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Longevity in Cave Animals

Enrico Lunghi and Helena Bilandžija*

Division of Molecular Biology, Institut Ruđer Bošković, Zagreb, Croatia

An extraordinary longevity has been observed in some cave species, and this raised the hypothesis that a longer lifespan may be considered one of the characteristic traits of these animals. However, only a few cave species have been studied thus far, and a firm conclusion remains to be drawn. Here we review the available knowledge on the longevity of subterranean species, point out the limitations of previous studies, and provide suggestions for future studies to answer important questions regarding the longevity in cave animals, its adaptive value and the related promoting factors. We also argue that studying the longevity in cave animals will contribute to the field of aging, especially to understanding the evolution of this phenomenon.

Keywords: adaptation, biospeleology, cave biology, lifespan, senescence, subterranean, troglobite, convergent evolution

Edited by:
Hope Klug,
University of Tennessee
at Chattanooga, United States

Reviewed by:
Oana Moldovan,
Emil Racovita Institute of Speleology,
Romanian Academy, Romania
Gabriel-Ionut Plavan,
Alexandru Ioan Cuza University,
Romania

***Correspondence:**
Helena Bilandžija
helena.bilandzija@irb.hr

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INTRODUCTION

With their unique ecological setting, subterranean environments are theaters of evolutionary processes that lead to fascinating adaptive traits in the species able to colonize them (Mammola, 2019). All subsurface habitats are characterized by a common feature, the absence of light (Culver and Pipan, 2014, 2019). Light can only penetrate and affect the area surrounding their connections to the surface (Lunghi et al., 2015; Culver and Pipan, 2019), limiting the effects of seasonality and the circadian cycle in deeper zones, a condition that contributes to highly stable microclimate characterized by high humidity and constant temperatures (Biswas, 2009; Lunghi et al., 2015). Without sunlight, photosynthetic processes are absent (Culver and Pipan, 2019), what leads to a strong reduction of the available organic matter, and therefore the subterranean food web is largely dependent on inputs of allochthonous organic material from the surface (Schneider et al., 2011; Barzaghi et al., 2017). This scarcity of food resources results in reduced abundance of species at all levels of the food web (Venarsky et al., 2014; Culver and Pipan, 2019; Manenti et al., 2020).

Colonization of subterranean environments by aboveground species is accompanied by numerous changes in their phenotypic traits (Hervant et al., 2001; Bilandžija et al., 2020; Lunghi and Zhao, 2020). The hallmarks of adaptation to subterranean environments are loss of eyes and pigmentation, which are so common in subterranean taxa that they are used as diagnostic traits to assess the degree of adaptation to these environments (Howarth and Moldovan, 2018; but see Lunghi et al., 2014). Some of the other conspicuous adaptive traits in subterranean species include elongation of body appendages, increase in fat stores, overexpression of mechanosensory and chemosensory systems (Jeffery, 2009; Bilandžija et al., 2012; Gonzalez et al., 2017). Although most obvious, morphological adaptations often represent the final chapter in a story that began with the behavioral and physiological changes that accompanied the early stages of cave colonization (Culver et al., 1995; Pigliucci et al., 2006; Bilandžija et al., 2020).

In this review we explore a poorly known aspect of subterranean species: their longevity. Among subterranean taxa, individuals with exceptional longevity have occasionally been reported (e.g., Voituron et al., 2011; Puljas et al., 2014), raising the idea that the dark passages within the earth harbor animals with extended lifespans. Over the years, most studies have aimed to estimate the age and lifespan of cave species (e.g., Trajano, 1991; Voituron et al., 2011; Puljas et al., 2014), but very few in a comparative framework that included a surface relative (Poulson, 1963). Ultimately, it has yet to be proven whether higher longevity is indeed a characterizing trait of subterranean animals, and eventually whether such trait is adaptive. Here, we review what is known about the longevity of subterranean species and provide recommendations for future studies to experimentally test whether these animals show higher longevity compared to their surface relatives and what the potential promoting factors might be.

LONGEVITY IN SUBTERRANEAN SPECIES

The limited information on the lifespan of cave species mostly comes from the few species that have been successfully reared in laboratory facilities (Poulson, 1963; Miaud and Guillaume, 2005; Hinaux et al., 2011; Voituron et al., 2011; Bichuette and Trajano, 2021). Animals kept under controlled conditions enable tracking their growth and development of specific growth rate curves can provide age estimates for wild populations (Brunkow and Collins, 1996; Gallo and Jeffery, 2012). However, controlled conditions may differ from those found in natural environments and may alter growth rates of individuals (Trajano, 1997; Simon et al., 2017). Luckily, growth rates can be estimated also in the wild for species that are marked (e.g., Lunghi and Bruni, 2018; Lunghi et al., 2019) and recaptured over time (Taddei Ruggiero, 2001; Venarsky et al., 2012; Balázs et al., 2020; Lunghi et al., 2022), or when individuals show reliable age marks (Simon et al., 2017; Riddle et al., 2018).

One of the most iconic cave species is the olm, *Proteus anguinus*, an aquatic salamander distributed in the Dinaric karst in the South-Eastern Europe (Sket, 1997; Gorički et al., 2017). Because it is extremely difficult to study *Proteus* in the wild (Buzzacott et al., 2009; Balázs et al., 2020), most of the available knowledge comes from captive observations (Juberthie et al., 1996; Ipsen and Knolle, 2017; Aljančič, 2019). This neotenic salamander has a slow development, becoming sexually mature after 14 years and reproducing every 12.5 for at least 50/60 years (Voituron et al., 2011; Ipsen and Knolle, 2017). The oldest known individual has an age between 48 and 58 years (Voituron et al., 2011). Given its slow growth rate and low reproductive activity, the average lifespan of the olm should be around 70 years, although some individuals can live more than 100 years (Bulog et al., 2000; Voituron et al., 2011). In comparison, the closest aboveground relatives are from the North American genus *Necturus*, and the longevity of *Necturus maculosus* has been estimated at 34 years (Petranka, 1998). Interestingly, the olm's small size, metabolic rate comparable to other salamanders, and lack of increased antioxidant activity are in stark contrast to the predictions of aging theory, which foresee higher lifespan in larger species with low metabolic rate and high antioxidant activity (Blanco and Sherman, 2005; Voituron et al., 2011).

Cavefish are within the best-studied subterranean animals, yet only a few studies on their lifespan exist. For example, the Mexican tetra, *Astyanax mexicanus*, is probably one of the widest used model species in cave biology (Wilkens, 1988; Rétaux and Casane, 2013; Keene et al., 2015; Jeffery, 2020), but reliable information on the potential lifespan of this species is missing. We know from captive breeding that both surface and cave forms of *A. mexicanus* can reach the age of 15 (Riddle et al., 2018). There is a divergence in growth rate and age distribution between several populations of cave and surface forms (Simon et al., 2017). Specifically, the range of estimated ages of fish was greater in cave populations (2–8 years) than in surface populations (2–5 years), and there is variability in age distribution even between cave populations (Simon et al., 2017). In another comparative study, Poulson (1963) used the scale and otolith to age five amblyopsid fishes, two surface species, *Chologaster cornuta* and *Forbesichthys agassizi*, and three subsurface, *Typhlichthys subterraneus*, *Amblyopsis spelaea*, and *A. rosae*. The results showed a higher lifespan in cave fishes, where the age of older individuals ranged from 3 to 7 years, up to three times more than for the surface fishes (Poulson, 1963). A similar age for *A. rosae* (about 4–5 years) has been estimated in another study (Brown and Johnson, 2001). However, more up to date techniques indicate a potential lifespan of 20–30 years for these cavefish (Poulson, 2001). For the Brazilian *Ancistrus cryptophthalmus*, an initial estimate determined a lifespan of 8–10 years (Trajano and Bichuette, 2007), while a subsequent study extended it to more than 15 years and provided evidence that the longest-lived individuals can live up to 20–25 years (Secutti and Trajano, 2009). An estimate of lifespan based on growth rate exists also for some other cavefish from the tropics: *Pimelodella kronei* (10–15 years; Trajano, 1991), *Trichomycterus itacarambiensis* (7 years; Trajano, 1997), *Caecobarbus geertsii* (9–15 years; Heuts, 1952; Proudlove and Romero, 2001), and *Ituglanis passensis* (>10; Secutti and Trajano, 2021). No comparable information on closely related surface species exists for these Brazilian cavefish; however, in comparison with other cyprinids (data from AnAge database; Tacutu et al., 2018) these species are among the longer living ones.

Studies in cave invertebrates also yielded extraordinary estimates of their lifespan. An analysis of the growth line formation in the shells of the cave bivalve *Congeria kusceri* found that the average lifespan was about 30 years. Importantly, authors also showed that growth lines form annually despite animals residing in stable underground waters (Puljas et al., 2014). The oldest individual in this study, a 14.3 mm long male, had an impressive lifespan of 53 years (Puljas et al., 2014). However, other studies have found much larger individuals, so the lifespan of this and possibly other *Congeria* species is likely much higher (Morton, 1969; Bilandžija et al., 2013). The average lifespan of other dreissenid species ranges between 2 and 5 years (Puljas et al., 2014), implying that cave bivalves have evolved lifespans 10 times longer than their surface relatives. As with *Proteus*, this is contrary to predictions which suggest that larger animals have longer lifespans (Blanco and Sherman, 2005), as *Congeria* is one of the smaller dreissenids. However, its slow growth rate and low investment in reproduction (Morton and Puljas, 2013) are consistent with disposable soma theory of aging (Kirkwood, 1977) which suggests a tradeoff between the investment in the reproduction and somatic maintenance; the latter leading to lifespan increase. Similarly, analysis of growth rate of the brachiopod *Neocrania anomala* from marine caves estimated that its lifespan may exceed 40 years (Taddei Ruggiero, 2001). The lifespan of *N. anomala* is about three times higher than *Waltonia inconspicua* and *Terebratalia transversa*, brachiopods that can reach a maximum age of 15 and 13 years, respectively, (Paine, 1969; Rickwood, 1977). Age estimation of an extinct brachiopod, *Gigantoproductus okensis*, indicates that this species could have lived up to 20 years (Angiolini et al., 2012), which is half of the lifespan estimated for the cave *N. anomala* (Taddei Ruggiero, 2001).

A capture-mark-recapture study conducted over 5 years provided important information on the lifespan of the crayfish *Orconectes australis* (Venarsky et al., 2012). Using growth rate data, the authors were able to re-evaluate the lifespan for this species, which was incorrectly estimated to be 100 years, and found out that the species can live over 22 years (Venarsky et al., 2012). In addition, these authors compiled a list of crayfish species for which lifespan estimates exist (see Table 2 in Venarsky et al., 2012), including two additional cave species: *O. inermis* (9–10 years), and *Procambarus erythrops* (>16 years). Of the 10 surface cambarids included in the list, one has an estimated lifespan of 13 years, while the others ≤7 years. Similar results have been obtained for other cave crustaceans. Based on the distribution of body size, Pacioglu et al. (2020) suggested that the lifespan of *Gammarus balcanicus* might exceed that of epigean gammarids, which have lifespan estimates of about 1 year. In another study, Magniez (1975) estimated that the cave *Stenasellus virei* can reach an age of 12–15, a lifespan up to 20 times longer than epigean congeneric species. Furthermore, a 40-year study performed by Carpenter (2021) showed that *Bahalana geracei* has probably the longest known lifespan (ranging from 24.5 to 35 years) among isopods. Capture mark recapture studies showed that the cave beetle *Laemostenus schreibersi* can reach the remarkable age of >6.5 (Rusdea, 1994), almost doubling

TABLE 1 | Summary of the lifespan data for cave species collected in this review.

Species	Average lifespan	Maximum lifespan	References
Vertebrates			
Proteus anguinus	70	>100	Voituron et al., 2011
Speleomantes italicus		25	Lunghi, 2022
Calotriton asper	∼12	16–19	Miaud and Guillaume, 2005
Astyanax mexicanus	2–8	15	Simon et al., 2017, Riddle et al., 2018
Typhlichthys subterraneus	1–2	4 (20–30)	Poulson, 1963, Poulson, 2001
Amblyopsis spelaea	2–5	7 (20–30)	Poulson, 1963, 2001
Amblyopsis rosae	2–3	4 (20–30)	Poulson, 1963, 2001
Ancistrus cryptophthalmus	15	20–25	Secutti and Trajano, 2009
Pimelodella kronei	6	10–15	Trajano, 1991
Trichomycterus itacarambiensis	7	7	Trajano, 1997
Ituglanis passensis		>10	Secutti and Trajano, 2021
Caecobarbus geertsii		9–13 (<15)	Heuts, 1952, Proudlove and Romero, 2001
Invertebrates			
Congeria kusceri	30	53	Puljas et al., 2014
Neocrania anomala		>40	Taddei Ruggiero, 2001
Orconectes australis		>22	Venarsky et al., 2012
Orconectes inermis		9–10	Retreived from Venarsky et al. (2012)
Procambarus erythrops		>16	Retreived from Venarsky et al. (2012)
Gammarus balcanicus		>1	Pacioglu et al., 2020
Stenasellus virei		12–15	Magniez, 1975
Bahalana geracei		24.5–35	Carpenter, 2021
Laemostenus schreibersi		>6.5	Rusdea, 1994

Data is shown in years and refer to both observed and predicted species average and maximum lifespan.

the maximum lifespan observed for epigean ground beetles (Lövei and Sunderland, 1996).

All information on cave species lifespan collected in this review are summarized in **Table 1**.

Although bats are not strictly bound to subterranean habitats, as they use caves primarily for sheltering purposes and do not exhibit classic cave-related adaptations (Howarth and Moldovan, 2018; Sadier et al., 2020), it is worth mentioning this animal group in the context of longevity, as they are the longest-lived mammals relative to their mass (Podlutsky et al., 2005; Wilkinson and Adams, 2019). Interestingly, cave use predicts the evolution of longevity in several bat lineages (Wilkinson and South, 2002; Salmon et al., 2009).

CONCLUSION AND FUTURE DIRECTIONS

The information assembled here suggests that longevity can indeed be considered a characteristic of cave animals. However, additional systematic studies encompassing a broader range of animal groups in a comparative framework which includes surface and cave relatives are needed to fortify this conclusion. The main remaining questions are: (1) is longevity adaptive for subterranean lifestyle or did it evolve as a physiological consequence of other adaptive traits, (2) what components of the subterranean environment contribute to the evolution of life extension in resident animals, and (3) what are the molecular and developmental mechanisms that lead to convergent evolution of longevity in cave organisms. Several hypotheses can be made regarding the links of aging with other cave adaptive traits and the characteristics of subterranean environments that may be promoting it. For example, adaptive traits in caves such as slower growth, lower metabolic rate and lower investment in reproduction, have been associated with increased lifespan (Flatt and Schmidt, 2009). Further, many environmental features of caves such as limited food resources (Aspiras et al., 2015), lower extrinsic mortality (lack of predators; Plath and Schlupp, 2008), hypoxia (Boggs and Gross, 2021; van der Weele and Jeffery, 2022) and lack of UV irradiation (Körner et al., 2006), are consistent with known ecological predictors of longevity (Speakman and Selman, 2011; Flament et al., 2013; Omotoso et al., 2021). These nonexclusive hypotheses can be tested using model systems that have closely related species or populations in caves and on the surface, have a reliable method for estimating their age, and can survive in the laboratory to be used for experimental perturbations.

Although important to understand the life history characteristics of subterranean species (e.g., sexual maturity, reproductive potential; Poulson, 1963; Lunghi et al., 2018; Lunghi, 2022), growth rate curves may not be the best method to estimate species ages. First, species generally do not grow indefinitely and their growth rate can only be estimated during a particular phase of their life cycle (Venarsky et al., 2012; Lunghi, 2022). A clear example of this is the aforementioned crayfish *Orconectes australis*, whose lifespan has been reduced by a factor of four using better-tuned methods (Venarsky et al., 2012). Another limitation to using this method stems from the ecological differences between cave and surface populations. For example, low availability of nutrients in subterranean environments (Huntsman et al., 2011; Culver and Pipan, 2019; Pacheco et al., 2020) strongly influences species growth (Simon et al., 2017). Without rearing cave and surface relatives under the same conditions, it is difficult to distinguish intrinsic from extrinsic effects on lifespan.

The use of molecular biomarkers of aging (e.g., SA-β-Gal, 4-HNE, or lipofuscin staining; Nelson et al., 2012; Dimri et al., 1995) may overcome some of these limitations. In addition to allowing reliable assessment of lifespan differences between subterranean and surface species, the use of markers for relevant physiological and molecular processes will enable following the basic processes underlying aging as well as the assessment of variability in aging on population or species levels (Robins et al., 2017).

Studies on cave animals may also provide important insights into the biology of aging, particularly in the areas of evolution and genetics of aging. One of the greatest challenges in the field of aging is to uncover the genes and processes that cause lifespan differences among species (Partridge and Gems, 2006). Because of the known direction of evolution -from surface to cave- and the ability to compare ancestral form with derived form, cave dwellers provide a rich source of information about mechanisms that lead to slowing rates of aging in nature. Knowledge of these mechanisms could be of great benefit and have implications for human welfare. Because of well-defined environmental characteristics and numerous convergently evolved physiological and life-history adaptations, the study of aging in cave dwellers can shed light on how longevity covaries and co-evolves with other organismal and environmental traits.

Aging is a complex phenotype, so it is important to incorporate research on nontraditional and atypical species and integrate approaches from multiple biological disciplines (Cohen, 2018). How and why senescence evolves in natural populations and how to maintain health in old age is still a major issue in contemporary biology. We propose that studies of aging in cave-adapted animals can provide new and original insights into how nature has solved the problem of extending lifespan.

AUTHOR CONTRIBUTIONS

EL drafted the manuscript. Both authors conceived the study and critically revised the manuscript.

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