Sensory Adaptations of Fishes to Subterranean Environments

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Caves and other subterranean habitats represent one of the most challenging environments on the planet. Other than salamanders, bony fishes are the only vertebrate group that has successfully colonized and are completely restricted to those habitats. Despite being known to science for over 150 years, only recently have cavefishes become model systems for evolutionary studies. Several cavefishes, such as the Mexican characid Astyanax mexicanus, *have provided valuable insights into how fishes have evolved to cope with life in perpetual darkness and often-limited food resources. Much less is known about the biology of other cavefishes and their sensory modalities. Here, we summarize the current understanding of nonvisual sensory modalities in cavefishes. Enhancement of mechanosensation appears to be the most common adaptive strategy, but little is known of other sensory modalities in these fishes. Only comparative studies nested within well-resolved phylogenies will clarify the sensory adaptation of fishes to subterranean habitats.*

Keywords: comparative, evolution, neurobiology, cave, troglomorphy

Subterranean organisms remain one of the least understood faunas in the world. This is partly explained by the difficulty in exploring and sampling the natural cavities below the surface of the Earth. Subterranean habitats are generally categorized into one of three main types: cave habitats, interstitial habitats, and superficial subterranean habitats (seeps, talus slopes, and small cavities in the uppermost areas of karst rocks; Culver and Pipan 2009). Caves are the best-known subterranean habitats, and most cavefishes occur in them. Animals that live in continually dark subterranean habitats are faced with unique challenges and require sophisticated solutions in order to locate and identify food, predators, and each other. Without vision, novel navigation strategies must also be adopted. Aside from darkness, several other abiotic factors influence subterranean ecosystems, such as relatively stable temperature, high humidity, and hydrological factors, such as periodic flooding (Culver and Pipan 2009). These factors have probably led to major constructive changes in behavior and phenotypes in organisms permanently restricted to subterranean habitats.

Organisms that are obligate residents of subterranean habitats are known as *troglobites*. These animals are no longer able to survive aboveground and have evolved unusual and highly specialized morphological and life history traits, termed *troglomorphy* (Christiansen 1962). Many independent lineages of troglobites have evolved regressive features, such as the loss or reduction of eyes and pigmentation, but also constructive traits, such as longer appendages and enhancements of nonvisual sensory systems (Culver and Pipan 2009). Other organisms are transient or semipermanent visitors to subterranean habitats and typically do not exhibit the same degree of troglomorphy that troglobites do. Some of these animals can complete their life cycles on the surface or underground but have not evolved troglomorphic traits. Others are only occasional visitors, using subterranean habitats for some aspect of their life histories, such as to shelter from harsh environmental conditions on the surface or to breed. Cave-roosting bats that rest during the day in caves but emerge at night to feed on the surface are an excellent example.

Although many species that exhibit differing levels of troglomorphy and adaptation can be found in subterranean habitats, here, we will focus on true troglobites—and cavefishes in particular. The continual darkness of caves and other subterranean habitats imposes a sensory constraint that offers a unique opportunity to examine not only how these nonvisual sensory modalities become transformed but also how they coevolve. Aquatic cave organisms, such as cavefishes, not only survive in perpetual darkness but also negotiate the challenges of an aquatic environment. Variation in water volume and flow can be large in subterranean streams, especially during floods. High flow can wash fish downstream deeper underground or out onto the

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surface. Farmers in some provinces in China, for example, report finding cavefishes in their rice paddies every rainy season. Torrential flash floods in Ecuador make the environment extremely hostile to any aquatic subterranean life, and yet, a population of cave-dwelling naked sucker-mouthed catfishes (Siluriformes: Astroblepidae) persists (Haspel et al. 2012). Such variation in water level and flow, however, along with more subtle changes in pH and temperature, may be important cues for reproduction during seasonal flood events for many cave animals (Culver and Pipan 2009).

Trophic factors may act as significant selective pressures for the evolution of behavior and sensory adaptations in subterranean organisms. Because of the absence of light, there is no photosynthesis in caves, and chemosynthesis rarely supplies much trophic support (Culver and Pipan 2009). Consequently, many cave systems are resource limited. With few exceptions, cave communities rely on external organic matter, typically from dissolved and particulate organic carbon transferred from the surface hydrologically (Simon and Benfield 2001) or from animals that fall or wander into caves and die, to drive cave ecosystems. In addition, the regular movement of animals into and out of caves, such as colonial bats that produce guano piles, may be particularly important in several otherwise energy-limited cave systems. These allochthonous resources often drive the community dynamics in subterranean ecosystems (Hüppop 2000, Huntman et al. 2011), which tend to have few trophic levels. Cavefishes are typically top predators in their subterranean ecosystems. In general, little is known about the abiotic characteristics of the caves inhabited by most cavefishes. The few ecological studies on this topic have included only basic measures, such as pH and water temperature, and in only two have time-series studies been conducted that characterized cavefish habitats (Trajano 1991, 1997). To our knowledge, these data have never been incorporated into studies of sensory neurobiology.

Cavefishes

Ray-finned fishes are the most diverse vertebrate class extant today (class Actinoptergyii). Of the approximately 32,000 global fish species (Eschmeyer 2013), over 300 have been reported to live in cave and other subterranean habitats, with more than 170 species living exclusively in freshwater caves and associated subterranean habitats and exhibiting some degree of troglomorphy. Cavefishes exhibit considerable phylogenetic and geographical diversity, representing 10 orders and 22 families and occurring on every continent but Europe and Antarctica (figure 1; Proudlove 2006, 2010). Obligate cave inhabitation has evolved many times, with the greatest cavefish diversity in the orders Cypriniformes (78 spp.) and Siluriformes (57 spp.). At the family level, the cypriniform families Cyprinidae (minnows; 40 spp.) and Balitoridae (loaches; 36 spp.) and the siluriform families Trichomycteridae (pencil catfishes; 19 spp.) and Heptapteridae (three-barbeled catfishes; 14 spp.) are most diverse (Proudlove 2010). The greatest species richness is found in China, followed by Brazil and Mexico (Proudlove 2010, Ma and Zhao 2012). Interestingly, regions of cavefish diversity do not necessarily correspond with regions of great biodiversity of other aquatic troglobites (Trajano 2001).

Although cavefishes are among the most well-known troglobites, there have been few comparative studies in which their ecology and sensory biology were investigated. This is likely because many cavefishes occur in habitats that are difficult to access or are in regions with few local resources for researchers, and most studies have been focused on describing new taxa and resolving systematic relationships. China, for example, has the greatest diversity of cavefishes in the world, with over 105 described species (Romero et al. 2009, Chen et al. 2010, Zhao et al. 2011), yet little is known regarding those species' habitats, ecology, behavior, and sensory biology. Most studies that have been published on this subject are written in Chinese and are of limited availability in Western libraries. Consequently, the cavefish literature is dominated by studies on a few Western species, predominately the blind Mexican characin (*Astyanax mexicanus*; Characiformes: Characidae, formally *fasciatus*; for reviews, see Jeffery 2008, 2009), followed by North American amblyopsids (Percopsiformes: Amblyopsidae; Niemiller and Poulson 2010, Niemiller et al. 2013). The two systems are complementary, because in the case of *Astyanax*, cave and surface morphs represent intraspecific variation, whereas in the amblyopsids, related species that live in caves or on the surface represent interspecific relationships. Furthermore, in few cavefish studies (less than 4%, according to Trajano [2001]) have aspects of ecology been examined. Most ecological studies have been conducted by Trajano and colleagues and have been concentrated on Brazilian cavefishes (for a review, see Trajano and Bichuette [2010]).

Cavefishes are uniquely suited for the comparative study of sensory neurobiology evolution, because (a) fish in general are a well-studied group from neurosensory perspectives; (b) many lineages around the world have independently evolved an obligate, cave-adapted existence allowing for natural replication; (c) their evolution covers varying timescales, from just tens of thousands to several million years; (d) the directionality of ecological shifts are known (from a surface environment to a cave); (e) their evolution can be directly linked to environmental conditions (e.g., the absence of light); and (f) compared with many other subterranean organisms, cavefishes are easier to capture, because their larger size and pale coloration make them conspicuous. Much of the interest in cave-adapted species is due to the fascinating suite of morphologies that enable those species to survive in caves. Their lack of eyes and pigmentation, elongated fins and increased numbers of skin sensory organs, such as taste buds and neuromasts, are all convergent traits that permit cavefishes to survive in subterranean habitats.

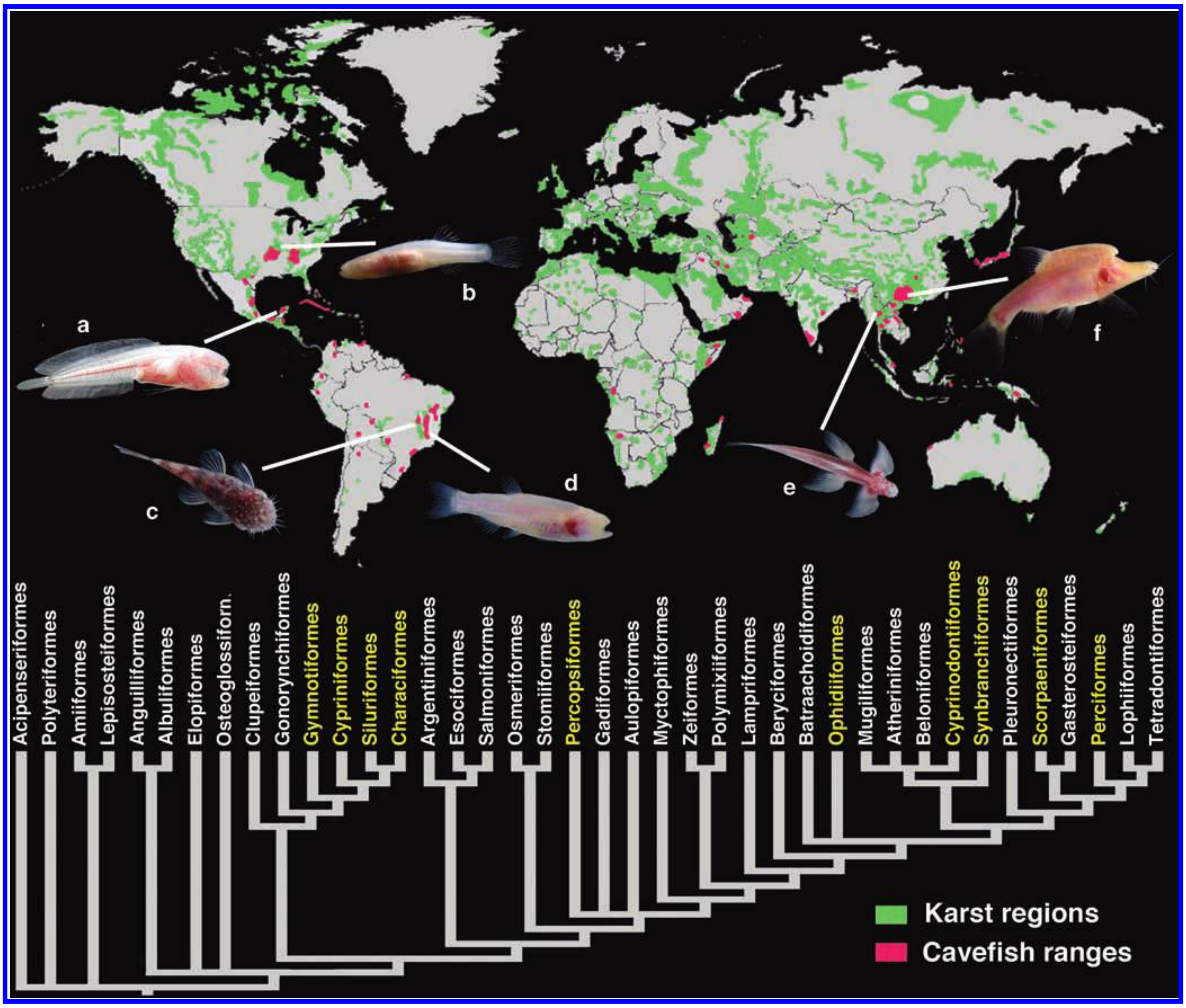

Figure 1. Cavefishes are known from 10 teleost fish orders (highlighted in yellow) and occur on every continent but Europe and Antarctica: (a) **Typhliasina pearsei** *(Ophidiiformes: Bythitidae) from Mexico. (b)* **Troglichthys rosae** *(Percopsiformes: Amblyopsidae) from the United States. (c)* **Ancistrus cryptophthalmus** *(Siluriformes: Loricariidae) from Brazil. (d)* **Stygichthys typhlops** *(Characiformes incertae sedis) from Brazil. (e)* **Cryptotora thamicola** *(Cypriniformes: Balitoridae) from Thailand. (f)* **Sinocyclocheilus furcodorsalis** *(Cypriniformes: Cyprinidae) from China. Sources: The karst regions were modified from those in Williams and Ford (2006), and the phylogenetic relationships are based on those in Li and colleagues (2008). Photographs: Thomas M. Iliffe (a) and Dante B. Fenolio (b–f).*

Cavefish sensory neurobiology

The physical characteristics of a habitat influence the evolution of sensory structures (Collin and Pettigrew 1988, Schellart 1992). It is likely that variation among cave habitats contributes to different types of sensory specializations. The association between habitat and sensory morphology has been examined in many species of surface fish. Morphological sensory diversity is high in fishes and is partly explained by a higher number of accessible sensory modalities in aquatic environments that result from the physical properties of water. It is generally agreed that the relative size and distribution of peripheral endorgans correlate with those of the related brain regions and that all three are a measure of the relative importance of a particular sensory modality in the species. Most surface fishes rely on vision and have a correspondingly large optic tectum. Cavefishes, on the other hand, have evolved to rely on other sensory modalities for behavioral decisions, which has given rise to distinct brain morphologies.

Mechanosensation. *Mechanoreception* refers to the sensation of mechanical stimuli, such as direct physical contact or the movement of the surrounding environment (e.g., sound or pressure waves in air or water). In aquatic habitats in which vision is limited, the mechanosensory lateral line system plays a critical role in sensing of the environment in teleosts. In cavefishes, and also in surface fishes, the lateral line system provides important information on water currents, for prey detection, and for hydrodynamic imaging (figure 2; Poulson 1963, Montgomery et al. 2001). The lateral line contribution to rheotaxis in *Astyanax* has a much lower threshold for the behavior in the presence of an olfactory cue (Baker and Montgomery 1999). Baker and Montgomery (1999) emphasized the interactive relationship between sensory modalities to direct and organize behavior.

Anatomically, the lateral line system consists of numerous sensory structures, called *neuromasts*, situated within recessed fluid-filled subepidermal canals (*canal neuromasts*) or externally on the skin (*superficial neuromasts*). Each neuromast comprises several hair cells (and associated nonsensory support cells), with bundles of cilia embedded in a gelatinous cupula. Water movement causes displacement of the cupula, and the cilia of the hair cells triggers an action potential.

Most of our knowledge of cavefish lateral line systems is from studies of the Mexican cavefish *Astyanax* and researchers of this species have made important contributions to the understanding of lateral line systems in general (Montgomery et al. 2001). The cave form of *Astyanax* not only has many more neuromasts than do its surface counterparts (figure 2c; Montgomery et al. 2001, Windsor et al. 2008, Sharma et al. 2009, Yoshizawa et al. 2010), but it has also evolved an adaptive behavior to enhance mechanosensory sensitivity. *Astyanax* has evolved a form of active sensing in which it uses a kick-and-glide swimming style to generate a relatively stable, dipole-like flow signal during the glide phase of the swimming cycle (Sharma et al. 2009, Patton et al. 2010). With this strategy, *Astyanax* uses the distortions of nearby obstacles in the self-generated flow field to sense those obstacles and spends more time gliding when investigating a new object (Patton et al. 2010). Cave amblyopsids also have more superficial neuromasts that are larger and that have longer cupulae (figure 2b) than their surface relatives, which allows the detection of moving prey at a greater distance than their surface relatives (Poulson 1963, Niemiller and Poulson 2010).

Cavefishes share this hypertrophy of the mechanosensory lateral line system with most deep-sea pelagic fishes. Because of the vastness and large water column of the pelagic environment, deep-sea fishes are able to rely on undisturbed pressure waves and low levels of background noise (Coombs and Braun 2003, Coombs and Van Netten 2005). Neither

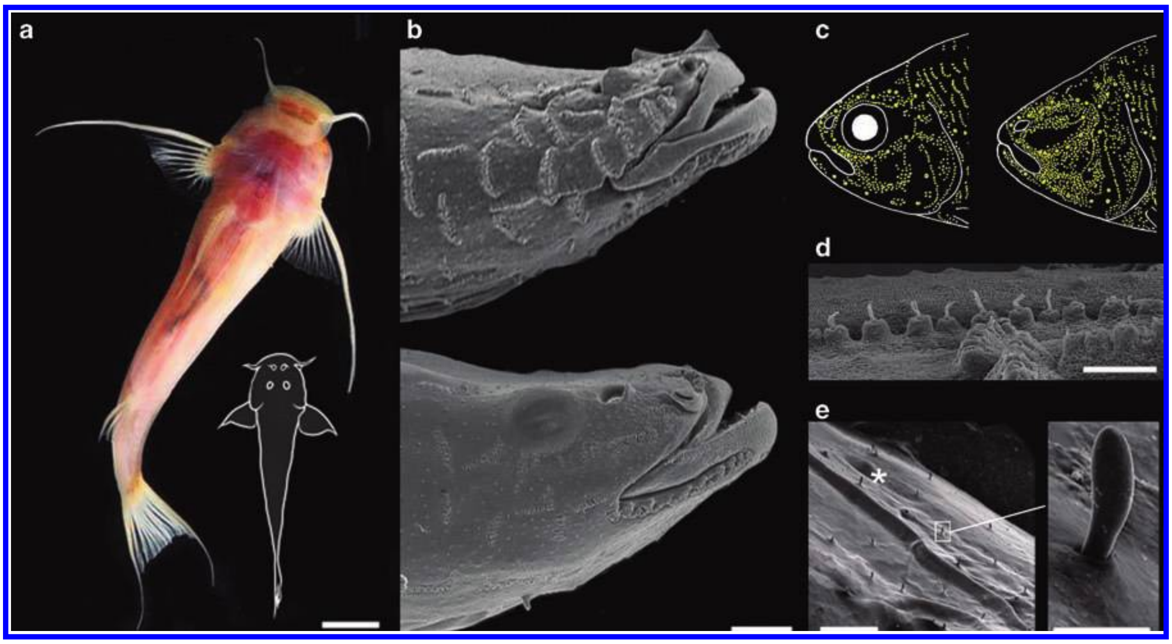

Figure 2. Mechanosensory specializations in cavefishes. (a) **Astroblepus pholeter** *showing longer barbs and fins than those of surface species (the insert diagram is of* **Astroblepus mancoi***; the scale bar represents 1 centimeter for the cavefish and 2 centimeters for the surface fish). (b) Lateral lines of cave (***Amblyopsis spelaea***) and surface amblyopsids (***Chologaster cornuta***). The scale bar represents 1 millimeter (mm). (c) Distribution of superficial and canal neuromasts in surface (left) and cave (right)* **Astyanax mexicanus***. (d) Close up of superficial neuromasts in* **Amblyopsis spelaea***. The scale bar represents 25 mm. (e) Mechanosensory skin denticles of* **Astroblepus pholeter***. The asterisk (*) indicates a vestigial eye. The scale bars represent 1 mm in the left image and 100 mm in the right. Photographs: Daphne Soares.*

characteristic is found in caves. Therefore, other evolutionary forces must underlie the evolution of mechanosensation in cavefishes.

Some cavefishes also have longer appendages (such as fins and barbels) than their surface counterparts, which they use to explore their environment. Cavefishes may use elongated fins (figure 2a), particularly pectoral fins, to touch obstacles and other objects, and they use this tactile information along with hydrodynamic imaging to sense their environment (Windsor et al. 2008). Another unusual mechanosensory strategy used by cavefishes is the use of skin teeth to detect current flow. Haspel and colleagues (2012) demonstrated that the cave loricarioid catfish *Astroblepus pholeter* has adapted not only to complete darkness but to life in fast, turbulent water. This species has unusually few neuromasts but shows a hypertrophy of mechanosensory skin denticles along the dorsal surface of the head and trunk (figure 2e). This fish is endemic to a single cave that contains a fast outgoing stream, which often becomes torrential after sometimes daily heavy rains. The direction of water flow is detected by deflection of the denticles, and the proximity to the substrate can be detected by changes in fluid velocity. This is the first report of a mechanosensory role of denticles and of a nonneuromast mechanosensory adaptation to subterranean habitats in fishes.

Hearing. Hearing is an important sense for aquatic organisms. Water is a better conductor of sound than air because of its greater density and allows for hearing over greater distances. In water, sound is composed of two distinct physical components—pressure waves and the motion of particles—which differ in the way in which they reach the hearing organ of fishes. The inner ear in ray-finned fishes consists of three fluid-filled chambers—the lagena, sacculus, and utriculus—which contain areas of sensory epithelium lined with sensory hair cells and overlain by otoliths. The otoliths of all fishes directly detect the particle-motion component. This is an outcome of inertial differences between sensory epithelia and the heavier otoliths. Because most fish tissues are of similar density to water, sound waves travel through fish at an amplitude and frequency that are similar to those at which they travel through the surrounding water. However, otoliths are denser than the rest of the fish's body and vibrate at an amplitude and a phase different from those of the sensory epithelium, and this difference causes the hair cells of the sensory epithelium to move, which triggers action potentials and the detection of sound. Ray-finned fishes have evolved accessory hearing structures to enhance hearing for greater sensitivity and a wider frequency range. The pressure component of sound can be detected indirectly through these specialized accessory anatomical structures. Other unique structures include a close connection between the swim bladder and the inner ear and *Weberian ossicles*, which are a modification of the anterior four or five vertebrae into movable bones that connect the inner ear to the swim bladder. Weberian ossicles are characteristic of otophysans, which account for two-thirds of freshwater fish diversity (Nakatani et al. 2011).

Enhancement of hearing abilities appears be adaptive in caves for several reasons, including working in association with other nonvisual senses to detect prey, conspecifics, or predators. In addition, because many cave systems are prone to dramatic changes in water levels and velocity caused by episodes of heavy precipitation, having greater sensitivity to detect sounds caused by flowing water at a greater distance allows these fish more time to seek shelter and reduces their risk of being washed out of a cave system, injured, or killed. However, the degree to which hearing abilities are enhanced, if they are at all, in cavefishes is largely unknown, because behavioral and neurophysiological studies on the acoustical biology of cavefishes have been extremely limited. In only two studies have the hearing profiles of cavefishes and those of surface fishes been compared. Popper (1970) showed that in *Astyanax*, there are no differences in hearing between cave and surface forms, because both forms have thresholds as low as those reported for other otophysan fishes (the minimum threshold is 1000 hertz [Hz]). No differences were found between the cave and surface forms of the molly *Poecilia mexicana* (family Poecillidae; Schulz-Mirbach et al. 2010). Both forms have greatest sensitivity between 200 and 300 Hz. Interestingly, Schulz-Mirbach and colleagues (2010) reported different otolith morphology between forms, which did not seem to affect general auditory sensitivity or hearing behavior. Although many fishes, including several cavefish-containing clades, have evolved a diversity of sound-generating mechanisms for acoustic communication (Ladich 2000), acoustic communication has yet to be demonstrated in any cavefish.

In an unpublished study, Niemiller and colleagues examined the relationship between background noises in cave habitats and the ability of cavefishes to detect auditory signals. In that study, the researchers compared the auditory brain stem responses of three species of amblyopsids and the acoustic profiles of their subterranean habitats. Cave amblyopsids have lost not only their eyes but also a significant portion of their hearing range. These fishes are unable to hear frequencies higher than 800 Hz, unlike their surface relatives, which hear up to 2 kilohertz. Congruent audio recordings from their home caves show that streams and water droplets from the ceilings of cave passages create loud, high-frequency background noise, generally above 800 Hz. These findings raise the intriguing possibility that cave amblyopsids may have lost hearing at high frequencies in response to the noisy acoustic environments in which they live.

Chemoreception. The senses of taste (gustation) and smell (olfaction) play important roles in many aspects of fish biology, including feeding, orientation, conspecific recognition, reproduction, and escape from predators. These senses may be particularly important to the detection of limited food resources and the location of potential mates during the breeding season in the complete darkness of caves.

Olfaction is accomplished through the binding of odorants to olfactory receptors in the olfactory epithelium, which is often highly folded as lamellae and arranged in rosettes located within paired olfactory sacs. Several cavefishes show increases in the number of lamellae and in the overall surface area of their olfactory epithelium relative to their surface relatives (figure 3; Jeffery 2008, Niemiller and Poulson 2010). In addition, cavefishes often have larger olfactory bulbs in the brain (Jeffery 2008, Niemiller and Poulson 2010). In the cave *Astyanax*, the region of the brain that processes chemoreception in the telencephalon is enlarged by 40% relative to that of the sighted morph (Peters et al. 1993). However, it remains to be seen whether these morphological changes translate into increased olfactory sensitivity or discrimination capabilities. Studies are needed to address whether cavefishes possess greater olfactory sensitivities than related surface fishes, whether olfactory sensitivities are indeed correlated with the surface area of the olfactory epithelium, and whether distantly related cavefish species that share a common ecology exhibit similar sensitivities.

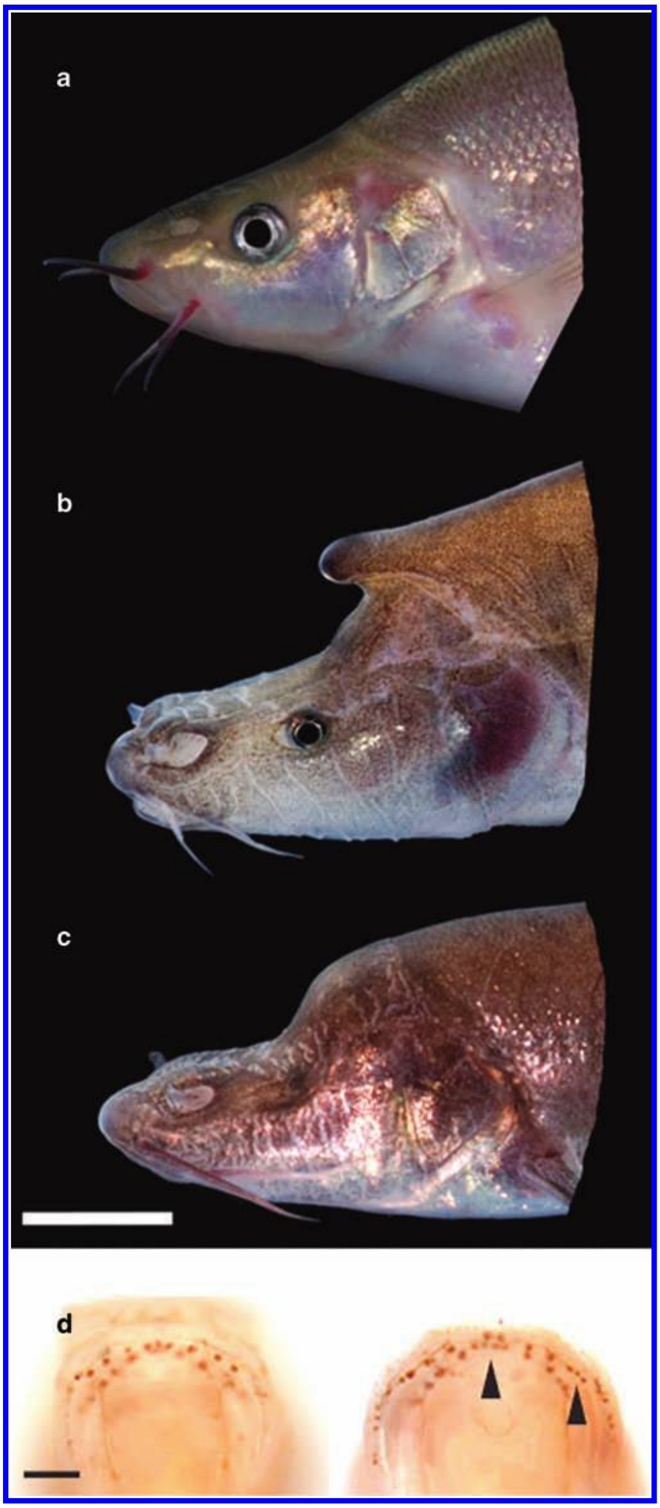

Figure 3. Chemosensory characteristics of three species of **Sinocyclocheilus***: (a)* **Sinocyclocheilus brevis***,* *(b)* **Sinocyclocheilus tileihornes***, and (c)* **Sinocyclocheilus anophthalmus***. Several cave-adapted species (b and c) exhibit hypertrophy of the olfactory rosettes relative to related surface species (a), which may be associated with greater olfactory sensitivity. The scale bar represents approximately 1 centimeter. Photographs: Dante B. Fenolio. (d) Calretinin-stained taste buds of surface (left) and cave (right)* **Astyanax mexicanus***. The scale bar represents 100 millimeters. Source: Adapted from Yamamoto and colleagues (2009).*

A large number of cavefishes belong to families that have prominent chemosensation, such as catfishes, but locating an odor source at a distance is not trivial in water because information transmitted through chemosensory channels is often complex. Therefore, sensitivities for individual substances may be high for dissolved chemicals, which are spread by turbulent flow and diffusion (Atema 1988).

Gustation is important for the location and identification of food and can be a very highly developed sense in some teleost lineages, such as cyprinids (minnows). Taste buds are the receptor organs of gustation; are bulbous in shape; and consist of receptor, supporting, and basal cells. Taste buds are primarily distributed on the epithelia of the lips, mouth, pharynx, and gill arches and around the head, but some species, such as catfishes, also have concentrations of taste buds located on well-developed barbels or even distributed all over their bodies and fins. In *Astyanax*, the gustatory system is expanded in the cave morph and is largely evident in an increase in taste bud density along the lips, pharynx, and ventral surface of the head, often with a five- to sevenfold increase in the number of taste buds (Schemmel 1967, Varatharasan et al. 2009, Yamamoto et al. 2009). In addition, taste buds contain more receptor cells, are innervated by more axon profiles, and have an accelerated rate of development relative to those in the surface morph (Boudriot and

Reutter 2001, Varatharasan et al. 2009). The cave *Astyanax* uses a different feeding posture from the surface morph's to better facilitate foraging on the bottom of cave pools (Schemmel 1980, Hüppop 1987); the surface morph prefers food items on the surface of the water. Cave populations of *Astyanax* also respond to alarm signals by avoiding an area but show a reduction in alarm behavior (e.g., erratic movements, rapid swimming and hiding) relative to that of surface populations (Fricke 1987). This change in behavior could be mediated through the olfactory and gustatory modality and is possibly associated with constructive changes in jaw size and taste buds and may be genetically linked to eye degeneration (Protas et al. 2008, Yamamoto et al. 2009).

In a well-studied population of the molly *P. mexicana* (Cyprinodontiformes: Poeciliidae), cave-dwelling individuals also exhibit increased numbers of taste buds on the dorsal surface of the head (Parzefall 2001). In addition to food detection, this may be an adaptation to improve communication between males and females during courtship. Most amblyopsid cavefishes show little reaction to chemical stimuli of living or dead prey that are found in their environments in a laboratory setting but will regularly react to mechanosensory stimuli (for a review, see Niemiller and Poulson 2010). However, at least one species (*Typhlichthys eigenmanni*) is attracted to exudates of both conspecifics and prey (Aumiller and Noltie 2003). The cave cyprinid *Phreatichthys andruzzii* (Cypriniformes: Cyprinidae) shows a negative response to chemical cues of unfamiliar conspecifics, which may be related to potential territoriality and the existence of distinct groups or stocks of this species (Berti and Zorn 2001). A more intense repulsion is exhibited to heterospecific cues, possibly representing an antipredator response. Studies have shown that *P. andruzzii* can distinguish different spatial regions through the perception of endogenous and exogenous odors (Paglianti et al. 2006, Ceccolini et al. 2010). The recognition of a fish's own odor or other chemical cues in the environment is likely to be adaptive in caves, because the risk of repeatedly exploring the same volume of water is minimized, which allows the fish to invest more time and energy for other functions, such as reproduction, in an energy-limited environment (Ceccolini et al. 2010).

Electroreception. Several clades of fishes have evolved the ability to detect faint electric fields in their environments created by other organisms (*passive electroreception*) or to generate their own electric fields using ampullary organs (*active electroreception*). Electroreception is particularly useful for navigating, orienting, and detecting prey in low-light conditions, such as at night or in deep, murky water. Consequently, these fish clades would be preadapted to living in caves. Electroreception is known from only the orders Siluriformes (catfishes) and Gymnotiformes (South American knifefishes) that also contain subterranean cavefish species. However, there is no evidence of an enhancement of electrosensory abilities in the few cave lineages within these groups that have been examined (Weber 1995).

Magnetoreception. Several species of vertebrates, including fishes, are known to orient themselves using the Earth's magnetic field (Lohmann and Johnsen 2000, Wiltschko and Wiltschko 2005). To our knowledge, no studies to date have demonstrated that cavefishes can self-orient to magnetic fields. However, aquatic European cave salamanders (Schlegel et al. 2009) can detect magnetic fields. Given their phylogenetic diversity, some cavefishes may be able to orient magnetically in order to navigate within subterranean habitats.

Conclusions

In this review, we summarized the current knowledge of the sensory biology of cavefishes. Most studies have been focused on the loss of vision, because the regression of eyes is often the most obvious morphological change seen in these animals. Constructive changes in nonvisual sensory modalities have received comparatively less attention. In addition, our understanding of the sensory biology of cavefishes has largely been focused on just a handful of species, particularly the characid *Astyanax*. Although much has been learned from the *Astyanax* model, several important questions remain. Have different lineages of cavefishes evolved similar adaptive strategies to sensory specialization, or are sensory modalities predominately governed by subtle variation in abiotic factors in subterranean environments? In addition, are sensory modalities constrained by ancestry—that is, by those sensory adaptations employed by related surface species? Comparative studies of different lineages are needed in order to better understand the morphological, behavioral, and physiological adaptations associated with nonvisual sensory adaptations.

Studies on the evolution of regressive traits have implicated the roles of both random and selective processes in the loss or reduction of eyes and pigmentation (Jeffery 2009). However, the evolution of nonvisual sensory adaptations has generally been considered from a deterministic viewpoint: Selection is the primary driver for constructive changes in nonvisual sensory traits, such as increased numbers of taste buds or neuromasts. The evolution of constructive sensory traits in subterranean organisms may also be influenced by random factors, such as mutation and genetic drift. The importance of random forces in the evolution of nonvisual sensory modalities in subterranean organisms is largely unknown. The independent derivation of cavefish lineages offers a unique opportunity to determine the contributions of the random and deterministic processes that shape the evolution of nonvisual sensory modalities. Several clades of closely related cavefish species exhibit varying degrees of troglomorphy, such as the cyprinids of Southeast Asia—the genera *Sinocyclocheilus* and *Triplophysa* in particular (Ma and Zhao 2012). Although comparative data are not yet available, these clades are especially suited to studies of

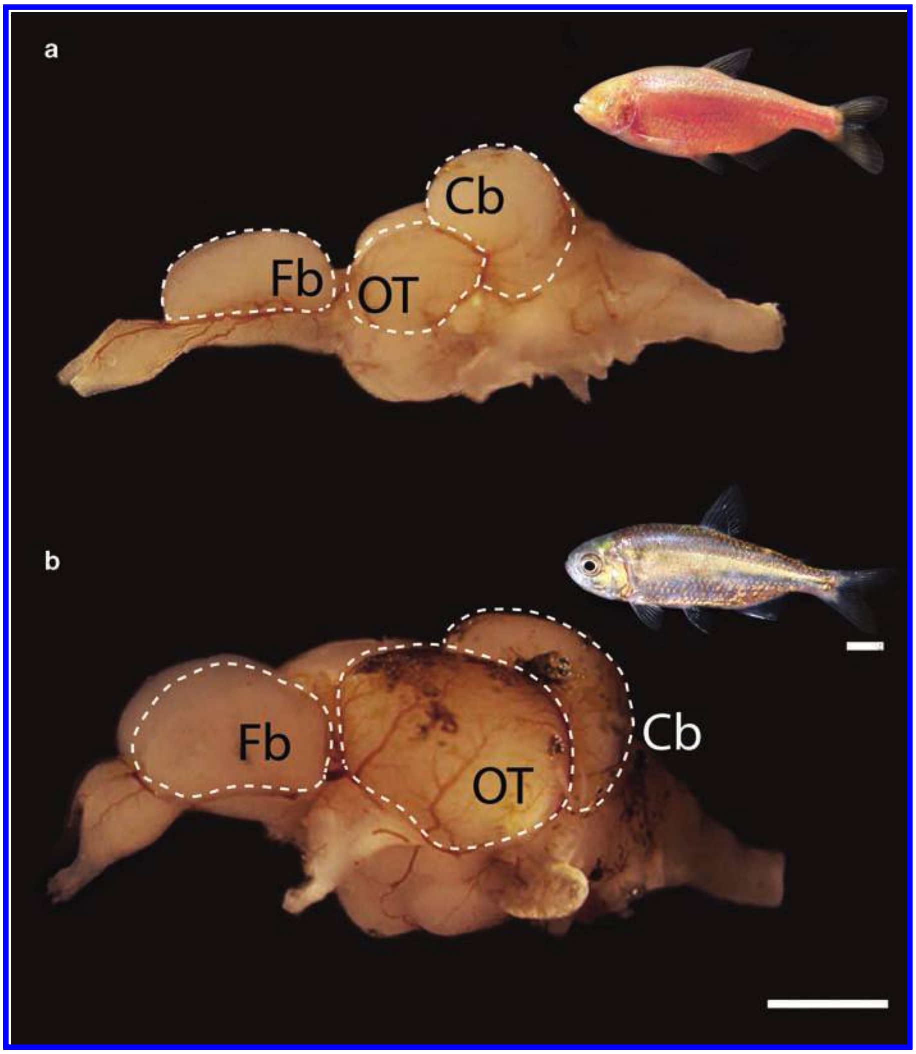

Figure 4. Differences in brain morphology of (a) cave and (b) surface **Astyanax mexicanus***. The scale bars represent 200 millimeters for the brains and 1 centimeter for the fish. Source: Adapted from Strickler and Soares (2011). Abbreviations: Fb, forebrain; OT, optic tectum; Cb, Cerebellum.*

the timing and factors influencing sensory adaptations to subterranean habitats.

Cavefishes may also become important models for understanding functional trade-offs among sensory modalities. Significant differences in brain morphology between related surface fishes and cavefishes have been noted, including the reorganization of neural connections of different sensory modules (figure 4; Soares et al. 2004, Jeffery 2008, Yoshizawa et al. 2010). However, our knowledge is hampered by a lack of data on how much phenotypic variation exists for most nonvisual sensory traits.

Cavefishes possess several attributes that make them ideal model systems for studies of sensory neurobiology. Comparative and molecular studies of surface and cavefish sensory neurobiology and ecology are in their infancies, but cavefishes have already made valuable contributions to the study of the changes and mechanisms underlying evolution to a novel environment. Further studies will continue to advance our understanding of the evolution of sensory adaptations, trade-offs between sensory modalities, and the neural basis of natural behaviors in vertebrates.

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