1</sup>; its biology and ecology remain poorly**  
16 **known due to the low number of specimens collected. Only two previous studies<sup>1,2</sup> have**  
17 **attempted to determine its age and growth. They suggested a maximum lifespan of 20**  
18 **years placing the coelacanth among the fastest growing marine fish. These findings are**  
19 **at odds with the coelacanth's other known biological features including low oxygen-**  
20 **extraction capacity, slow metabolism, ovoviviparity, and low fecundity, typical of fish**  
21 **with slow life-histories and slow growth. In this study, we use polarized light microscopy**  
22 **to study growth on scales based on a large sample of 27 specimens. Our results**  
23 **demonstrate for the first time nearly imperceptible annual calcified structures (circuli)**  
24 **on the scales and show that maximal age of the coelacanth was underestimated by a**  
25 **factor of 5. Our validation method suggests that circuli are indeed annual thus**  
26 **supporting that the coelacanth is among the longest-living fish species, its lifespan being**  
27 **probably around 100 years. Like deep-sea sharks with a reduced metabolism, the**  
28 **coelacanth has amongst the slowest growth for its size. Further reappraisals of age at**  
29 **first sexual maturity (in the range 40 to 69 years old) and gestation duration (of around**  
30 **5 years) show that the living coelacanth has one of the slowest life histories of all marine**  
31 **fish and possibly the longest gestation. As long-lived species with slow life histories are**

32 **extremely vulnerable to natural and anthropogenic perturbations, our results suggest**  
33 **that coelacanths may be more threatened than previously considered.**

34 **Keywords :**

35 Scalimetry, Growth patterns, Polarized light, long-lived species, life-history traits

36

37 **Results and Discussion**

38 **A new ageing methodology**

39 Extant coelacanths were discovered in 1938 and are the only surviving members of an  
40 extinct lineage<sup>3</sup>. The coelacanths are large lobe-finned fish (sarcopterygians). The African  
41 coelacanth *Latimeria chalumnae*<sup>3,4</sup> is considered critically endangered. This species is  
42 characterized by a large body size that can reach up to two meters in length and weigh up to  
43 105 kg<sup>5</sup>, with large length at maturity (around 150 cm<sup>6,7</sup>). These animals are ovoviviparous,  
44 produce a relatively small number of offspring, and have a large size at birth (around 35 cm).  
45 The coelacanth is thought to be a nocturnal languid drift-hunter and its unique locomotory  
46 movements are generally slow<sup>8</sup>, though it can exhibit fast-start escape responses<sup>9</sup>. These fish  
47 have a slow metabolism<sup>10,11</sup> often thought to be associated with its energy-saving mode of life,  
48 typical of deep water species. African coelacanths are found most commonly at water  
49 temperatures between 15 to 19°C where their oxygen uptake capacity is optimal<sup>10</sup>. These life-  
50 history, physiological and behavioural traits initially positioned coelacanths at the slow end of  
51 the slow-fast life-history continuum<sup>12</sup>. Growth estimates presented in two previous studies<sup>1,2</sup>  
52 using the same dataset of 12 specimens, however, placed coelacanths among the fastest  
53 growing fishes, comparable to tunas<sup>13</sup>. The inconsistency between a suggested fast body  
54 growth and other life-history traits indicative of slow life-history prompted us to revisit the  
55 age and body growth estimations of coelacanths. In this study, age and growth were estimated  
56 from scales collected from 27 coelacanths captured of the coast of the Comoros Islands (13

57 females, 11 males, 1 juvenile, and 2 embryos) with total length ranging from 30.5 to 180 cm.  
58 These specimens were captured between 1953 and 1991 (See also Table S1). The scales of  
59 coelacanths present an anterior field with ridges radiating from the apex and concentric  
60 macroscopic circuli<sup>1</sup> (called macro-circuli hereafter) observable under transmitted light  
61 microscopy (Figure 1). Both previous ageing studies interpreted these macro-circuli as marks  
62 of growth rate variation with alternating translucent and opaque bands suggesting fast and  
63 reduced growth, respectively; however, these studies did not agree on the periodicity of band  
64 formation. The earliest study suggested that macro-circuli were seasonal with two being laid  
65 down each year in association with the alternation of two wet and two dry seasons annually in  
66 the tropics<sup>1</sup>, whereas the most recent study interpreted macro-circuli as annual, only one being  
67 laid down each year<sup>2</sup>, arguing that, as for the majority of fish<sup>14</sup>, tropical fish exhibit a  
68 circannual rhythm despite climate seasonality.

69         Following these earlier studies, we analysed our extended sample under transmitted  
70 light microscopy to count the macro-circuli along the longest growth axis of each scale  
71 (Figure 1a). The age of the individuals was estimated to range between 0 to 8 years and  
72 between 1 to 17 years under the hypothesis that macro-circuli are seasonal and annual,  
73 respectively (See also Table S1). These age ranges and the total length range of our sample  
74 are comparable to those of the previous ageing studies, thus suggesting an equally fast body  
75 growth inconsistent with other life-history traits. We therefore decided to use another  
76 observation method, namely polarized-light microscopy. As expected, polarized light revealed  
77 much more detail on scale topography than transmitted light<sup>15,16</sup> (Figure 1b), the quality of the  
78 image being equivalent to micro-computed tomography (See also Figure S1). More  
79 specifically, we identified new circuli that were thinner and more numerous than the macro-  
80 circuli observed under transmitted light (Figure 1b vs. Figure 1a). These circuli were also  
81 formed by alternating thin translucent and opaque bands suggestive of growth rate variation.

82 Counting circuli in the same manner as macro-circuli and under the assumption that they are  
83 annual, we obtained individual ages ranging from 5 to 84 years (See also Table S1).  
84 Comparing our results under transmitted and polarized light, the number of circuli appeared  
85 linearly related to the number of macro-circuli ( $P = 0.009$ ;  $R^2=0.84$ ) with a slope of 5.16,  
86 which indicates the appearance of a macro-circulus roughly every five circuli.

## 87 **Validation of coelacanth age**

88 Only direct validation methods, i.e., those using individual-level temporal reference  
89 marks on scales relative to natural marks to assess the periodicity of the latter, would allow  
90 indisputable confirmation of the interpretation of circuli as annual growth marks. The main  
91 direct validation methods are (i) mark-recapture of wild individuals tagged externally and  
92 labelled with a chemical depositing a mark on their scales and (ii) captive rearing of either  
93 chemically-labelled fish of unknown age or of fish of known age (e.g. produced in controlled  
94 conditions). These methods are, however, not applicable to coelacanths due to conservation  
95 and ethical issues.

96 Instead, we used indirect validation methods. The most widely used method is Marginal  
97 Increment Analysis (MIA), which assesses the periodicity of increments in calcified  
98 structures, here macro-circuli and circuli. When growth has a circannual rhythm, increments  
99 are formed during the growth period of the year. The size of the increment under formation,  
100 named the marginal increment and measured as the distance between the last fully formed  
101 (macro-) circulus and the edge of the scale, should thus exhibit some intra-annual periodic  
102 pattern when plotted against the month at which the individual was captured. Applying MIA  
103 to macro-circuli, no such intra-annual periodic pattern was evident ( $P = 0.61$ ; Figure 1 lower  
104 panel) suggesting that they are not formed annually. In contrast, the application of MIA to  
105 circuli allowed detection of intra-annual variation in their growth ( $P < 0.001$ ; Figure 1 upper  
106 panel), revealing a circannual rhythm in circuli formation.

107 A second indirect validation method is to assess the internal and/or external consistency  
108 of the population-level mean body growth pattern, or length-at-age data, obtained for each  
109 scale. Three growth models are widely used in ecology to describe length-at-age data for  
110 species with indeterminate growth because they conform to the observed shape of growth  
111 curves: the von Bertalanffy, Gompertz, and logistic growth models. For both macro-circuli  
112 and circuli ageing, the von Bertalanffy growth model appeared to best described the resulting  
113 length-at-age data based on minimization of the small-sample bias-corrected AIC (See also  
114 Table S2). The body growth curve estimated from length-at-age data obtained using macro-  
115 circuli for ageing (Figure 2 dashed blue curve) was characterized by a combination of a large  
116 asymptotic length ( $TL_{\infty} = 296.1$  cm) reached at a fast rate ( $K = 0.05 \text{ year}^{-1}$ ; note that  
117 coefficient  $K$  in the von Bertalanffy model represents the rate at which asymptotic length is  
118 reached and not size change per unit of time). Consequently, the largest ( $TL = 180$  cm) and  
119 oldest (17 years) specimen of our sample appeared as being still in a fast growth phase and at  
120 about only 61% of the estimated asymptotic length  $TL_{\infty}$ . Moreover,  $TL_{\infty}$  was estimated to be  
121 much larger than both the largest individual ever captured<sup>17</sup> ( $TL = 190$  cm) and the maximum  
122 length ( $TL_{\text{max}} \pm \text{c.i.} = 199 \pm 24$  cm) estimated independently from length-at-age data using  
123 extreme value theory<sup>2</sup>. The same holds when using length-at-age data obtained by the  
124 previous ageing study assuming annual macro-circuli (Figure 2 dashed dark blue curve). In  
125 contrast, the body growth model fitted to length-at-age data obtained using circuli (Figure 2  
126 red curve) estimated a smaller asymptotic length ( $TL_{\infty} = 203.8$  cm) reached at a slower rate  
127 ( $K = 0.02 \text{ year}^{-1}$ ) such that the largest ( $TL = 180$  cm) and oldest (85 years) individual in the  
128 data set is in a slow growth phase and much closer to its asymptotic length (88%). In addition,  
129  $TL_{\infty}$  is in much better agreement with the length of the largest individual ever captured and  
130 with the previously independently estimated maximum length. The growth pattern obtained  
131 using circuli ageing appears thus to outperform other estimates.

132 We further used a double logarithmic plot of the von Bertalanffy rate coefficient  $K$   
133 versus asymptotic length  $TL_{\infty}$  (so-called auximetric plot), and the growth performance index  
134  $\phi'$  to compare the global body growth of coelacanths with other marine fish species (1383  
135 populations distributed across 1313 species extracted from FishBase<sup>18</sup>) for each ageing  
136 method. Ageing based on macro-circuli would position the coelacanth among the fastest  
137 growing fishes with a similar asymptotic length (Figure 3A) and above the 90<sup>th</sup> percentile of  
138 the growth performance index  $\phi'$  distribution across all marine fish (Figure 3B). Such high  
139 body growth capacity is almost equivalent to that of tunas<sup>13</sup> (Figure 3) that have evolved  
140 unique morphological: streamlined body and fin shapes, large mass-specific gill surface area,  
141 and physiological: high oxygen-affinity blood, combined with endothermy, high proportion of  
142 red muscle, high cardiac performance<sup>13</sup>, characteristics to support their high growth  
143 performance and very active lifestyle. These traits differ strongly from those of coelacanths,  
144 which are typical of fish with low growth performance and high longevity<sup>19</sup> like deep-sea fish  
145 with low metabolic rates. In contrast, the body growth pattern obtained from circuli would  
146 place *L. chalumnae* among the slowest growing fish within the same range of asymptotic  
147 length (Figure 3A) and close to the mode of the growth performance index  $\phi'$  distribution  
148 (64<sup>th</sup> percentile, Figure 3B). This growth is similar to that of deep-sea sharks, concurring with  
149 the morphological and physiological traits of the living coelacanth, as well as its lifestyle.

150 These results suggest that ageing coelacanths by interpreting circuli as annual growth  
151 marks provides the most realistic estimates of seasonal scale formation and lifelong body  
152 growth, with the longevity of the coelacanth estimated to be close to one century. This  
153 observed longevity is five times greater than previously estimated. Only one study had  
154 hypothesised such an extended lifespan<sup>6</sup> but with no direct evidence. Our study unequivocally  
155 demonstrates for the first time the coelacanth exceptional longevity and positions it as one of  
156 the most long-lived fish species. The factor of five between longevity estimates originates

157 from the fact that the macro-circuli used by the previous studies for ageing do not exhibit a  
158 circannual formation rhythm and appear with an approximately 5-year periodicity throughout  
159 the lifespan of both males and females (See also Figure S2). Two hypotheses may explain the  
160 presence of these macro-circuli, the first one being of exogenous origin, namely periodic  
161 environmental events, and the other of endogenous origin, i.e. periodic  
162 physiological/behavioural events. Regarding the former, strong variations in environmental  
163 conditions such as salinity or temperature are known to leave marks on scales and large-scale  
164 climate oscillations such as the Indian Ocean Dipole (IOD) or the El Niño-Southern  
165 Oscillation (ENSO)<sup>20</sup> could produce periodic scale marks. However, an exogenous origin  
166 would imply a mark deposition on scales that is synchronized across individuals. This  
167 synchrony is not observed in the years of appearance of the macro-circuli for the different  
168 individuals in our sample (See also Figure S2A). The hypothesis of an endogenous origin  
169 (periodic physiological or behavioural stresses) seems thus more likely. Periodic events that  
170 affect both sexes equally, as macro-circuli are found in both females and males, such as  
171 migration or reproductive behaviour are potential candidates. Unfortunately, knowledge on  
172 the biology and behaviour of the coelacanth remains too fragmented to address this hypothesis  
173 further.

#### 174 **Implications for life history and conservation**

175 In addition to longevity and body growth, two other aspects the coelacanth's life-history can  
176 be reappraised with our new age estimation method: the duration of gestation and the age at  
177 first sexual maturity. The early life of coelacanth is not well known and developmental stages  
178 available in collections are rare. In our sample, two different *pre-partum* embryos (CCC29.5  
179 and CCC162.21), one early *post-partum* juvenile (CCC94), and another slightly older juvenile  
180 were available (See also Table S1). The age of both *pre-partum* specimens is estimated at 5  
181 years based on circuli whereas that of the two *post-partum* individuals is estimated at 9 and 12



182 years, respectively. This indicates that the gestation duration is at least five years contrary to  
183 the 1 to 2 years suggested by earlier studies. The length at birth is uncertain but the size of the  
184 largest observed *pre-partum* individual from a litter of 26 near-term embryos<sup>21</sup> ranging from  
185 30.8 to 35.8 cm total length found in a gravid female could be a good estimation. Based on  
186 our estimate of the von Bertalanffy growth model and under the assumption that embryos  
187 follow the same growth pattern as post-partum individuals, such length at birth would also  
188 give a gestation period close to five years. The earlier hypothesis of a long gestation is thus  
189 confirmed<sup>2</sup> but largely extended, placing the coelacanth among the vertebrates with the  
190 longest gestation period, alongside the deep-sea frilled shark *Chlamydoselachus anguineus*  
191 (three years)<sup>22</sup>.

192 The length at first sexual maturity was estimated to range between 120 and 129 cm for  
193 males and between 160 to 179 cm for females<sup>6,7</sup>. These values were obtained from the  
194 anatomical and morphological differences between juveniles and matures specimens. In light  
195 of our ageing data (See also Table S1), these length ranges would correspond to ages at first  
196 maturity ranging from 40 to 69 years for males and from 58 to 66 years for females. These  
197 new estimates of age at first maturity are also close to those of the frilled shark and  
198 correspond to an onset of maturation much later in life (ratio of age maturity to maximum  
199 longevity: 0.47-0.81 for males and 0.68-0.78 for females) than in teleost fishes (range: 0.16-  
200 0.39 and typical values: 0.25-0.30<sup>23</sup>). This pattern is consistent with the reproductive strategy  
201 of both coelacanth and elasmobranches<sup>24</sup>. Species that rely on internal fertilization and  
202 produce a few large fully-developed offspring after a long gestation, especially ovoviviparous  
203 and viviparous ones, tend to mature later in life than species that lay very large number of  
204 eggs, rely on external fertilization and produce undeveloped larvae (most teleost fishes<sup>25</sup>).  
205 This conforms to life-history theory which predicts that an increased survival probability of  
206 immature life-stages, such as in case of ovoviviparity and viviparity, favours the evolution of

207 delayed maturation<sup>26</sup>. The delayed maturity of the coelacanth relative to its longevity also  
208 implies a shorter relative reproductive lifespan than teleost fishes. This results in very  
209 different benefits and demographic consequences of extreme longevity. In teleost, long-lived  
210 species have an extended reproductive lifespan and thus “sample” multiple reproductive  
211 events. In a variable environment resulting in fluctuating recruitment, this allows taking  
212 advantage of occasional favourable environmental conditions to produce strong year classes  
213 literally “stored” in the adult population until conditions for strong recruitment return, a type  
214 of bet-hedging strategy also called “storage effect”<sup>27</sup>. In contrast, the coelacanth demography  
215 is likely to rely on a continuous influx of weak recruitment insured by very high survival rates  
216 of a few offspring per individual whatever the environmental conditions.

217         Based on our re-appraisal of time-related life-history traits of the coelacanth, namely  
218 growth rate through the von Bertalanffy rate coefficient  $K$ , maximum observed longevity, age  
219 at first sexual maturity and gestation duration, we assessed its location along the slow-fast  
220 life-history continuum in marine fish. A Principal Component Analysis was performed on  
221 these four life-history traits across 147 populations in 131 marine fish species extracted from  
222 FishBase<sup>18</sup>. By focusing on life-history traits with time dimensionality, we avoided the  
223 problem of heterogeneous dimensions across traits that may prevent correct interpretation of  
224 life-history strategies in terms of the slow-fast continuum<sup>12</sup>. Ideally, the phylogenetic  
225 relatedness between species should have been accounted for in this analysis. However, as far  
226 as we are aware, no phylogeny relating the coelacanth, Actinopterygii and Chondrichthyes  
227 with a sufficiently fine granularity, i.e. including most species of our life-history dataset, is  
228 currently available. In addition, past analyses in other taxa have shown that phylogenetic  
229 inertia does not affect strongly the detection and strength of the slow-fast continuum<sup>12</sup>. The  
230 first Principal Component observed trades-off high longevity and late maturity against fast  
231 rate of approach towards asymptotic size, and thus can be considered as the main component

232 of the slow-fast life-history continuum, whereas the second one is mostly determined by  
233 gestation duration (inversely related to spawning frequency used in the analysis; Figure 4A).  
234 The estimation of life-history traits based on macro-circuli ageing places the coelacanth in the  
235 main bulk of marine fish, close to the cluster formed by tunas (Figure 4A). In contrast, life-  
236 history traits estimated from circuli position the coelacanth towards very slow life-histories,  
237 close to deep-sea sharks and roughies (Figure 4A). Taking the first PC as a metric of the slow-  
238 fast life-history continuum, ageing based on circuli places the coelacanth among the slowest  
239 life-histories (0<sup>th</sup> percentile) together with roughies and deep-sea sharks whereas ageing based  
240 on macro-circuli would correspond to a faster, moderate pace of life (26<sup>th</sup> and 13<sup>th</sup> percentile  
241 for macro-circuli ageing of our data and previous data, respectively; Figure 4B).

242 The new ageing method developed in this study shows that the African coelacanth, *L.*  
243 *chalumnae*, may live for about a century, making it one of the most long-lived fish species.  
244 Alongside its exceptional longevity, this study showed that the African coelacanth has one of  
245 the slowest life histories among marine fish, and possibly all vertebrates, characterized by a  
246 slow body growth relative to its size, very late age at first sexual maturity, and exceptionally  
247 long gestation time, which is in concord with its ovoviviparity, relatively small clutch size,  
248 and reduced metabolism. These life-history and physiological characteristics are partly similar  
249 to those observed in the human fish (*Proteus anguinus*)<sup>28</sup>, a small cave salamander with one  
250 of the slowest life-histories among vertebrates. Long-lived species characterized by slow life  
251 history and relatively low fecundity are known to be extremely vulnerable to perturbations of  
252 a natural or anthropic nature due to their very low replacement rate<sup>29</sup>. Ignoring such  
253 characteristics has been shown to be detrimental to conservation and management as  
254 exemplified by some deep-sea fisheries<sup>30</sup>. The African coelacanth is assessed as critically  
255 endangered (Red List of Threatened Species of IUCN). Our results suggest that it may be  
256 even more threatened than expected due to its peculiar life history. Further studies on the

257 biology and ecology of the coelacanth, especially on its reproductive biology and behaviour,  
258 are needed to be able to preserve this unique component of life on Earth.

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## 271 **Author contributions**

272 M.H., K.M. and B.E. contributed conception and design of the study. M.H. performed the  
273 sampling. K.M. organized the image acquisition and ageing data collection. K.M.. performed  
274 the analysis of growth patterns and the marginal increment analysis and B.E. the auximetric  
275 analysis and the slow-fast life-history continuum analysis. All authors provided inputs for the  
276 results and discussion. K.M. wrote the first draft of the manuscript and B.E. wrote sections of  
277 the manuscript. All authors provided critical comments and were involved in the revision and  
278 editing of the manuscript. All authors accepted the final version of the manuscript.

## 279 **Declaration of interests**

280 The authors declare no competing interests.

281

282 **Figure Legends**

283 **Figure 1: Analysis and periodicity of the circuli and macro-circuli of the African**  
284 **coelacanth scale.** The same scale of *L. chalumnae* CCC4 (female of 109 cm caught in  
285 January 1954) is analysed based on a reconstructed image under either transmitted light  
286 microscopy (a.) or polarized light microscopy (b.) (Horizontal white scale bar = 1 mm).  
287 Macro-circuli (a.) and circuli (b.) are marked (dots) along the longest growth axis (red line).  
288 For each type of circuli, temporal dynamics of monthly marginal increments (mm) on scales  
289 of *L. chalumnae* (n = 27) based on the hypothesis of annual circuli (red) or annual macro-  
290 circuli (blue) are shown. The bottom and top of each box are the first and the third quartiles of  
291 the marginal increment distribution for the considered month (x-axis), the horizontal segment  
292 and the diamond inside the box are respectively the median and the mean, and whiskers  
293 represent the most extreme data point within 1.5 interquartile range. For three specimens  
294 (CCC162.21, CCC29.5 and CCC42.5), only macro-circuli could be identified and no  
295 individual was collected in November and December so that no marginal increment was  
296 available for month 10 and 12. The thin continuous curve in each panel represents the fit of a  
297 sinusoidal regression of marginal increments against month with a period of 12 month to test  
298 for annual periodicity. Under the hypothesis of annual circuli, a significant intra-annual  
299 periodicity of marginal increment growth is detected by the sinusoidal regression. In contrast,  
300 under the assumption of annual macro-circuli, no evidence of a periodic pattern is found (See  
301 also Figure S1 and S2).

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308 **Figure 2: Body growth pattern of the African coelacanth according to different scale**  
309 **interpretations.** Observed length-at-age data for different scale interpretations for age are  
310 shown (red solid circles: circuli ageing, blue open squares: macro-circuli ageing, dark blue  
311 crosses: previous age interpretation<sup>2</sup>) together with the corresponding fitted von Bertalanffy  
312 growth models (dashed light blue curve: macro-circuli, continuous red curve: circuli, dashed  
313 dark blue curve: previous age interpretation).  $TL_{\infty}$  and  $K$  are the asymptotic total length (cm)  
314 and the rate coefficient, i.e. the rate at which the asymptotic length is reached ( $\text{year}^{-1}$ ),  
315 respectively, estimated from the von Bertalanffy growth models and  $\phi' = \log(K) +$   
316  $2 \log(TL_{\infty})$  is the growth performance index ( $\text{cm} \cdot \text{year}^{-1}$ ) that allows overall growth  
317 performance comparison across populations or species. The grey area represents embryos *in*  
318 *utero*. The black horizontal line indicates the size of the largest specimen ever captured (See  
319 also Table S1 and S2).

320 **Figure 3: Comparison of the African coelacanth growth rate characteristics to other**  
321 **marine fish under the various ageing hypotheses. A.** Auximetric plot of the coelacanth  
322 under the various ageing hypotheses (red diamond: annual circuli, light blue diamond: annual  
323 macro-circuli from present study; dark blue diamond: annual macro-circuli from previous  
324 study) relative to other taxonomic groups of marine fish species (solid circles; orange: tunas;  
325 purple: deep-sea sharks; green: roughies; grey: other fish species). The auximetric plane is the  
326 plane defined by two logarithmic axes representing the von Bertalanffy rate coefficient  $K$   
327 versus asymptotic total length  $TL_{\infty}$  where a population characterized by a set of von  
328 Bertalanffy growth parameters  $(TL_{\infty}, K)$  is represented by a point. Populations of a given  
329 species or species having similar growth characteristics will tend to form clusters of points  
330 that delimit the growth space of that species or group of species. 95% ellipses, i.e. contours  
331 enclosing 95% of the data points under the assumption of a bivariate-normal distribution, are  
332 drawn to illustrate the growth space of tunas (orange circle), deep-sea sharks (purple circle)  
333 and roughies (green circle) for better comparison. The auximetric plot allows comparison of  
334 species according to their speed of growth at a given asymptotic size (vertical direction) and  
335 according to their body size for a given speed of growth (horizontal direction). It also allows  
336 comparison of species in terms of their global growth capacity by superimposing isolines of  
337 the growth performance index  $\phi' = \log(K) + 2 \log(TL_{\infty})$  since these have a known slope of  
338 2 (dashed black lines labelled with the corresponding  $\phi'$  value). **B.** Growth performance  
339 index  $\phi' = \log(K) + 2 \log(TL_{\infty})$  of the coelacanth (diamonds) under the various ageing  
340 hypotheses (same colors as in A) relative to other taxonomic groups of marine fish species  
341 (boxplots; same colors as in A). Labelled vertical lines give the percentiles of the distribution  
342 of  $\phi'$  values across all marine fish species corresponding to the  $\phi'$  values of the African  
343 coelacanth under the various ageing hypotheses. Boxplots are defined as in Figure 1. Von

344 Bertalanffy growth parameters for other marine fish were extracted from FishBase in June  
345 2020 (1383 populations distributed across 1313 species).

346

347 **Figure 4: Locating the African coelacanth along the slow-fast life-history continuum in**  
348 **marine fish under the various ageing hypotheses. A.** Biplot of the two first axes of a  
349 Principal Component (PC) analysis on time-related life-history traits (von Bertalanffy rate  
350 coefficient  $K$ , sexual maturity age, maximum observed longevity and spawning  
351 frequency/inverse of gestation time) of marine fish after log<sub>10</sub>-transformation, removal of the  
352 effect of body size, centering and scaling. The coelacanth projection (diamonds) on the PC  
353 plane under the various ageing hypotheses (same colors as in Figure 3) can be compared to  
354 the projections of other taxonomic groups of marine fish species (solid circles; same colors as  
355 in Figure 3). The percentage of variance explained by the PCs is indicated between  
356 parentheses in axis labels. Arrows indicate how much each life-history trait contributes to  
357 each PC according to its projection on each PC axis and the angle between the arrows is  
358 indicative of the correlation between life-history-traits, orthogonality meaning independence  
359 and opposite directions meaning negative correlations. Clearly, the first PC corresponds to the  
360 slow-fast life-history continuum as it trades-off high longevity and late maturation on the left  
361 hand side against fast approach rate towards asymptotic length on the right hand side whereas  
362 the second PC mainly involves spawning frequency. **B.** Position of the coelacanth (diamonds)  
363 under various ageing hypotheses (same colors as in Figure 3) relative to other taxonomic  
364 groups of marine fish species (boxplots; same colors as in Figure 3) along the slow-fast life-  
365 history continuum (scores along PC1, panel A). Labelled vertical lines give the percentiles of  
366 the distribution of the scores along PC1 of all marine fish species that correspond to the scores  
367 of the coelacanth under the various ageing hypotheses. Boxplots are defined as in Figure 1.



368 Life-history traits for other marine fish were extracted from FishBase in June 2020 (147  
369 populations distributed across 131 species).

370

371

372

## 373 **STAR METHODS**

### 374 **RESOURCE AVAILABILITY**

#### 375 **Lead contact**

376 Further information and requests for resources should be directed to and will be fulfilled by  
377 the Lead Contact, Kélig MAHE (kelig.mahe@ifremer.fr)

#### 378 **Materials availability**

379 This study did not generate any reagents or other materials.

#### 380 **Data and code availability**

381 All data on coelacanth specimens are available in the Supplementary Material. Data on the  
382 other marine fish species were extracted from FishBase in June 2020 (see Key resources  
383 table). All data extracted and R codes supporting the current study have been deposited in  
384 SEANOE (<https://doi.org/10.17882/80498>).

### 385 **EXPERIMENTAL MODEL AND SUBJECT DETAILS**

386 Between 2 and 5 scales were sampled from the basal part of the first dorsal fin of coelacanth  
387 specimens from public natural history collections: two specimens of the Zoologischen  
388 Staatssammlung München (ZSM; The Bavarian State Collection of Zoology) and 25 of the  
389 Collections des pieces anatomiques en fluide from the Muséum National d'Histoire Naturelle  
390 de Paris (MNHN; The French National Museum of Natural History). For each specimen, we  
391 provide its inventory number of the institution that houses the collection and the Coelacanth  
392 Conservation Council (CCC) number<sup>17</sup> (See also Table S1). The specimens of the MNHN and  
393 ZSM are stored in 10% formalin and 70° alcohol, respectively. The MNHN's specimens are

394 conserved in the formalin since their capture and, with time, the un-buffered conservative  
395 solution became acid, which could have damaged the structure of some scales.

## 396 METHOD DETAILS

### 397 Sclerochronology

398 The coelacanth has an elasmoid-type scale that has evolved several times independently in the  
399 evolutionary history of fish. All scales were rehydrated and cleaned. After this preliminary  
400 step, they were photographed under transmitted light using a Zeiss microscope equipped with  
401 a camera to observe the series of concentric macroscopic circuli (macro-circuli). In a second  
402 step, they were photographed under polarized light microscopy in order to increase the  
403 contrast between structures. Polarized light microscopy reveals topographical details on  
404 anisotropic materials, including bio-calcified structures such as scales, which are difficult to  
405 observe under transmitted light. Polarized light revealed more numerous circuli, thinner than  
406 the macro-circuli and formed by alternating translucent and opaque bands suggestive of  
407 growth rate variation. Several scales were scanned using a micro-computed tomography  
408 scanner (CT scan) providing a high resolution 3-dimensional representation of the object. In a  
409 few cases, the structures on the scale were not distinguishable due to degradation by the  
410 formalin solution and thus scale interpretation was not possible in the corresponding  
411 specimens (See also Table S1).

412 The image processing was performed using the image analysis system TNPC (Digital  
413 processing for calcified structures) for pictures under both transmitted and polarized light.  
414 Two sclerochronology experts analyzed each scale by identifying macro-circuli under  
415 transmitted light and circuli under polarized light along the longest growth axis, i.e. from the  
416 proximal to the distal end of the scale (Figure 1). Several scales per specimen were used to  
417 obtain a robust estimate of the number of (macro-) circuli and thus of the age of the specimen  
418 under the assumption of an annual growth periodicity (see age validation method below).

419 Age validation method: Marginal Increment Analysis

420 Calcified structures in fish have the potential to grow throughout the life of the individual  
421 without resorption. Variations in the individual's body growth are translated into variations in  
422 the growth of the calcified structures. These variations are revealed by the optical properties  
423 of the bio-calcified material that appears either opaque or translucent. Hence, circannual  
424 rhythm in body growth and calcified structure formation produces an alternation of  
425 translucent and opaque bands on the latter. Pairs of translucent-opaque bands correspond to  
426 annual increments and can thus be used for ageing individuals. However, for using observed  
427 increments on calcified structures (here macro-circuli and circuli on coelacanth scales) to age  
428 individuals, it is necessary to validate their annual frequency of formation as any event  
429 affecting growth may produce such a mark (e.g. transition from endogenous to exogenous  
430 nutrition in larvae, migration, gestation, thermal shock). Such age validation is required for  
431 establishing the accuracy of an age estimation method<sup>31</sup>.

432 Marginal Increment Analysis (MIA) is the most commonly used age validation method  
433 and allows assessing the periodicity of increment formation in bio-calcified structures<sup>32</sup>. It is a  
434 quantitative approach that relies on a measure of the size of the increment under formation  
435 (named the marginal increment), i.e., the distance between the most recently formed (macro-)  
436 circuli and the edge of the scale, relative to the size of the last fully formed increment, i.e., the  
437 distance between the last-but-one and the most recently formed (macro-) circuli. In  
438 mathematical notation, the relative measure of the marginal increment, MI, is given by:

439 
$$MI = \frac{R_0 - R_n}{R_n - R_{n-1}}$$

440 Where  $R_0$  is the radius of the scale measured from its focus to the edge (Figure 1),  $R_n$  is the  
441 distance between the focus and the last (macro-) circuli formed  $n$ , and  $R_{n-1}$  is the distance  
442 between the focus and the last-but-one (macro-) circuli  $n - 1$ . If (macro-) circuli are formed

443 annually, the marginal increment MI will thus exhibit an intra-annual periodic pattern that can  
 444 be observed by plotting its measure against the date of its origin, i.e. the month at which the  
 445 specimen was captured. MI was measured for each specimen using macro-circuli under  
 446 transmitted light and circuli under polarized light and plotted against the month of capture. A  
 447 sinusoidal regression of MI against the month of capture  $m$  with a period of 12 months was  
 448 used to test for the annual periodicity of (macro-)-circuli formation after linearization:

$$449 \quad MI \sim a + b \sin\left(\frac{2\pi}{12}m + c\right) = a + b \sin(c) \cos\left(\frac{2\pi}{12}m\right) + b \cos(c) \sin\left(\frac{2\pi}{12}m\right) \quad (1a)$$

450  
 451 so that,

$$452 \quad MI \sim \alpha_0 + \alpha_1 \cos\left(\frac{2\pi}{12}m\right) + \alpha_2 \sin\left(\frac{2\pi}{12}m\right) \quad (1b)$$

453  
 454 with  $a = \alpha_0$ ,  $b = (\alpha_1^2 + \alpha_2^2)^{1/2}$ , and  $c = \arctan\left(\frac{\alpha_1}{\alpha_2}\right)$ .

455 The global significance of the linear regression provided a statistical validation for an intra-  
 456 annual pattern in (macro-) circuli MI. The classical assumptions of the linear models  
 457 (normality of, homoscedasticity of, and absence of trends in the residuals) were verified and  
 458 met.

#### 459 [Body growth models](#)

460 The mean body growth patterns of the sampled specimens obtained by interpreting scales  
 461 using macro-circuli and circuli were described using three different growth models including:

462 a) the von Bertalanffy<sup>33</sup> model:

$$463 \quad TL_t = TL_\infty - (TL_\infty - TL_1) \cdot e^{-K \cdot (t-1)} \quad (2)$$

464 b) the Gompertz<sup>34</sup> model:

$$465 \quad TL_t = TL_\infty \cdot e^{\ln\left(\frac{TL_1}{TL_\infty}\right) \cdot e^{-K \cdot (t-1)}} \quad (3)$$

466 c) the logistic model<sup>35</sup>:

$$467 \quad TL_t = \frac{TL_\infty}{1 + \left( \frac{TL_\infty}{TL_1} - 1 \right) * e^{-K \cdot (t-1)}} \quad (4)$$

468 Where  $TL_1$ ,  $TL_t$ , and  $TL_\infty$  are respectively the length at age 1, at age  $t$  and the asymptotic  
469 length, and  $K$  is the rate at which the asymptote is reached, called the rate coefficient in this  
470 paper. Notice that the models started at age 1 as no data was available for age 0 individuals,  
471 hence the age offset of 1 in the exponential:  $t - 1$ .

472 [Auximetric plot and growth performance comparison](#)

473 The body growth patterns obtained for coelacanth macro-circuli and circuli were compared  
474 with those of other marine species using two complementary approaches.

475 First, an auximetric plot<sup>36</sup>, which is a double logarithmic plot (base 10) of the von Bertalanffy  
476 growth model parameters  $K$  versus  $TL_\infty$ , was produced. Given that  $K$  represents the rate at  
477 which  $TL_\infty$  is reached in inverse time units whereas  $TL_\infty$  represents the size range of the  
478 species in size units, it is difficult to compare multiple growth patterns while accounting for  
479 both dimensions at the same time. In addition, the fact that  $K$  and  $TL_\infty$  are negatively  
480 correlated complicates the matter. The auximetric plot allows circumventing these difficulties.  
481 A population characterized by a set of von Bertalanffy growth parameters ( $TL_\infty, K$ ) is  
482 represented by a point and populations of a given species or species having similar growth  
483 characteristics will tend to form clusters of points that delimit the growth space of that species  
484 or group of species. Moreover, the auximetric plot allows the comparison of species according  
485 to their speed of growth at a given asymptotic size (vertical direction) and according to their  
486 body size for a given speed of growth (horizontal direction).

487 Second, the “growth performance index”<sup>36</sup> was computed:

$$488 \quad \phi' = \log_{10} K + 2 \log_{10} TL_\infty \quad (5)$$

489 This index has the interesting property of having the same dimension as a growth rate, i.e. size  
490 per unit time, and thus allows to compare the global growth performances across species. A

491 very high growth index would correspond to species growing fast to large sizes relative to  
492 species with a low one. Empirically, the index  $\phi'$  is shown to be distributed normally for  
493 populations of the same species or phylogenetically close species. Isolines of the index  $\phi'$  can  
494 be superimposed to the auximetric plot since these have a known slope of 2, thus allowing  
495 both approaches to be used at the same time.

496 Both approaches were used for the comparison of the coelacanth with other marine fish  
497 species. Von Bertalanffy parameters for the other marine fish species were extracted from  
498 FishBase in June 2020 (Popgrowth table<sup>18</sup>). Only populations for which size was measured as  
499 total length were kept for comparison, resulting in 1383 populations distributed across 1313  
500 species.

#### 501 [Slow-fast life-history continuum analysis](#)

502 The location of the coelacanth along the slow-fast life-history continuum<sup>12</sup> in marine fish was  
503 assessed using estimates of time-related life-history traits obtained from both macro-circuli  
504 and circuli ageing: the von Bertalanffy rate coefficient  $K$  ( $\text{yr}^{-1}$ ), the maximum observed  
505 longevity (yr), the age at first sexual maturity (yr), and the gestation duration (yr) transformed  
506 into a spawning frequency ( $\text{yr}^{-1}$ ). These four traits were extracted for other marine fish species  
507 from FishBase in June 2020 (Popgrowth, Species, Maturity, Fecundity and Spawning tables<sup>18</sup>)  
508 and were available together for 147 populations distributed across 131 species.

### 509 [QUANTIFICATION AND STATISTICAL ANALYSIS](#)

#### 510 [Body growth models](#)

511 For both macro-circuli and circuli ageing, the best growth model was identified as the one  
512 minimizing the small-sample, bias-corrected form of the Akaike Information Criterion  
513 ( $\text{AICc}^{37,38}$ ). The  $\text{AICc}$  balances the trade-off between the quality of fit and the number of  
514 parameters used<sup>38</sup> while accounting for small-sample bias and is defined as:

$$515 \quad \text{AICc} = 2k - 2 \ln(L) + \frac{2k(k+1)}{n-k-1} \quad (6)$$

516 where  $n$  is the sample size,  $k$  is the total number of parameters of the model and  $L$  is its  
517 likelihood.

#### 518 Slow-fast life-history continuum analysis

519 As time-related life-history traits are known to be affected by body size<sup>12</sup>, the four traits were  
520 regressed against asymptotic total length  $TL_{\infty}$  after log10-transformation of the five variables.  
521 A Principal Components (PC) analysis was then carried out on the residuals of the regressions  
522 of the four life-history traits after centering and scaling. The two first PCs explained 78.9% of  
523 the variation. A biplot on the plane defined by the two first PCs was produced in order to  
524 identify the slow-fast life-history continuum and to position the coelacanth life-history as  
525 estimated by the two ageing methods. The biplot represents both populations' projection on  
526 the PC plane as dots and life-history trait projection as arrows.

527 Statistical analyses and plots were performed using the following packages in the statistical  
528 environment R: Rfishbase<sup>39</sup>, ade4<sup>40</sup>, ggplot2<sup>41</sup>, factoextra<sup>42</sup>, ggpubr<sup>43</sup>.

#### 529 ADDITIONAL RESOURCES

530

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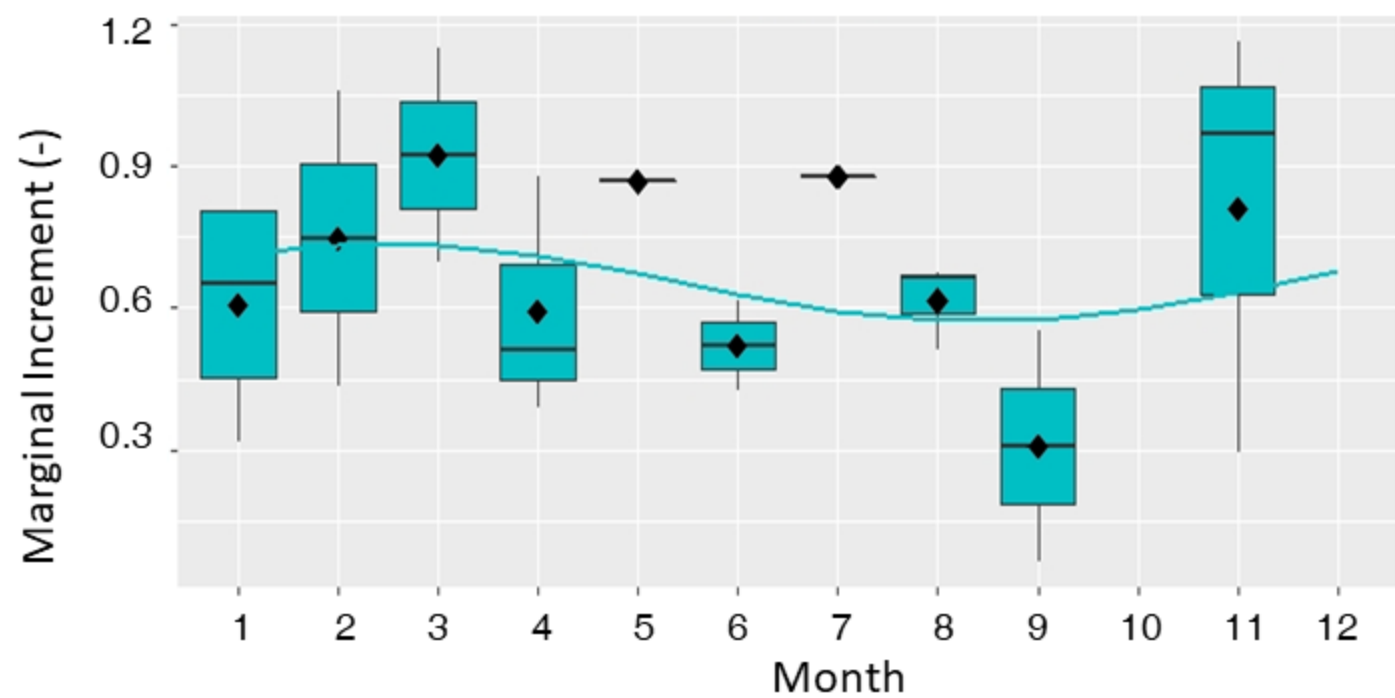
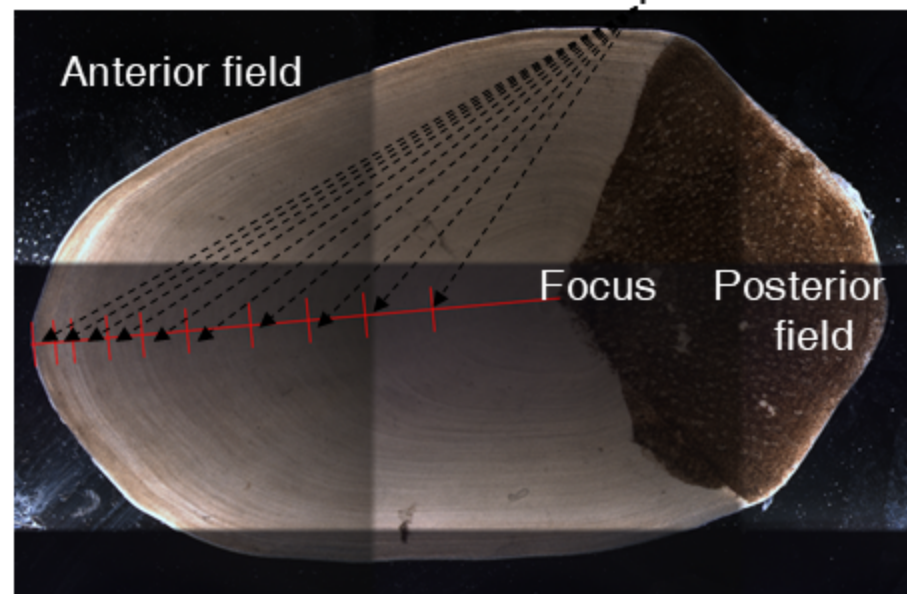
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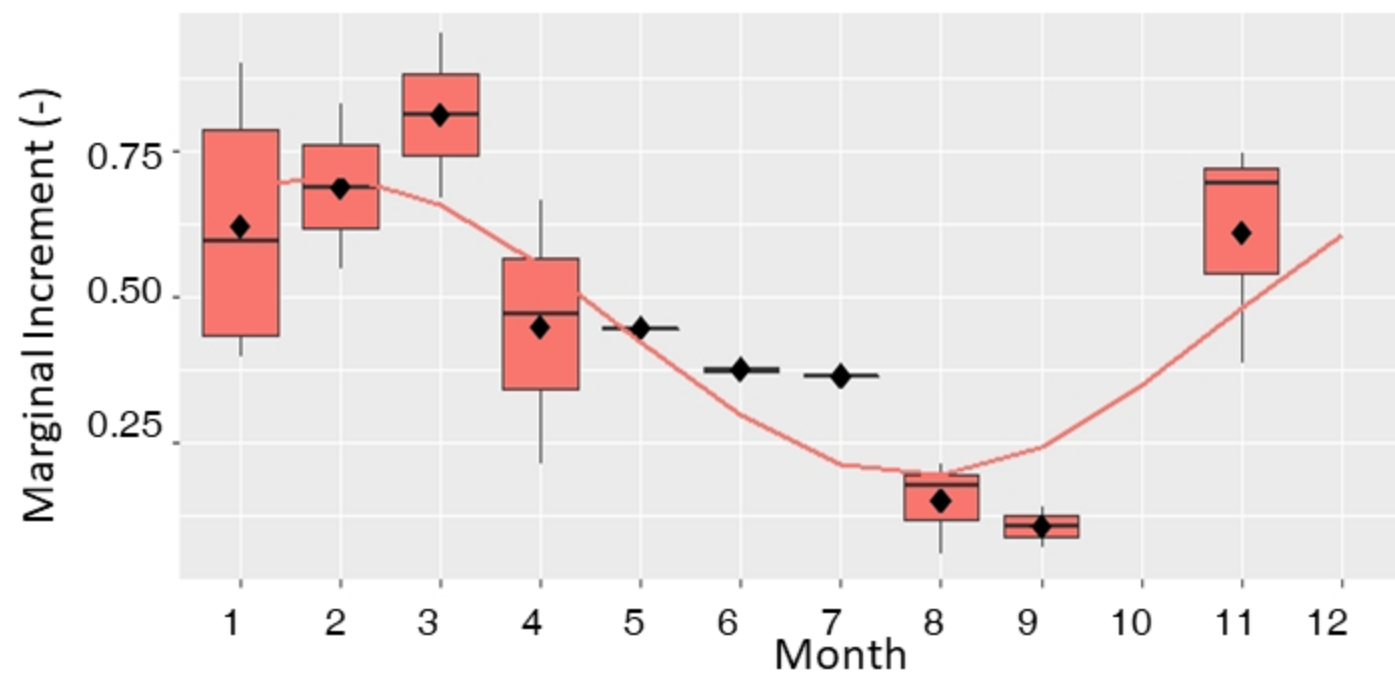
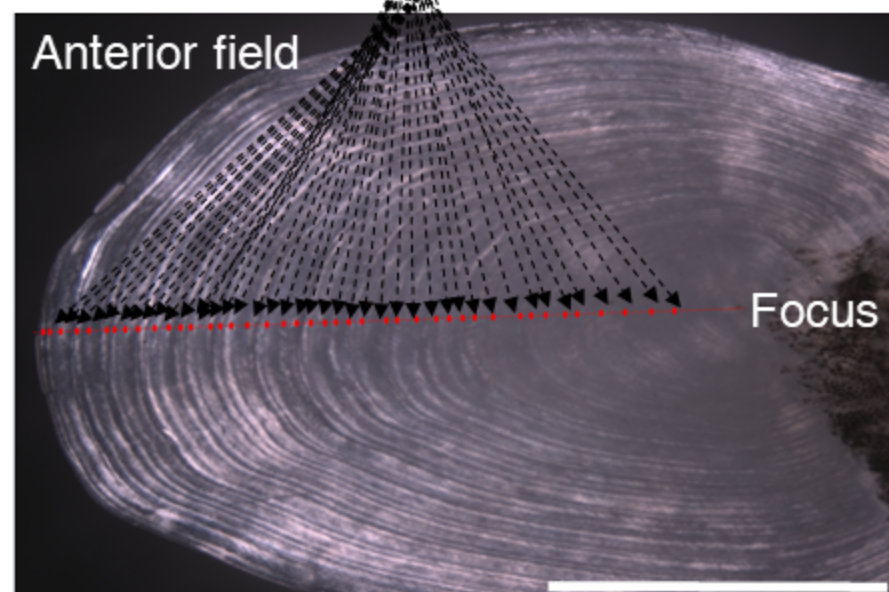
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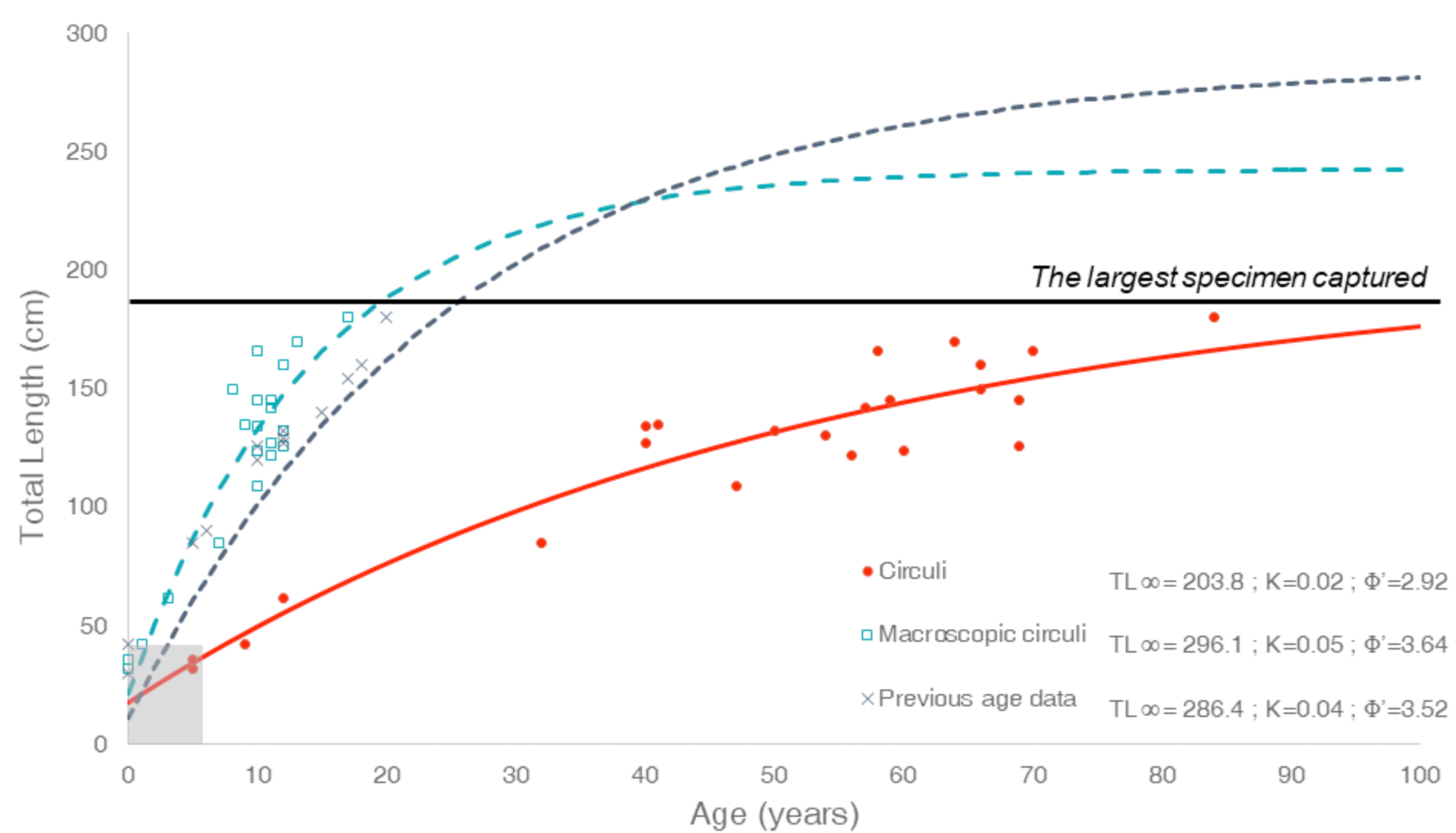
10 Macroscopic circuli

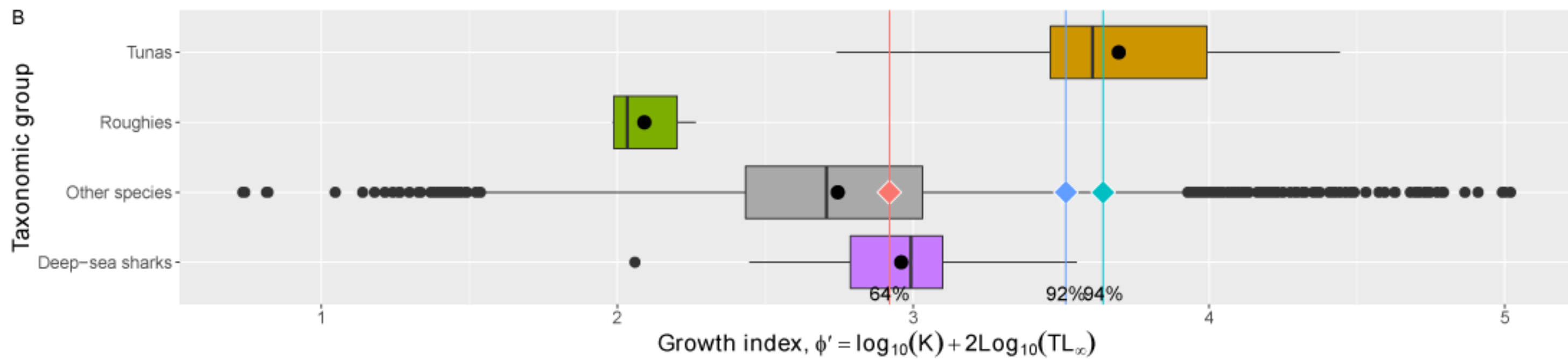
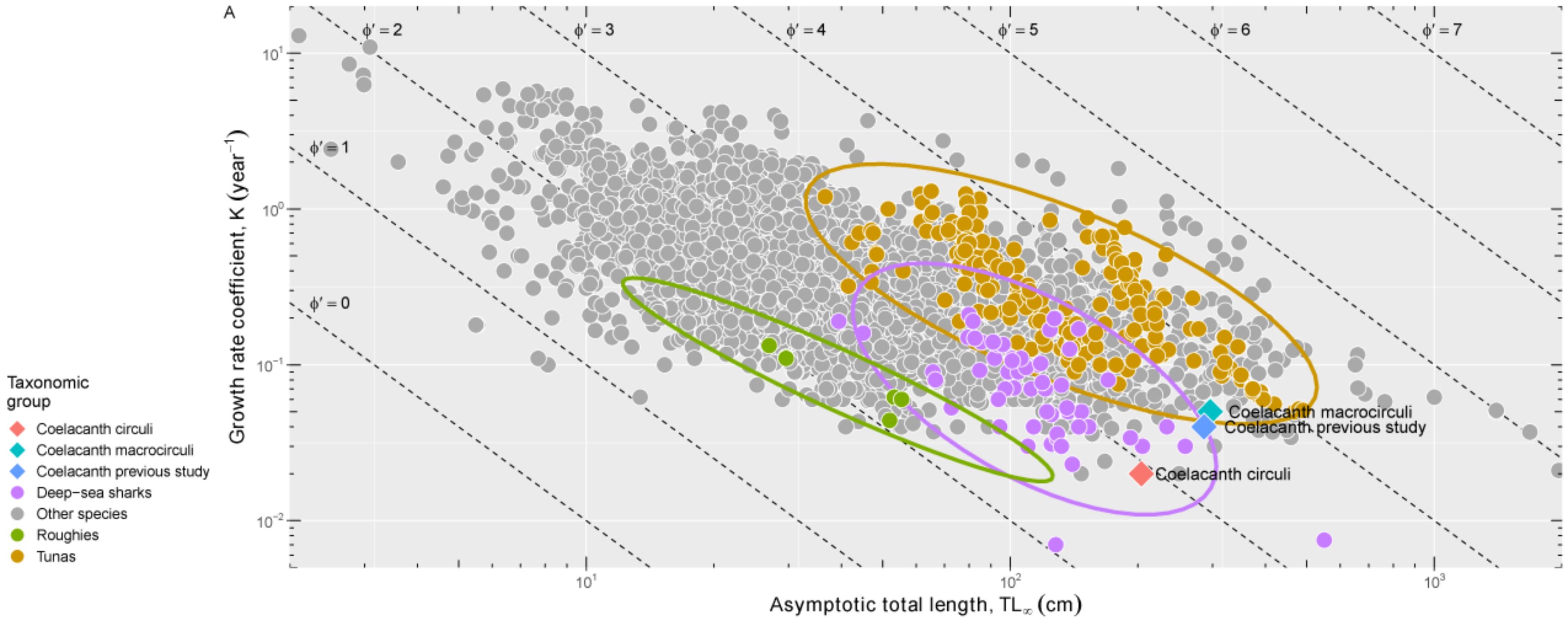


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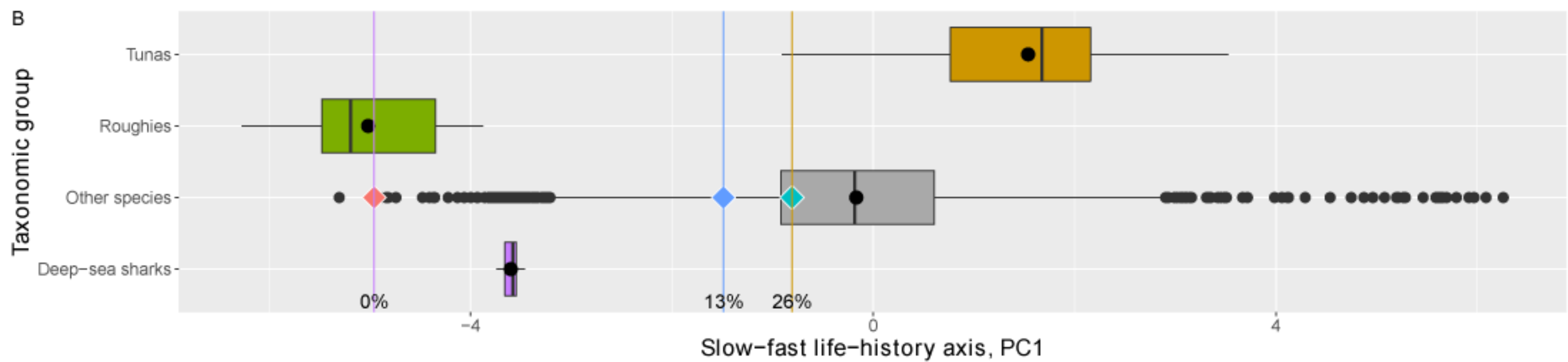
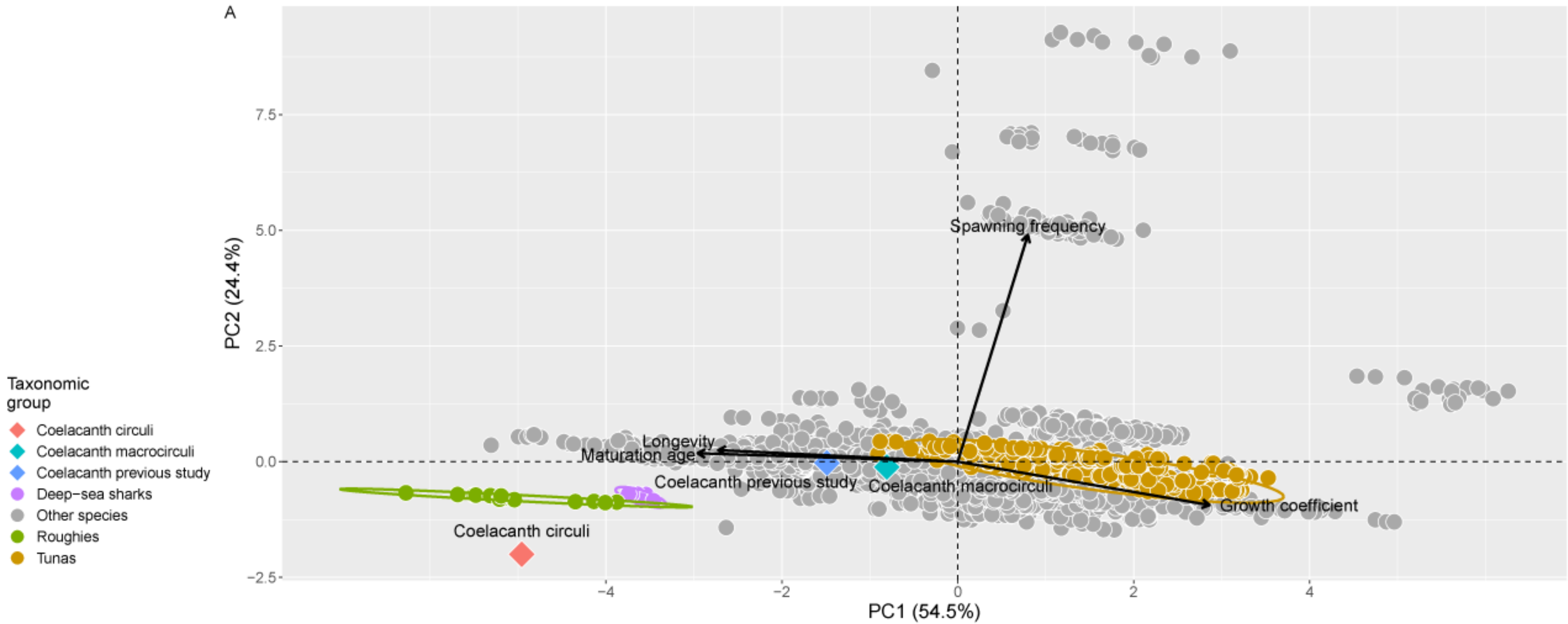
47 Circuli













**Earlier ageing**  
Transmitted light



**New ageing**  
Polarized light

Scale observation

Ageing validation

Life History Reappraisal

Length

190 cm

Slow growth

Long  
gestation

Late  
maturity

High  
longevity

5 yr

40 yr

70 yr

100 yr

Age

