Occurrence, distribution and troglomorphisms of subterranean fishes of peninsular India

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During the period 2007–2011, two species of an enigmatic genus of siluriform fish, two species of another siluriform fish of the family Clariidae and a blind eel of the synbranchiform fish of the family Synbranchidae, were collected from nine different artificial wells located at the south-eastern part of Thrissur District, Kerala. These include three of the only six species reported from subterranean freshwaters of peninsular India and two undescribed species. Here we examine their morphological and behavioural peculiarities and report on their geography. We also discuss their troglomorphisms in relation with their observed habitat.

Keywords: Autapomorphy, laterite, subterranean fishes, troglomorphisms.

THE subterranean environment comprises a network of interconnected subsoil spaces, of variable sizes, filled with air or water[1]. In the western periphery of the Western Ghats, South India, subsurface material (mostly laterite) in the underground water-filled zone (water table, phreatic zone), when it contains a network of hollow spaces through which water flows, can form subterranean conduits. Such hypogean channels constitute subterranean streams[2]. Subterranean aquifers and streams are sometimes found open to the epigean realm through springs or sink holes. Some fish species are specially adapted to live in these subterranean waters and are called subterranean fishes or hypogean fishes. The troglomorphisms or a series of autapomorphies[3] found in the species that are adapted to a subterranean habitat include smaller body size compared to their epigean relatives, absence or reduction of the eyes, reduction of fin elements or the fins themselves, absence of body pigmentation, exaggerated appearance of chemo- and mechanoreceptors, etc.[4].

In the Indian subcontinent, six of the eight known subterranean fish species were collected only from deep wells containing subterranean fauna which may have entered through groundwater springs. The hill-stream loach *Nemacheilus evezardi* (*Indoreonectes evezardi*), though known to be a hypogean[5,6] and distributed in flooded caves of Central and NE India, has epigean forms also, and the hypogean forms of this species do not show complete troglomorphy[5]. Similar is the case with *Schistura sijuensis*, another cave loach[6]. In contrast to these hypogean fish species that live in accessible hypogean habitats like the caves, a detailed survey is presently not practical to explore the faunal diversity and status of the less studied, inaccessible subterranean channels. *Horaglanis krishnai* (Menon), a clariid, Indian blind catfish (family Clariidae) with typical troglomorphisms, is the first fish species recorded from such a true subterranean habitat in South India. This catfish is subterranean because of its troglomorphic attributes such as complete absence of the eyes, absence of skin pigmentation and that it had been collected only from wells that receive water gushing from subterranean source[7,8]. Also, three species of synbranchiform fishes (eels or snake-like fishes with a single, common gill opening) of the genus *Monopterus*, namely *M. eapeni* Talwar[9], *M. roseni* Bailey and Gans[10] and *M. digressus* Gopi[11] were also reported as 'cavernicoles' from wells in Kerala.

Recently, an enigmatic genus of a primarily subterranean catfish, *Kryptoglanis* Vincent and Thomas[12], was reported from Thrissur District, Kerala. The artificial well from where this fish was first collected was found to receive water only from subterranean springs. This article describes the habitat and troglomorphisms of these less studied endemic fishes.

Materials and methods

Unexpected collection of an unknown fish genus in May 2007 from a newly dug artificial well[12], made the present author to consider the relation between the presence of subterranean fauna in springs and the occurrence of such springs in the segmented valleys and wetlands associated with the numerous lateritic foothills found distributed along the western periphery of Western Ghats. It was understood that subterranean streams can be located at varying depths from the earth's surface. If a well is dug in an area where subterranean fishes exist, and if this causes the subterranean water channels to be exposed, there is a chance of getting subterranean fish from the well. Areas which are known to have good groundwater recharge from natural springs were visited during the period 2007–2009 and the people who dig wells for domestic usage were interviewed. In addition to the voluntary

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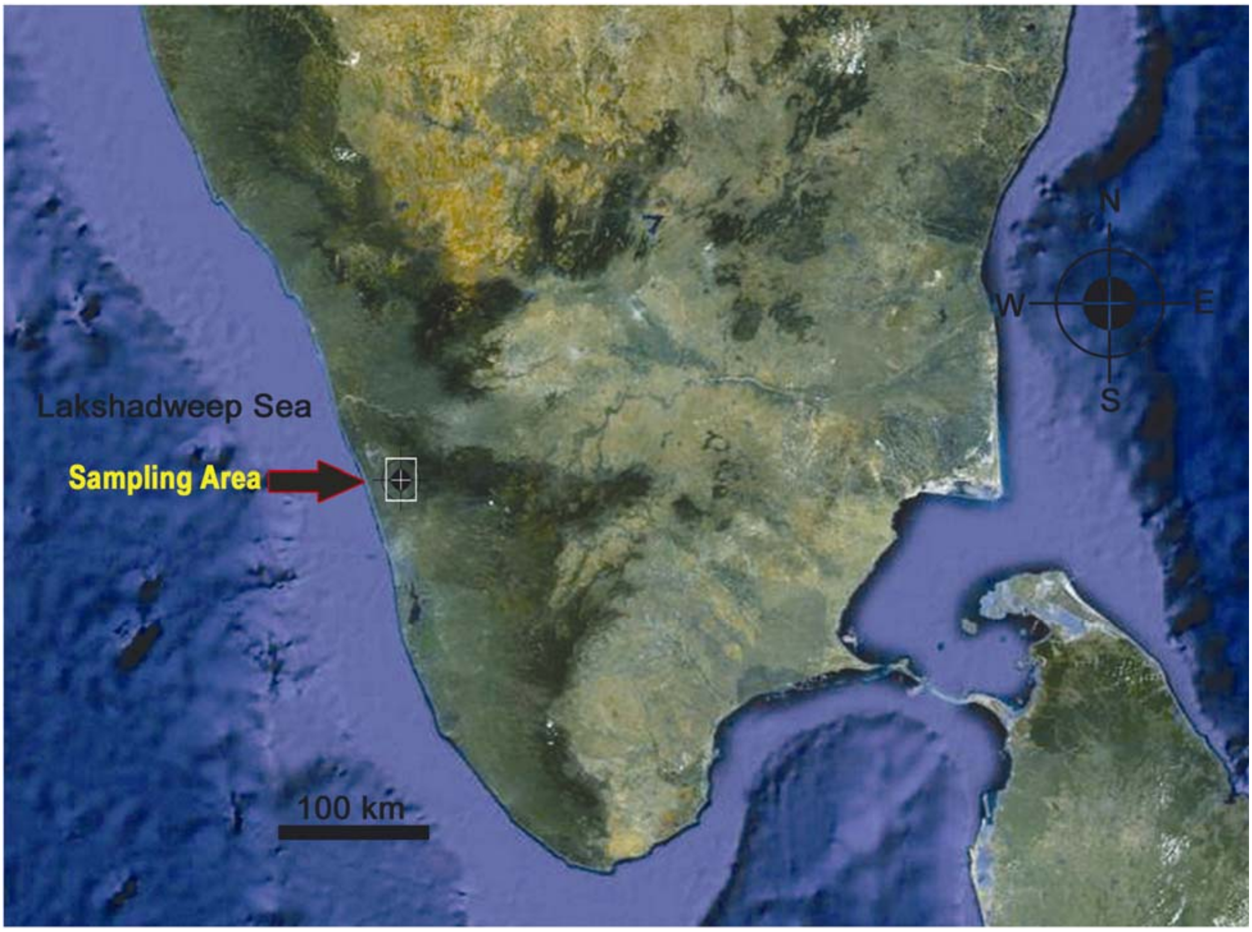

Figure 1. Map of South India showing the study area.

surveys made by the present author, field visits and sample collection were also made when information was received about any unfamiliar fish in a well. All the fishes identified in the present study were first collected from nine different wells located between lat. 10°20′N and 10°23′N, and long. 76°16′E and 76°23′E (Figure 1).

Whenever available, the fishes were collected alive and transported to the laboratory where they were kept in good condition. Identification was based primarily on Gopi[11] and Jayaram[13]. Behavioural studies were made by direct observation on fishes in the author's laboratory. Specimens of undescribed species were deposited in the laboratory facility for thorough studies, or deposited in the Zoological Survey of India, Southern Regional Station, Chennai; Zoological Survey of India, Calicut and Zoology Museum, Christ College, Irinjalakuda.

Results

Altogether five different subterranean species belonging to three genera of fishes were identified during May 2007–June 2011. A brief description of each genus is given below.

Kryptoglanis

Nineteen live specimens of a catfish of an unreported genus of siluriform fishes were collected during May 2007. Later this genus was named *Kryptoglanis* (Figure 2). Fishes of this enigmatic genus can be distinguished from all other described genera in the order Siluriformes (the catfish order), by possession of a unique combination of morphological characters, viz. absence of the dorsal fin; presence of four pairs of barbels, including one nasal pair; relatively small and subcutaneous eyes; a superior mouth with a distinctly projecting lower jaw; fan-like pectoral fins, lacking any hardened elements; anal fin with a long base, confluent with the caudal fin and caudal fin with less than eight fin-rays. The type species of this genus, *Kryptoglanis shajii*, the enigmatic subterranean spring catfish (ESS catfish), is called 'Middu' in Malayalam[14,15], owing to its resemblance with the stinging catfish, *Heteropneustes fossilis.* Because of its autapomorphies, it is not yet placed in any of the catfish families reported from around the world and described as *Incertae sedis* in the order Siluriformes. Figure 3 shows the comparative morphology of this catfish with its seemingly related families naturally distributed in the Indian subcontinent. This genus is presently comprised of two species that show considerable morphological differences from each other. The type species, *K. shajii*, is distinct from the undescribed species (*Kryptoglanis* species 2) in its body shape in lateral profile (Figure 3 *a* and *b*) and fin-ray counts. Both these species were first collected together from a 5.5 m deep artificial well located on the slope of a hilly terrain and later from thickets of water plants in a stream habitat that originates within 150 m near the well. In fact, specimens of fish belonging to this genus was first collected during August 2003, also from a stream located amidst a valley which was originally a freshwater wetland in Aloor village, near Chalakudy, Thrissur District. However, at that time they were misidentified as aberrant specimens of juvenile *H. fossilis*.

Horaglanis

Two different types of this clariid fish were identified in a collection made by a villager, from two different wells in May 2011. One of them, with 23 fin-rays in the dorsal fin and 16 fin-rays in the anal fin, was identified as *Horaglanis krishnai* (Figure 4 *a*) and the other one with 20 fin-rays in the dorsal fin and 15 fin-rays in the anal fin together with other marked variations is presently treated as *Species inquirenda*. Two species of this genus are already known, viz. *H. krishnai* (Menon) and *H. alikunhii* (Subash Babu & Nayar). Both these species were first recorded from deep wells in Kerala state. The present collection locality (10°22′N, 76°22′E) is about 12.5 km (air distance) east of the collection locality specified for *H. alikunhii*[8] and about 92 km north from Kottayam, the first collection site of *H. krishnai*.

The fishes collected in the present study were red in colour and remained so for two months in the laboratory until they died. One of the most notable morphological features of these fishes was the prominence of the mouth at the anterior terminus of head (Figure 4 *b*; also note the terminal positioning of anterior nostrils and minute blood vessels appearing though the transparent skin). Together with the miniaturization of pectoral fin into a vestigial bud (Figure 4 *c*), its ability to move its head up and down by hinging at the level of pharyngeal region is otherwise not normally reported in fishes. Figure 4 *a* shows an entire live specimen raising its head. Other remarkable troglomorphic characters of *H. krishnai* are available in the literature[6,13].

Figure 2. Photograph of a live ESS catfish *Kryptoglanis shajii* (scale bar = 5 mm).

Monopterus digressus

This earthworm-like fish (Figure 5), an eel (order Synbranchiformes, family Synbranchidae), with no external characters of a fish, except gill aperture and characteristic swimming movements, may be considered as the most adapted in a subterranean habitat. It lacks eyes and fin elements, except a membranous caudal fin tip. No dorsal, anal, pectoral or pelvic fins are present. Its body is scaleless, sub-cylindrical, elongate and cord-like.

Two pairs of nasal apertures and a series of sensory pores of the cephalic–lateralis system form the main sense organs. The body was red in colour when collected. Six specimens of this fish were collected from four different wells. The largest specimen collected had a total length of 186 mm. For collection localities, see Vincent and Thomas[2].

Observations on troglomorphic traits

Depigmentation of the skin

In *Kryptoglanis*, body was reddish-brown at the anterior part and the posterior part was translucent, when newly collected from the well. The reddish-brown colouration is in part due to the translucent nature of the skin which reflects the colour of the muscles and internal organs. However, fishes collected from the stream and those reared in laboratory under shaded daylight (< 500 lux) were darker bodied. Skin was found to carry minute, dark specks (chromatophores) in fishes grown under shaded daylight.

In *Horaglanis* the absence of skin pigmentation makes the minute blood vessels visible beneath the skin, which is the reason for the body being blood-red in colour. The excessive skin vascularization is believed to be an adaptation to facilitate respiratory gas exchange through the skin when the fish inhabits the narrow subterranean channels. Live specimens of *Kryptoglanis* became darker bodied a few hours after collection from the wells and specimens of *Monopterus* need more than 3 days to became darker bodied, whereas *Horaglanis* retained the original red colouration for at least two months or until the whole period they were kept alive.

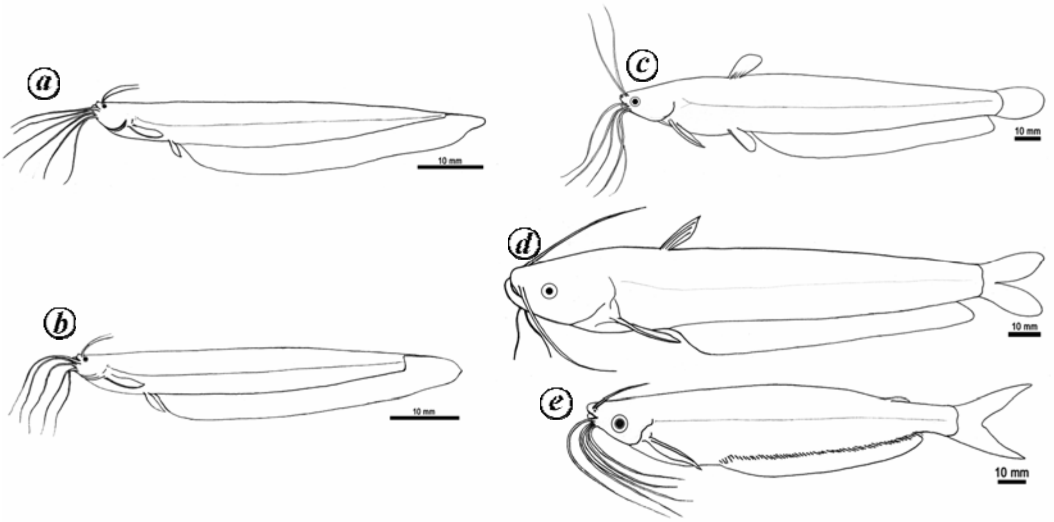

Figure 3. Outline of (***a***) *Kryptoglanis shajii* and (***b***) *Kryptoglanis* species 2 together with other morphologically comparable catfishes of three families of order Siluriformes, naturally distributed in the freshwaters of India, namely (***c***) *Heteropneustes* (Clariidae), (***d***) *Ompok* (Siluridae) and (***e***) *Ailia* (Schilbidae).

Figure 4. Photographs of the Indian blind catfish *Horaglanis krishnai*. ***a***, Entire fish raising its head. ***b***, Close-up view of the mouth; ***c***, Enlarged view of the head region. Arrow points to the rudimentary pectoral fin.

Photophobic behaviour and extra-visual orientation

In *Kryptoglanis*, eyes are subcutaneous and the eye diameter is only 10% (± 0.5%) of head length. Whenever the aquarium was slightly illuminated, the fishes disappeared into the crevices of lateritic stones. However, they soon came out when food (minced earthworm/*Artemia* nauplii/ larvae of cyprinid fishes) was introduced into the water. The reaction of *H. krishnai* to light has been described by Mercy *et al.*[7]. The two types of *Horaglanis* collected in the present study were found to refrain from the illuminated area and always tend to remain under some hides. *M. digressus* did not respond to light and did not show any startling or hiding behaviour when exposed to bright sunlight. However, like *Horaglanis* they too avoided lighted area and tend to remain inside or under the hides provided. Two types of hideouts were provided for

M. digressus; one was a piece of laterite with an irregular shape and which carried some narrow tubular spaces within and the other was a transparent and flexible plastic tube (length, 275 mm) with an internal diameter of 4.0 mm. In both cases the fish easily sensed the hollow space and took refuge in it.

Distinctive cephalic sensory pores

In the genus *Kryptoglanis,* head and anterior part of the body bear an array of sensory pores, in addition to the lateral line system. These sensory pores are well distinguishable in live fishes and have a greater proportionate diameter in the total surface area of the head (Figure 2) compared to other catfish species inhabiting epigean waters of the same locality. In *Horaglanis* and *Monopterus*, the cephalic sensory pores are less distinct than those in *Kryptoglanis*. The cephalic–lateralis system of *M. digressus* has been elaborated by Gopi[11] in the original description of the species.

Absence of spines/fins

Absence of any structures that may offer resistance during movement through narrow crevices and passages in the lateritic subsurface material (Figure 6) in the water table or phreatic zone can be considered to be an adaptation to the subterranean environment. In three of the studied genera of subterranean fish, reduction or complete absence of fin structures and associated hardened elements (spines) were observed. These traits may prove to be adaptive in their natural habitat. In *Kryptoglanis* complete absence of dorsal fin is remarkable. Pectoral fin-spines which are usually present in most of the siluriform fishes are replaced by a flexible and simple ray in *Kryptoglanis*, while in *Horaglanis* the pectoral fin itself is in a vestigial form. In *M. digressus* complete absence of pectoral and pelvic fins and miniaturization of caudal fin (to a 2–3 mm long membranous structure) can be considered as an adaptation to the habitat. However, for *Monopterus*, the absence of fin structures is widespread in the genus.

Figure 5. *Monopterus digressus*.

Cutaneous respiration

Live specimens of *Kryptoglanis* were found to be capable of spending considerable time (> 5 min) in scanty amounts of water, that is only enough to moisten their skin. Microscopic examination of their delicate body parts such as anal fin showed that they are highly vascularized. No other accessory respiratory mechanism/structure in this fish genus was noticed. Similarly, no accessory respiratory organ was reported in *Horaglanis*. However, *M. digressus* has supra-branchial air chambers and the fish was observed to be spending a long time over surfaces that are just above the water level. It was able to take short trips through moist surfaces. It was also found to keep its head elevated from the water surface and periodically open its mouth in the air, if the water in which it was kept became foul.

In contrast to the fishes collected in the present study, other hypogean fishes of India, such as *Nemacheilus evezardi* and *Schistura sijuensis* are known to have a depigmented body, but not with red colouration. This may be due to the fact that depigmentation can result from darkness pertaining to their cave habitats, but blood-red colouration is not present as they need no accessory respiratory mechanisms in the waters of the caves where space is not much limited and chances of getting adequate amounts of dissolved oxygen are more (also see Trajano[1]).

Foraging behaviour

In laboratory, both species of *Kryptoglanis* were given different types of feeds, including *Artemia* nauplii and live fish larvae. In addition to the live feed, small minces of beef and fish flesh were also consumed by the fishes. It was found that they feed voraciously after a 24 h break in regular feeding. Feeding in *Kryptoglanis* was observed to be associated with tactile perception. They took the food material while swimming below the water surface. The fish took the food only when it touched it with their barbels while moving around the place where food was introduced. It was observed that even if the prey was nearby, and outside the barbel sweep area the fishes swam past the location of the prey, as they could not touch the food with their barbels. In addition to tactile stimulation from the barbels, it is assumed that they use chemosensory ability to locate the food, because whenever extracts from the food materials were added to the water, resting fishes soon came out from their hideout and exhibited foraging movements.

The present author maintained the undescribed species of *Horaglanis* for more than two months inside the laboratory. During this time feeding with minced earthworms

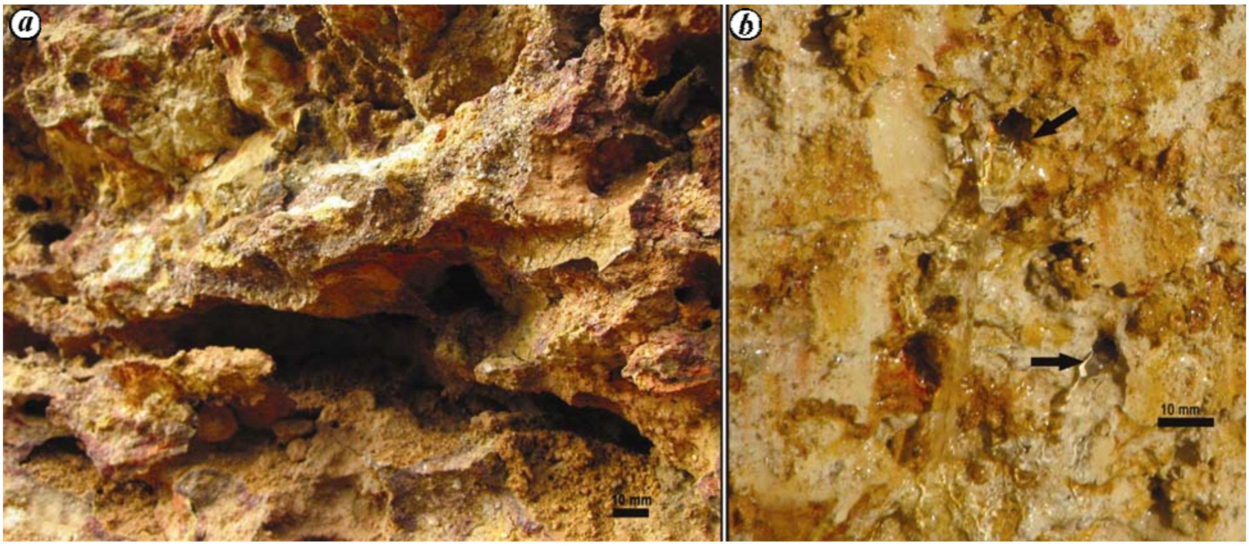

Figure 6. ***a***, Photograph of a section of the canaliculated lateritic subsurface material exposed at a mining area near one of the collection localities of *M. digressus* (see the interconnected spaces). ***b***, Photograph showing spring flow from small crevices in the lateritic sidewall of a well from where three specimens of *K. shajii* were collected in January 2010. Arrows point to the origins of spring flow.

and live larvae of a cyprinid fish species was found successful. *M. digressus* feeds on *Artemia* nauplii, and finely minced, small-sized earthworms. Dependence on olfactory and tactile stimuli for foraging in the absence of visual cues is described in Vincent and Thomas[2].

Notes on geography

The nine wells from where all the collections were made were situated in places where the chance of getting a subterranean fish was high as expected from the combined observation of geomorphology, direct observation of landscape, GPS reading of altitude variation and ecological indicators (thick growth of riparian vegetation or fauna that exclusively depend on water for propagation). As described earlier and mainly from casual observations, the present author put forward a relationship between the presence of subterranean fishes and peculiarity of the geographic formation. He was also influenced by observations made in a series of wells around the collection locality and from where subterranean fishes could not be collected. All places from where the fishes are collected have some common features. First, all the wells are located on the slopes of lateritic hills close (within 300 m) to a temporary freshwater wetland or at the fringe of a wetland itself. In all the places, the subsurface material was lateritic. Secondly, all localities are not far (within 400 m) from an ephemeral freshwater stream originating from groundwater recharge during June–December. Two species of the genus *Kryptoglanis* were also found living in the streams that originate at the fringes of these wetlands during the later half (June–December) of the year. It was observed that these streams are the result of groundwater outflow from the foot of lateritic hills bordering the temporary wetlands. These temporary wetlands are considered to be remnants of ancient freshwater wetland systems, as evidenced by the natural deposits of huge amounts of river sand and relicts. Figure 6 *a* shows the laterite formation carrying interconnected spaces or vermiform hollows[16] and (Figure 6 *b*) the spring flow from such a subsurface conduit that empties water into a well from where specimens of *Kryptoglanis* were collected during January 2010, 2 km southwards from the type locality. Note the scale bar to get an idea of space limitation in the subterranean channels.

It was also found that all the fish collection localities are under the pressure of active urbanization, with the number of artificial wells increasing at a fast rate, which can form traps for these fish species.

Discussion

The primary work on subterranean ichthyofauna of the study area was on *H. krishnai* from wells in Kottayam District. *H. krishnai* was not reported from any other place. The present conservation status of this fish is ‘data deficient’[17,18]. However, this article provides an account of *H. krishnai* from outside Kottayam District, that is more than 90 km away from the distribution range of this catfish species and thus forms the range extension report for the species. Between these two places of distribution, there are four epigean rivers, however, this species has not been reported from any of these rivers or their epigean drainage areas. Similarly, this article may be considered as a range extension report for *M. digressus*, which was first reported from a well at Calicut (Kozhikode) and is now reported from wells more than 115 km away from the initial collecting place (type locality of this species). Also, there are four epigean rivers that separate the collection localities at Calicut and the present collection sites in the southern region of Thrissur District. Does this indicate the spread of subterranean habitat along the western periphery of the Western Ghats (that is, at least between Kottayam and Calicut spanning a distance more than 200 km)? Or, do these species are able to disperse over epigean realm? Also, subterranean channels and associated freshwater wetland habitats can be found at many places along the entire range of the Western Ghats and, since it is found that the water table and phreatic region at some of these areas are also occupied by lateritic subsurface material, the present study area may not be the only place where subterranean fishes exist in peninsular India.

The troglomorphic character states such as absence of the eyes, presence of blood-red body colour (indicating possible low oxygen levels in subterranean waters) and lack of fin-related structures (that may offer resistance to movement in their observed habitat, the narrow passages through which water can flow in the water table or phreatic zone) are considered as the product of regressive evolution in a habitat where light is absent and space may be limited[2]. However, Romero and Green[4] point out the unwanted notion of regressive evolution in explaining troglomorphisms. And as indicated by Borowsky and Wilkens[19], changes that occur in regressive evolution are not different from those that occur in constructive evolution, for which troglobites also exhibit convergence, as, for example, increase in sensory modalities other than vision. Without regressive evolution all species would be encumbered by billion-year-long lists of superannuated traits[19]. It is important to note that the conceptive differentiation between constructive and regressive evolution is mostly arbitrary and that the presence or absence of selection pressures is always guiding the tempo of evolution. In other words, the morphological and behavioural adaptations discussed as troglomorphic character states, whether they are called products of regressive or constructive changes, are ultimately aimed to enhance the fitness of individuals of a species that live in a particular era of situations that modulate their survival, either to persist as a species or to transform into a new species as time advances and selection pressure changes.

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