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OPINION
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Why Coelacanths Are Almost “Living Fossils”?

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INTRODUCTION

Darwin pointed out that “species of different genera and classes have not changed at the same rate” (Darwin, 1859, chapter X). Besides, he coined the expression “living fossils” for lineages whose “new forms will have been more slowly formed, and old forms more slowly exterminated” (chapter IV), among other characteristics. This expression has become popular, but has sometimes been misunderstood as meaning that some organisms do not evolve. It has also been commonly used by paleontologists and evolutionary biologists to describe a general pattern of relative stasis in morphological evolution in some lineages. Darwin’s definition of the concept was imprecise and he considered that “species and groups of species, which are called aberrant, and which may fancifully be called living fossils, will aid us in forming a picture of the ancient forms of life” (Darwin, 1859, Chapter XIV). For more than 200 years, nevertheless, debates have raged on the definition of the concept (e.g., Bennett et al., 2017, 2018; Lidgard and Love, 2018; Turner, 2019), and more generally on the merits of its use in the life sciences (e.g., Casane and Laurenti, 2013; Naville et al., 2015). Although Darwin (1859) cited several taxa of fish as examples of “living fossils,” he did not mention the coelacanths, or actinistians, which were only known as fossils at his time. Huxley, however, soon after (1866) noticed the low anatomical disparity of coelacanths throughout their history. Since that time, and especially after the discovery of the living *Latimeria* in 1938 (Smith, 1939), the coelacanth has become an iconic symbol of the “living fossil” due to the slow morphological evolution illustrated by the fossil record of the clade, and its supposed affinities with tetrapods. Only the question of evolutionary rate is addressed here, not the question of ancestral status or other “living fossil” characteristics attributed to coelacanths. The low rate of evolution based on a lasting generalist morphological Bauplan has been confirmed by most subsequent authors who have worked on the group (Schaeffer, 1952; Cloutier, 1991; Forey, 1998; Schultze, 2004; Zhu et al., 2012; Cavin and Guinot, 2014), knowing that there are also exceptions to this general Bauplan (e.g., Friedman and Coates, 2006; Wendruff and Wilson, 2012; Cavin et al., 2017). However, part of the community of researchers working on fossil and living coelacanths avoids using this expression.

Most twenty-first century genetic studies have confirmed that the substitution rate of the genome of *Latimeria* was found to be slower than that of other vertebrate lineages in the mitochondrial (Sudarto et al., 2010; Nikaido et al., 2011; Lampert et al., 2012; Kadarusman et al., 2020) as well as in the nuclear genome (Nikaido et al., 2013) at least for the genes encoding proteins (Amemiya et al., 2010, 2013), when measured in substitution per year, although alternative interpretations remain (Bockmann et al., 2013; Casane and Laurenti, 2013; Grandcolas et al., 2014; Minelli and Baedke, 2014; Naville et al., 2015). It should be noted that although there is evidence for active transposable dynamics in the *Latimeria* genome (Smith et al., 2012; Chalopin et al., 2014; Naville et al., 2015), these elements have found to be highly conserved (Smith et al., 2012). The fact that at the level of transposable element activity, the coelacanth genome does not reveal slow dynamics (Chalopin et al., 2014) is thus not related to the global substitution rate.

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RATE OF EVOLUTION

The debate over the concept of "living fossils," in the sense of slowly evolving organisms, is part of a larger research agenda dealing with the rate of evolution. The rate of morphological evolution is usually measured as a unit of change per generation time (Haldane, 1949; Gingerich, 2001; Evans et al., 2012), while molecular evolution is usually measured as substitution rate per site per year (e.g., Lanfear et al., 2010). Substitution rates are affected by evolutionary and life history traits, such as population size, body size, mutation rate, and generation time (Martin and Palumbi, 1993; Pulquerio and Nichols, 2007; Thomas et al., 2010). Among these factors, generation time imposes a minimum time for the transmission of the genome throughout the generations, in particular when it carries mutations under selection. In order to control for this critically important factor when modeling gene evolution over time, substitution rates are generally given per generation rather than per year (Loewe and Hill, 2010). This allows, for instance, to compare gene dynamics in a population genetics or in a macroevolutionary context assuming that species have similar generation times (Vinciguerra and Burns, 2021). However, when studying the tempo of evolutionary change through time across species within a broader evolutionary framework, molecular evolution is usually given as a function of the number of years or rather million years instead of generations (Folk et al., 2019; Yohe et al., 2020). First discussed in the early 1990s (Ohta, 1993), the relationship between molecular evolution and generation time is actually more complex than expected, notably given that other factors are also at work. Among those is the number of germline cell divisions per generation (Lynch, 2010). For instance, the number of germ line divisions per generation varies greatly among mammalian species: while the human male germline is estimated to have 401 cell generations over an individual's lifetime, the male mouse germline has an average of only 62 (Drost and Lee, 1995; Bromham, 2011)—meaning that the number of copy errors per generation is expected to be more than 6 times higher in humans than in mice. As each cell division in the germline is expected to face the same mutation rate, this difference thus partly buffers the difference in generation time between humans and mice in an attempt to compare their molecular evolution across millions years. In her seminal review, Bromham (2011) points to factors, which in addition to differences in generation time and number of copy errors per generation in the germline, also affect rates of molecular evolution. Among those are the DNA damage level induced by metabolic and environmental energy. For instance, endothermic vertebrates that use metabolism to maintain a constant body temperature (birds and mammals) have higher absolute rates of molecular evolution than ectothermic vertebrates, such as reptiles and ray-finned fish (Martin et al., 1992). Another factor pointed by Bromham is body size and longevity, which might directly trigger selection for DNA repair mechanisms and thus lower levels of molecular evolution (Promislow, 1994). The impact of fecundity on molecular evolution might be driven by a similar selective process in which selection to reduce the rate of harmful mutations would be stronger in species producing smaller number of offspring per year (Welch et al., 2008). Additional factors encompass population sizes, with species characterized by smaller populations experiencing larger molecular evolutionary rates, owing to faster rates of fixation in arising mutations (i.e., substitution rates) along the selection-drift equilibrium (Charlesworth, 2009).

DISCUSSION

Neither the generation time nor the number of copy errors per generation in the germline can be easily identified in non-model species. These life history traits, as well as others such as fecundity or metabolic rates, also cannot be identified when dealing with extinct taxa, in which only a few life history traits are accessible to paleontologists. Some parameters affecting molecular evolution rates can, however, be identified directly on fossil material, such as body size, or can be indirectly inferred, such as generation time. Starting from the importance underlined above of the generation time in the estimation of the nucleotide substitution rate, and evolution rate in general, recent studies shed new light on a probable cause of the slow rate of evolutionary change in the coelacanth lineage.

In a new analysis of the growth lines on a set of scales of *L. chalumnae*, Mahé et al. (2021) showed that the lifespan in this species is probably around 100 years, the sexual maturity reached about 50 years old at the earliest (49–69), and the gestation time lasts around 5 years. Accordingly, the time before genetic transmission between generations is 54 years at minimum. This is 12.5 times longer that an average time calculated for a set of actinopterygian species (4.4 years when 50% of individuals attain their first reproduction years calculated on 215 individuals from 98 populations of 76 species) and 4.2 times longer that an average time calculated for a set of shark species (13 years calculated for 19 individuals from 11 populations of 9 species) (He and Stewart, 2001) (**Figure 1A**). In addition to longevity and body size, the slow gestation time might select for DNA repair mechanisms more strongly than in actinopterygians and chondrosteans. So far, no analysis has estimated the number of copy errors per generation in the germline but any other parameter considered equivalent, the evolutionary rate of *Latimeria* is slower in the same proportion compared to the other two clades, i.e., more than 10 times slower than ray-finned fish and almost 5 times slower than sharks. The discovery by Mahé et al. (2021) is limited to *Latimeria* among coelacanths, and it has been hypothesized that this life history trait is associated with the stable environments in which these animals live (Cupello et al., 2019). However, Mesozoic coelacanths lived in a variety of marine and freshwater aquatic environments that were very different from the extant mesobenthic habitat, and the stable environmental conditions are not enough to explain a slow rate of evolution.

There are exceptions to the slow evolutionary pace observed in Mesozoic coelacanths. For instance, morphological outliers from the generalist coelacanth Bauplan, such as the Middle Triassic *Foreyia*, may have resulted from heterochronic evolution caused by a change in the expression of developmental

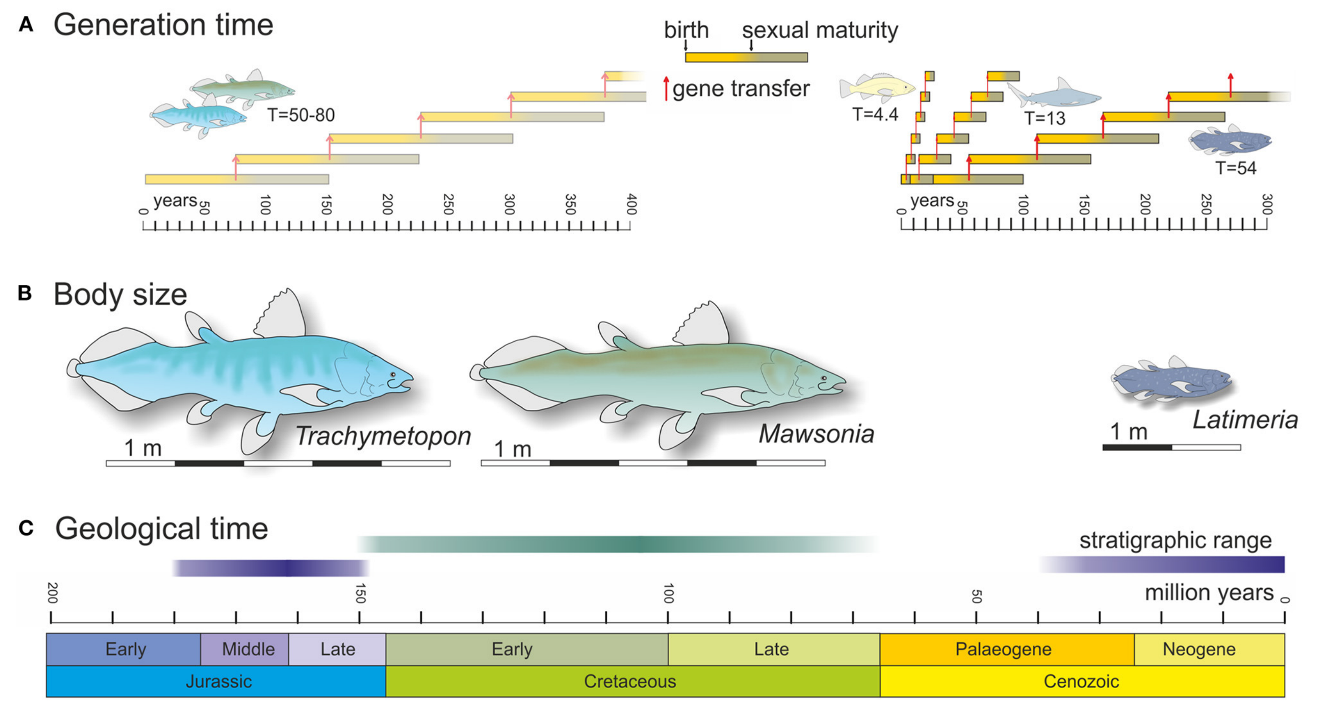

FIGURE 1 | Selected life history traits and stratigraphical range for *Latimeria* and two Mesozoic mawsoniid coelacanths, *Trachymetopon* and *Mawsonia*. **(A)** Generation time for *Latimeria* (from Mahé et al., 2021), and for actinopterygians and sharks (from He and Stewart, 2001) (right), and estimated for extinct *Trachymetopon* and *Mawsonia* (left). **(B)** Body size of *Latimeria*, *Trachymetopon* and *Mawsonia* (from Cavin et al., 2021a). **(C)** Stratigraphical ranges of *Latimeria*, *Trachymetopon* and *Mawsonia* (from Cavin et al., 2021b).

patterning genes (Cavin et al., 2017). But overall, new fossil data shows that Jurassic and Cretaceous coelacanths from the mawsoniid family, the sister family to the latimeriids, also evolved morphologically very slowly and probably had a very long generation time, as expressed by their giant body size, and this despite living in coastal marine, brackish and freshwater environments (Cavin et al., 2021a). The marine genus *Trachymetopon*, which reached about 5 m in length, stretched from the Toarcian to the Kimmeridgian of Europe, during about 30 million years, while the Late Jurassic to Late Cretaceous *Mawsonia*, which occurred in brackish and fresh waters from western Gondwana and North America, and reached 5.3 m in length, lasted from 50 to 80 million years as revealed by the identification of some specimens from the Late Cretaceous (Cavin et al., 2021a,b) (**Figures 1B,C**). Although there is no direct way to estimate fecundity and metabolic rates, as well as the age of sexual maturity on these extinct forms, the large body size attained by these coelacanths indicates that the first two of these parameters were likely low and the third likely high. If *Latimeria*, which barely reached 2 m in length can reach 100 years, the giants *Trachymetopon* and *Mawsonia* may have lived centuries to reach 5 meters in body length. Following the comparison, sexual maturity should have been reached even later in these giants than in *Latimeria* (**Figure 1A**). These points are partly speculative, but they might explain why these Mesozoic genera have spanned tens of millions of years with almost no morphological change. More generally, long generation and gestation times may explain the slow morphological evolution of coelacanths through deep times, without necessarily introducing other physiological or environmental peculiarities.

AUTHOR CONTRIBUTIONS

LC and NA contributed equally to the analysis of the data and to the writing of the manuscript. All authors contributed to the article and approved the submitted version.

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