Uiblein, F., Ott, J., Stachowitsch, M. (Eds): Deep-sea and extreme shallow-water habitats: affinities and adaptions. - Biosystematics and Ecology Series 11: 91-122.

Behavioural and morphological changes caused by light conditions in deep-sea and shallow-water habitats

J. PARZEFALL

Abstract: Animals living permanently in the total darkness of caves and those living in the ocean at depths below 1200 m seem likely to share morphological and behavioural specializations due to the lack of light. Both these habitats can in general be characterized as old, climatically stable, and non-rigorous. But there are also differences: the presence of luminous organs and drumming organs is restricted to deep-sea animals only. Cave dwellers - except inhabitants of phreatic waters - do not have to live under high hydrostatic pressure. Deep-sea species, unlike the cave-living ones, are not isolated in smaller habitats. These facts will be used to compare morphological reductions of visual organs and pigmentation in fish and invertebrates as well as the progressive traits in other sensory systems. Besides these changes, the behaviour of various characters also differs compared with epigean relatives. These include phototactic behaviour, locomotory activity, food and feeding, reproduction, aggression, dorsal light reaction, and circadian clock. Life histories of cave- and deep-sea dwellers also show parallels.

Introduction

The following paper deals with animals living in lightless habitats. In this context, the situation in caves and the deep sea beginning at a depth of about 1200 m will be compared (CLARKE 1970). Some of the cave dwellers presented have marine ancestors and now inhabit freshwater caves. They apparently first colonized marine marginal caves and adapted step by step to brackish and finally to freshwater conditions. All these cave habitats and deep-sea regions at about 1200 m can be characterized as lightless and more or less climatically stable. In comparing the morphological and behavioural changes in these habitats in relation to relatives living in epigean daylight habitats, one cannot neglect the high hydrostatic pressure as an important factor for deep-sea inhabitants. This factor is only effective in those cave dwellers found in artesian wells of phreatic waters like the Edwards Aquifer in Texas. In this region, animals can be caught from the outlets of wells that penetrate the Edwards formation between 402 m and 582 m (LONGLEY and KARNEI 1979). This condition, however, is an exception. Cave animals are usually not exposed to high hydrostatic pressure. This report begins with regressive traits found in cave and deep-sea inhabitants compared with epigean relatives. It continues with progressive adaptations to the lightless habitats. The final topic is behavioural changes.

Regressive traits

Eye reduction

Many species of different taxa living in caves or the deep sea have been described as eyeless, blind, or eye-reduced. Going into the detail, one can find specimens whose eye size is diminished to different degrees up to an absence of visible external traces of the eyes. In the latter case the eye remnants are buried deep under the body surface.

Tab. 1 shows some taxa of cave- and deep-sea dwellers in which eye reduction has been reported: The polynoid polychaete *Macellicephala hadalis,* which has been photographed swimming over the bottom (LEMCHE et al. 1976) and which occurs in the deepest part of the Pacific (Fig. 1), has no visible eyes. The same is true for *Gesiella jameensis* (Fig. 2) living in the Jameos del Agua, a lava tube in the coastal region of Lanzarote (Canary Islands). We observed this species slowly swimming close to the bottom (PARZEFALL 1986). In another family of polychaetes - the pelagic Alciopidae - two species of *Vanadis* caught at about 300 m have eyes whose retina is light-sensitive at about 460 nm to 480 nm (WALD and RAYPORT 1977). Gastropods are prominent among the slow-moving carnivores in the deep sea. In the Woods Hole transect from New England to Bermuda, samples taken by epibenthic sled between 478 m and 4862 m contained 93 species of prosobranchs and 30 species of opisthobranchs. More than half of them are predators (REX 1976, 1977). Many of them seem to be eyeless or eye-reduced. Aquatic gastropods have also colonized caves around the world. True cave dwellers, however, have only been found in freshwater or phreatic wells. They show different degrees of eye reduction. The family Ellobiidae, for example, contains 19 blind species living in caves of the karstic region of former Yugoslavia and Italy as well as in the Pyrenees (BERNASCONI and RIEDEL 1994). In the cephalopods, deep-sea species of the genus *Chiroteuthis* have regressed but functional eyes. There is only one blind cephalopod - the finned octopod *Cirrothauma murrai* (Fig. 3). CHUN (1914) found reduced eyes without lens or iris and very regressed retinal tissues. The eyeballs were completely closed. To date, no true cave-dwelling cephalopod has been described.

Tab. 1: Taxa with eye and pigment reduction

TAXON	DEEP SEA	CAVES	DEGREE RED.	AUTHORS
POLYCHAETA				
Polynoidae	*Macellicephla hadalis*	*Gesiella jameensis*, m.	eye abs. pigm. abs.	ELOFSSON & HALBERG 1977, HARTMANN-SCHRÖDER 1974
MOLLUSCA				
Gastropoda	var. species	var. species freshw., phrea.	eye variab. pigm. variab.	MARSHALL 1979, BERNASCONI & RIEDEL 1994, CHUN 1914
Cephalopoda	*Cirrothauma murray* *Chiroteuthis*		blind pigm. abs. eye variab. pigm. variab.	MARSHALL 1979
CRUSTACEA				
Mysidacea	var. species	var. species m, frw., phrea.	eye variab. pigm. variab.	LAGADERE 1985, PESCE et al. 1994
Mictacea	*Hirsutia bathylis, H. sandersetalia*	*Mictocaris halope*	eye abs. pigm. abs.	BOWMAN 1994, SANDERS et al. 1985
Isopoda	var. species "giants"	var. species m., frw., phrea.	eye bl. -> var. pigm. variab.	WÄGELE 1989, COINEAU et al. 1994
Amphipoda	var. species "giants"	var. species m., frw., phrea.	mostly eyeless & pale	HOLSINGER, 1994 MARSHALL, 1979
Decapoda Anomuran crabs Galatheidae	*Munidopsis spec.*	*Munidopsis polymorpha*, m.	eye variab. pigm. variab.	BIRSTEIN & ZARENKOW 1970, HARMS 1921
Reptantia & Natantia	var. species	var. species m, frw., phrea.	eye variab. pigm. variab.	GAGE & TYLER 1991, GUINOT 1994
TELEOSTEI				
Ictalurid catfish		*trogloglanis pattersoni, Satan eurystomus*, phrea.	blind unpig.	LANGECKER & LONGLEY 1993
Ophidiiformes Ophidiidae	var. species	var. species m, brackish, frw.	blind -> variab. pigm. abs. -> variab.	THINES 1969 GAGE & TYLER 1991

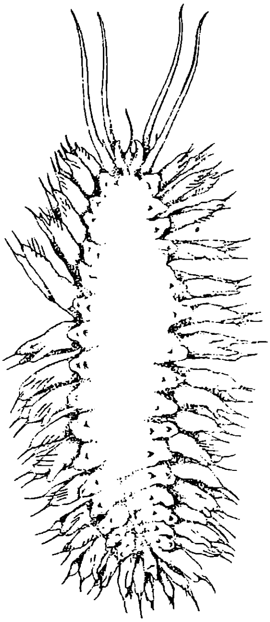

Fig. 1: *Macellicephala haddalis,* polynoid polychaete from the Kermadec Trench (6600-8300 m) (MARSHALL 1979).

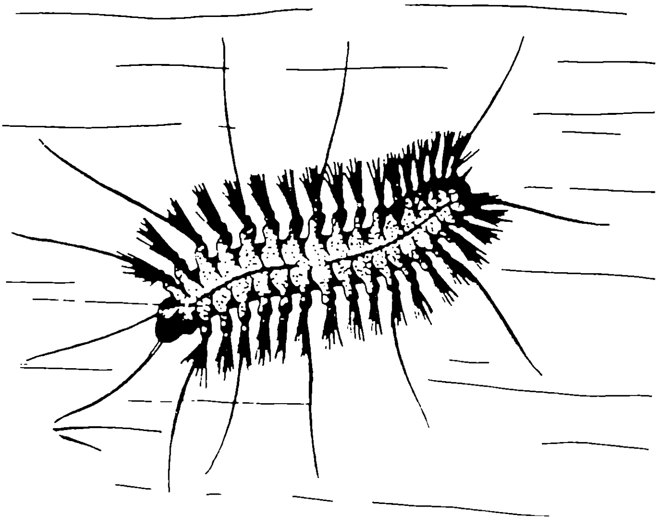

Fig. 2: *Gesiella (Macellicephala) jameensis,* polynoid polychaete from the marine lava cave Jameos del Agua, Lanzarote, Canary Islands (PARZEFALL 1986).

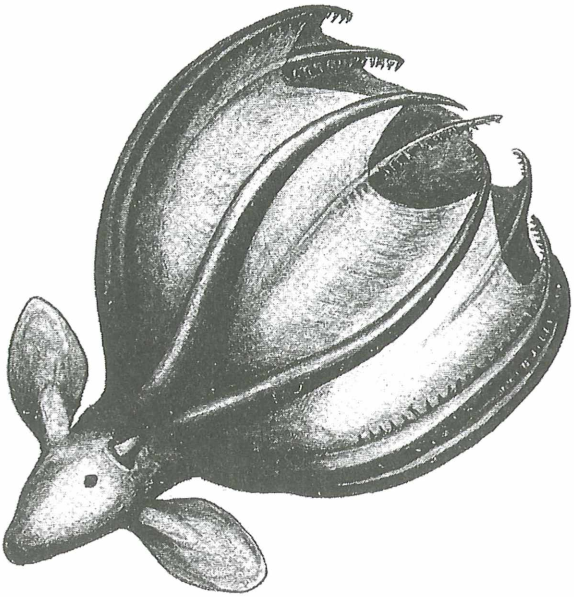

Fig. 3: *Cirrothauma murray*, blind cephalopod caught by net in 3000 m depth in the North Atlantic in 1910 (CHUN 1914).

Within the crustaceans there are many taxa with deep-sea and cave representatives having reduced eyes. The Mysidacea, although being predominantly bathypelagic (LAGARDÈRE 1985), have also evolved benthic species with reduced eyes. At present, 17 stygobiont mysid species are known from coastal caves, phreatic waters, and anchialine habitats of inland caves. Most of them are usually blind (PESCE et al. 1994). Species living in dim-light caves like *Heteromysoides cotti* from the Jameos del Agua on Lanzarote have slightly reduced eyes (WILKENS and PARZEFALL 1974). The three known species in the recently discovered order Mictacea lack visual elements in the eyestalks (Fig. 4) (BOWMAN 1994).

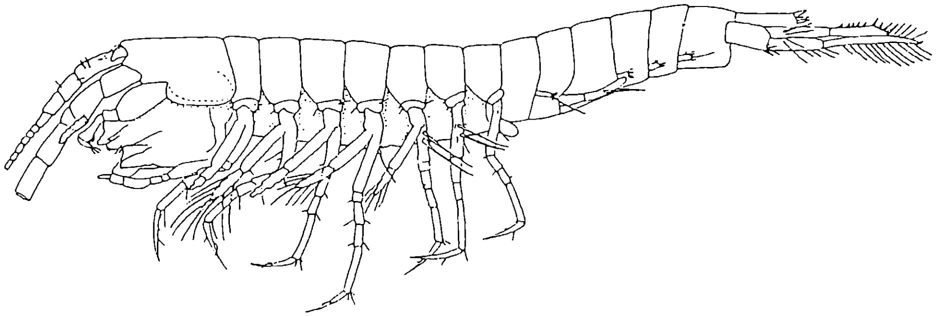

Fig. 4: *Mictocaris halope*, mictacean crustacean (BOWMAN 1994).

Isopod species of deeper waters have no eyes (MENZIES et al. 1973): in 11 species taken at a depth of 2000 m to the abyssal plain of 4500 m the eyes were absent. In species of *Serolis* from subantarctic and antarctic habitats, a progressive reduction of the eyes in relation to depth range has been observed. Cave isopods, which very sucessfully colonized the different types of cave habitats, contain many eyeless species (COINEAU et al. 1994). A similar situation has been found in the amphipods inhabiting the abyssal, whereas mesopelagic species still possess eyes (MARSHALL 1979). Among the 711 cave-dwelling species many are blind (HOLSINGER 1994). The various anomuran families, which include squat lobsters and hermit crabs, are the most diverse of decapods in the deep sea. The squat lobsters - family Galatheidae - are, for example, the most varied, with over 100 species in the essentially bathyal genus *Munidopsis,* but with less than 20 species being found deeper than 3 km (BIRSTEIN and ZARENKOV 1970, GAGE and TYLER 1991). *Munidopsis sarsi* occurs in high densities above 800 m in the Porcupine Seabight, NE Atlantic; *Munidopsis subsquamosa* are found clustered around hydrothermal vents in the Pacific. In shallow-water caves, however, there is only one species - *Munidopsis polymorpha* - living in different parts of the Jameos del Agua on Lanzarote, Canary Islands. They all show variously reduced eyes. *M. polymorpha* (Fig. 5), for example, is only able to detect light differences (WILKENS and PARZEFALL 1974).

In other decapod taxa like euphausiids and prawns, bathypelagic species tend to have small eyes, i.e., giant species of *Thysanopoda,* or regressed ones, i.e., *Bentheuphausia amblyops* (MARSHALL 1979). Cave decapods also tend to reduce their eyes: The palaemonid prawn *Typhlocaris galilea,* living in sulphurous and brackish water of a subterranean tract near lake Tiberias in Israel, is blind (TSURNAMAL 1978). GUINOT (1994) reports about 80 cave-living brachyuran decapods with different degrees of eye reduction. In the deep sea, brachyuran crabs are also present. They show an impressive radiation. Some, like the genus *Ethusina*, range from 500 m to abyssal depths of 4300 m and have more or less reduced eyes (MARSHALL 1979).

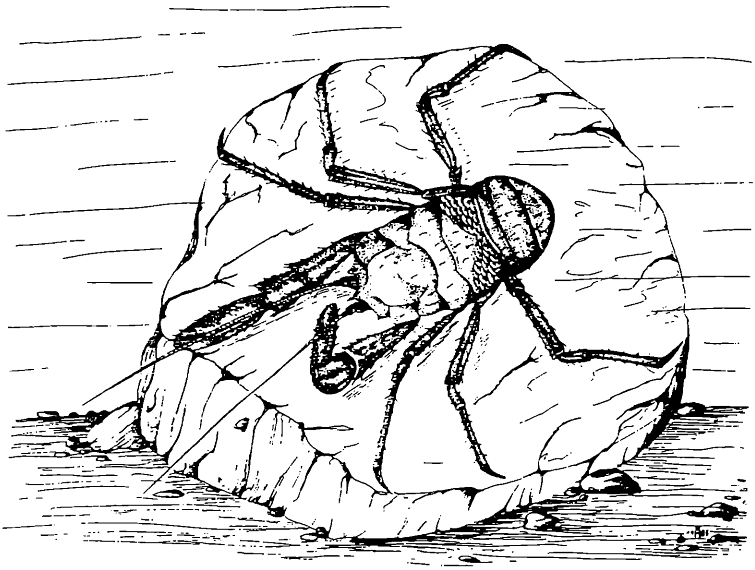

Fig. 5: *Munidopsis polymorpha*, galatheid crab from the marine lava cave Jameos del Agua, Lanzarote, Canary Islands (PARZEFALL 1986).

Among the various fish families living in the deep sea, the Ophidiiformes, which include the families Ophidiidae and Bythitidae, also occur in shallow, warm waters. In the deep sea as well as in cave habitats, eye reductions of different degrees have been observed: *Caecogilbia galapagosensis*, a brackish water form near the coast of Santa Cruz, Galapagos Islands, has regressed but variable eyes. However, *Ogilbia pearsi* from freshwater caves on Yucatan, Mexico, has a small eye remnant hidden under the body surface. The same is true in *Typhlonus nasus*, caught at about 4000 m depth (THINÈS 1969). Other ophidiiforms have small but visible eyes, as in the case of two abyssal brotulids shown in Fig. 6. Following ANDRIASHEV's (1953) division of the deep-sea fishes into "ancient deep-water forms" and "secondarily deep-water forms", these fish belong to the first group. The eyes of bathypelagic and bathybenthic fishes living below the threshold of light tend to be small and deficient. However, slope-dwelling species centered at depths between 250 m and 1000 m often possess large eyes. This fact has been also observed in families representing ancient deep-water forms such as the rattails, Macrouridae (MARSHALL 1979).

In general we can state that deep-sea and cave dwellers show a comparable degree of eye reduction, which can have different functional aspects. These will be analyzed later in this paper. Detailed comparative studies of the eye reduction in different populations of cave amphipods (FONG 1989) and Mexican cave fish (WILKENS 1988, LANGECKER et al. 1993) revealed a genetically based reduction of this trait. The eye reduction in cave *Astyanax* is due to mutations of regulator genes; the structural genes are still present (LANGECKER et al. 1993).

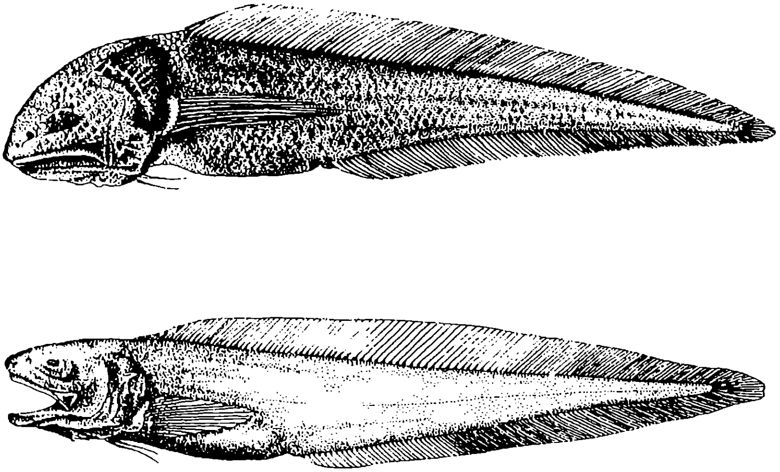

Fig. 6: Two abyssal brotulids. Above, *Abyssobrotula galatheidae* from Kermadec Trench 5230-5340 m. Below *Bassogigas* sp. (MARSHALL1979).

Pigment reduction

Besides the eye, the body pigmentation in deep-sea animals as well as in cave dwellers also undergoes a reduction process. The animals become increasingly pale: this is the case in polychaetes (Tab. 1), molluscs, crustaceans, as well as in deep-sea and cave fishes. Cephalopods become gelatinous and transparent, like jellyfishes. Many cave gastropods have thin, transparent shells compared with epigean relatives.

Most of cave and deep-sea fishes are unpigmented. The depigmentation is normally correlated with the degree of eye reduction. The ophiidid species *Caecogilbia galapagosensis*, for example, with its variable eye size as already reported above - also shows a variable body pigmentation (THINÉS 1969).

Detailed studies on the Mexican cave fish *Astyanax fasciatus* have demonstrated that this phenomenon is caused by partial or total loss of melanin in the melanophores and by a decrease in the number of melanophores. Hybridisation experiments of different populations show that recessive genes are responsible for the reduction of the melanophores and also for the absence of a genetic linkage between eye and pigment reduction (WILKENS 1970, 1976). Some of the Reptantia, like the euryonids, are pink or reddish. The deep-sea crab *Geryon quinqidens* which is very abundant at upper slope levels, is therefore called red crab (MARSHALL 1979). The shrimp *Stenopus spinosus* caught in the lava tube of the Jameos del Agua, is also red (ILIFFE et al. 1984).

Constructive traits

In eye-reduced animals, constructive traits can be observed which seem to compensate the disadvantages of life in dark habitats.

Elongation of body-appendages

Many of the species living in such dark habitats, regardless of whether they are pelagic or not, developed long antennae or other body appendages. Polychaetes like *Gesiella jameensis*, for example, have very long, fragile setae.

In nearly all crustaceans, examples of extremely long antennae and legs can be found. Fig. 7 presents *Typhlatya iliffei* from Tuckers cave, Bermuda (HART and MANNING 1981) and, for comparison, the deep-sea penaeid prawn *Sergestes corniculum* (MARSHALL 1979).

In fishes, barbels and fins can form long appendages. Deep-sea fishes of the family Melanostomiatidae, for example, developed barbels of variable length and form (Fig. 8). Cave-dwelling catfish of the families Ictaluridae and Pimelodidae reveal a comparable situation. Ophidiid fishes of different habitats have small filamentous ventral fins of variable length. In contrast, tripoid deep-sea fishes (Bathypteroidae) have extremely long fin rays that resemble a system of multiple antennae.

Light organs

Light organs only exist in deep-sea colonizers: in aquatic cave dwellers, bioluminescence has not been found. The only light-producing animals in caves are larvae of *Arachnocampa luminosa* living on the ceiling of Waitomo cave, New Zealand (VANDEL 1964).

In the deep sea, the most luminous depths are in the mesopelagic zone. Below 1000 m, light flashes become more and more sporadic due to the much smaller standing stocks of zooplankton at bathypelagic levels. Of the main taxa in the mesopelagic zone, only Chaetognatha and pteropod molluscs seem to lack luminescent members (MARSHALL 1979). In the permanent benthopelagic fauna, however, light organs are known only in fishes of the gadiform and perciform orders. The main light producers are rattails, Macrouridae, and deep-sea cods, Moridae (order Gadiformes). Their light organ opens near the anus or into the rectum and contains luminous bacteria. In rattails the light organ is apparently confined to the slope-dwelling species centred above 2000 m. In the deeper abyssal species, the light organ is lacking (MARSHALL 1979).

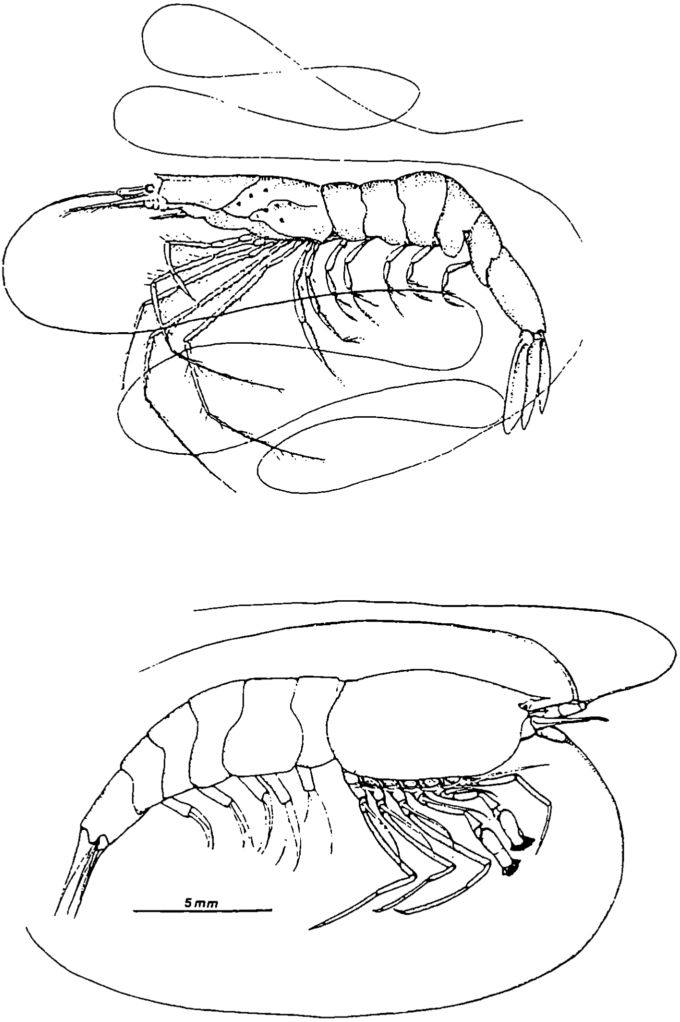

Fig. 7: *Sergestes corniculum* (above), penaeid prawn from the deep sea (MARSHALL 1979) and *Typhlatya iliffei* (below), atyid shrimp from Tuckers Town cave, Bermuda (HART and MANNING 1981).

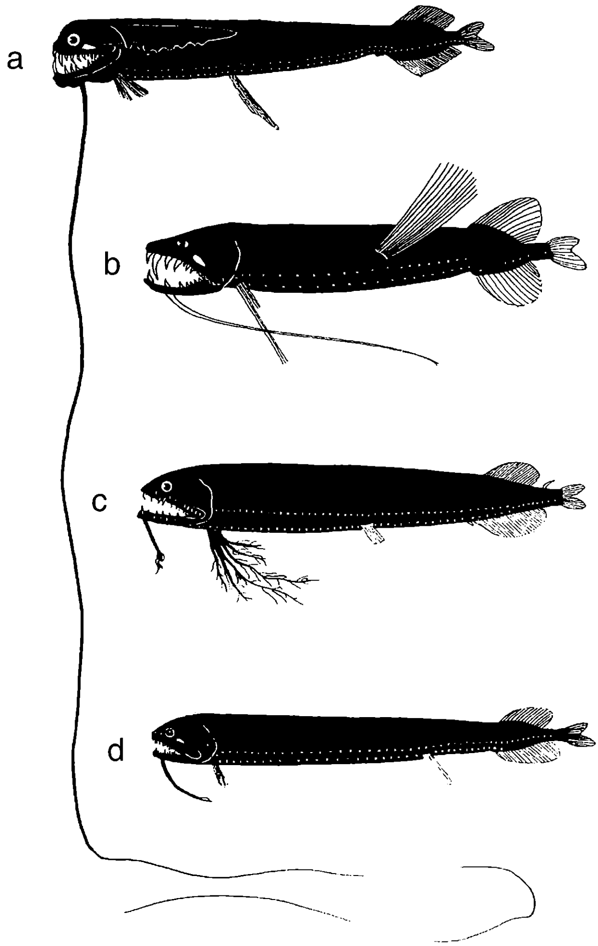

Fig. 8: Fishes of the family Melanostomiatidae, showing variation in length and form of luminous chin barbel: *Grammatostomias flabellibarba* (a), *Bathophilus longipinnis* (b), *Chirostomias pliopterus* (c), *Melanostomias spilorphynchus* (d) (MARSHALL 1979).

Diverse kinds of invertebrates on the deep-sea floor are luminescent, including echinoderms (HERRING 1974), sea-spiders (Pycnogonida), alcyonarian cnidarians, sea pens (Penatulacea) and siphonophores. All these forms have their main distribution in midwater-regions.

Sound production and registration

Certain deep-sea fishes bear paired drumming muscles on the forward part of the swimbladder. These muscles, which are homologous with those of drum-fishes and other sound-making fishes, are restricted to males in morids and macrourids. In the brotulid fishes, males of the oviparous species also have large drumming muscles, although both sexes have large sacculi in macrourids and oviparous brotulids. All viviparous brotulid species studied thus far have drumming organs in both sexes. All these species have a well-developed inner ear with large otoliths in each sacculus. Surprisingly, sound making and correlated hearing is confined to species with large eyes and light organs adapted for vision and communication in twilight. In species which tend to live at depths of 1000 m or more and in abyssal genera neither sex has drumming muscles (MARSHALL 1962, 1964, 1979). No drumming muscles have been described in blind cave brotulids (VAN MOL 1967, SCHEMMEL 1977). In aquaria, we observed head-shaking movements in the Mexican cave brotulid *Ogiliba pearsii* at a distance of a few centimeters that released flight behaviour in conspecifics. However, we were unable to register any sound signals using a hydrophone (PARZEFALL unpubl.).

The explanation for this difference might be that sound communication is virtually confined to near-field displacement described by a radius of $1/r^2$ from the sound producer. It would thus appear not to be a good communication form for fishes living in low densities.

Abyssal macrourids, as shown by a detailed photographic survey at a depth of around 2500 m, live in small groups of 2-5 fishes separated by much more than the radius of the near field. Individuals of slope-dwelling species, which can be very abundant, seem to be within near-field earshot of one other (MARSHALL 1971).

The cave-living brotulids we observed in different dark habitats on Yucatan, Mexico, were single specimens in very low densities (PARZEFALL unpubl.)

Lateral-line senses in fishes and invertebrates

The neuromasts of fishes are either housed in mucus-filled canals or freely exposed on the body surface. This system serves mainly to detect and locate moving animals such as prey, enemies, or social partners at short range on the basis of current-like water disturbances. In addition, obstacles of different size can be distinguished when the blind cave fish is gliding through the water and setting a current field around (HASSAN 1985). In adaptation to the dark habitats, the free neuromasts are extended on short stalks like in amblyopsid cave fish or in certain bathypelagic species (MARSHALL 1971). Moreover, cave amblyopsids carry more neuromasts and larger lateralis centres in the cerebellum than epigean species (POULSON 1963). Free neuromasts and canal neuromasts have been studied by SCHEMMEL (1977) in the Mexican cave brotulid *Ogilbia pearsei:* the neuromasts are also placed on stalks (Fig. 9), as in amblyopsids. The lateral line system is highly developed and concentrated on the head (Fig. 10). The head shaking described above in this species probably transmits signals to this system.

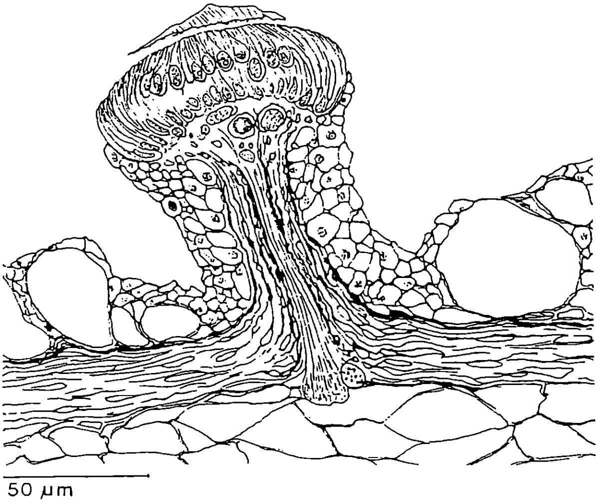

Fig. 9: Neuromast on an extented stalk in *Ogilbia pearsei* (SCHEMMEL 1977).

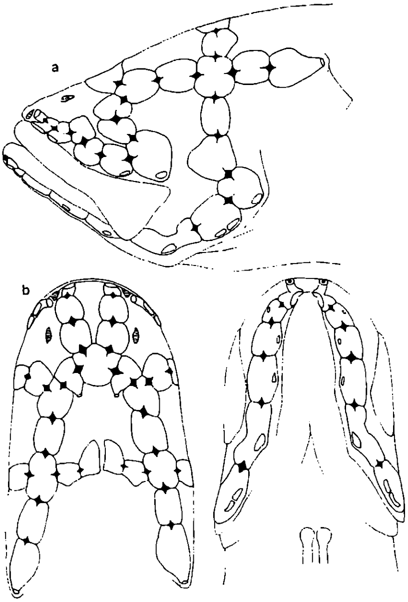

Fig. 10: Chambers of the lateral line canal system in *Ogilbia pearsei*. Black dots are neuromasts. Note the openings in the canal system. The nostrils are hatched (SCHEMMEL 1977).

Such a mixed neuromast system is also found in most benthopelagic fishes. The most striking feature is the development of very wide head canals with large neuromasts, such as found in cave and deep-sea brotulids and other benthopelagic fishes including macrourids and halosaurs (MARSHALL 1971).

Some invertebrates also have displacement receptors comparable to free neuromasts in fishes: in arrow-worms, hair-bearing sensory cells are distributed along the body (HORRIDGE and BOULTON 1967). In crustaceans antennal setal tubes function in mechanoreception (BALL and COWAN 1977). It seems possible that the long appendages in some of these species also improve mechanoreception.

Behavioural changes

Comparative data about behavioural changes have been reported mainly for cave dwellers.

Phototactic behaviour

A central question for animals living in darkness is how to react to light. This reaction has been studied extensively in cave-dwelling fishes. In choice tests with different populations of the characid *Astyanax mexicanus,* LANGECKER (1992) was able to demonstrate that this behaviour in the epigean population depends on light intensity (Fig. 11). Juveniles show a slightly positive response under all tested conditions, while adult fish are slightly photonegative. The photonegative behaviour greatly increases in blinded fish. Blinded fish that have been pineal-ectomized reveal the importance of the pineal for light perception and phototactic behaviour. The phototactic index is at the same level as for the tested cave population. In contrast to the epigean fish, the removal of the pineal organ has no significant effect on the cave fish. Thus, the differences in the phototactic behaviour in the cave fish could be caused by a reduction in parts of the pineal organ. Ultrastructurally, however, there is surprisingly little change in this organ. In addition, the degree of differentiation of the photoreceptor cells indicates that they are still sensitive (LANGECKER 1990). Therefore, the different phototactic response of the cave *Astyanax* must be a true behavioural regression. The persistence of the photoreceptor cells in the pineal organ of even the phylogenetically old Pachon cave fish suggests that there is an as yet undiscovered biological significance.

All cave dwellers studied appear to be significantly photonegative with respect to light intensities above 30 lux (Tab. 2). The phototactic index in Tab. 2 has mainly been calculated by LANGECKER (1992). The only reported positive data (BREDER and RASQUIN 1947) have been controlled and reexamined (LANGECKER 1990, ROMERO 1985). They seem to be incorrect. Within the Ophiididae, the 3 species tested demonstrate a photonegative reaction (Tab. 2). Among the invertebrates, cave isopods and amphipods are photonegative: the isopod *Caecidothea stygia* already reacts at 80 lux (BANTA 1907) and the amphipod *Niphargus orcinus* between 50 and 100 lux (GINET 1960). The galatheid crab *Munidopsis polymorpha* from the marine lava cave Jameos del Agua on Lanzarote, Canary Islands, already reacts at a light intensity of 3 lux by hiding (RODRIGUEZ 1996).

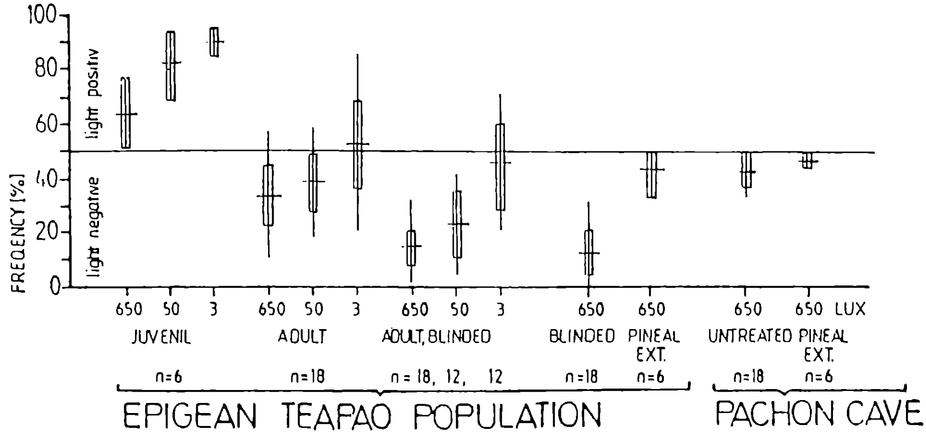

Fig. 11: Phototactic reaction: Preference for the lighted area in a light-dark choice experiment of different populations in the characid fish *Astyanax fasciatus* (PARZEFALL 1992 after LANGECKER 1992).

Based on the reactions seen on video sequences, most deep-sea animals are apparently also photonegative. On the other hand, certain species do not avoid light: the galatheid crabs *Munida sarsi* collected by otter trawl from 240 m near Bergen (Norway) were studied in aquaria for three weeks in daylight without any mortality (BERRILL 1970).

Tab. 2: Phototaxis in various species of fishes and crustaceans

Species	Light intensity	Result (Mean phototactic index)	Authors
TELEOSTEI			
(1) Characidae			
Astyanax fasciatus:			
"Anoptichthys jordani"	c. 500 lux	negative: 21%	BREDER & RASQUIN, 1947
= Chica fish			LÜLING, 1954
	daylight	slightly negative	THINÈS, 1954
	45 lux	negativ: 30%	GERTYCHOWA, 1970
	daylight	negative: 38%	ROMERO, 1985
	c. 1000 lux	negative 23-42%	BREDER & RASQUIN, 1947
"Anoptichthys antrobius"	c. 500 lux	positive: 54%	ROMERO, 1985
= Pachon fish			LANGECKER, 1989, 90
	c. 1000 lux	negative: 37-43%	LANGECKER, 1990
	c. 1400 lux	negative: 42%	BREDER & RASQUIN, 1947
"Anoptichthys hubbsi"	c. 600 lux	negative: 43%	LANGECKER, 1990
= Sabinos fish	c. 500 lux	positive: 55%	BREDER & RASQUIN, 1947
			BREDER & RASQUIN, 1947
Arroya fish	c. 1400 lux	negative: 32%	LANGECKER, 1989, 90
	c. 500 lux	negative: 48%	LANGECKER, 1989, 90
Tinaya fish			
	c. 500 lux	positive: 66%	
Piedras fish			
Yerbaniz fish	c. 1400 lux	negative: 41%	
	c. 1400 lux	negative: 32%	
(2) Cyprinidae			
Caecobarbus geertsii	45 lux	negative: 4%	THINÈS, 1954
	c. 50 lux	negative	THINÈS, 1958
Phreatichthys andruzzii	90x103•w/m^2	negative: 13%	ERCOLINI & BERTI, 1975
Barbopsis devecchii	137x103•m/m^2	negative: 46%	ERCOLINI & BERTI, 1978
Typlogarra widdowsoni	30 lux	negative: 42%	MARSHALL & THINÈS, 1958
(3) Pimelodidae			
Pimelodella kronei	150 lux	negative: 41%	TRAJANO, 1987
Rhamdia reddelli	c. 600 lux	negative: 21%	WILKENS et al., 1991
Rhamdia spec., Ostoc fish	c. 600 lux	negative: 6%	WILKENS et al., 1991
(4) Clariidae			
Uegitglanis zammaranoi	137x103•w/m^2	negative: 47%	ERCOLINI & BERTI, 1977
(5) Amblyopsidae			
Chologaster agassizi			
	daylight	negative	EIGENMANN, 1909
Amblyopsis spelaea		negative	POULSON, 1964
		negative: 22%	PAYNE, 1907
Amblyopsis rosae	daylight	negative: 36%	EIGENMANN, 1909
		negative	POULSON, 1963
(6) Ophiidae			
Lucifuga subterranea	daylight	negative	EIGENMANN, 1909
Stygocola dentatus	daylight	negative	EIGENMANN, 1909

Species	Light intensity	Result (Mean phototactic index)	Authors
CRUSTACEA			
Galatheidae *Munidopsis polymorpha*	3 lux	negative	RODRIGUEZ, 1996
Isopoda *Caecidothea stygia*	80 lux	negative	BANTA, 1907
Amphipoda *Niphargus orcinus*	50-100 lux	negative	GINET, 1960

Locomotory activitiy

In general, most of the cave fishes studied have a quite different swimming behaviour versus their epigean relatives. The epigean characid *Astyanax fasciatus*, for example, living in clear Central American freshwaters, is active during the day and feeds by rapid swimming movements on every prey that moves. It can immediately switch from hovering motionless in the free water to rapid darting. This type of locomotion is also involved in territoriality and aggressive behaviour. The blind population, however, shows a permanent gliding through the free water at a low velocity (PARZEFALL unpubl.). This type of swimming behaviour is also common in the cave brotulid *Typhliasina (Ogilbia) pearsei* (unpubl. observ.) from Yucatan, Mexico. The brotulids *Caecogilbia (Ogilbia) galapagosensis* and *C. deroyi* from coastal brackish cave waters have been described by VAN MOL (1967) as slow swimmers. An epigean relative *Grammonus (Oligopus) ater* with well-developed eyes has been observed by RIEDL (1966) in the Mediterranean Sea during the night in marginal caves swimming near the walls.

Many cave-dwelling invertebrates have been characterized as less active in connection with a low metabolic rate (HÜPPOP 1985), but exact comparative data on swimming speed in cave dwellers are lacking. On the other hand, more data are available for the deep sea; they reveal a comparable situation for the animals there: the bathypelagic mysid *Gnathophausia ingens,* for example, has a reduced swimming capacity compared to shallower-living species. This mysid species is described as constantly swimming, without a tendency for hanging motionless in the water (COWLES and CHILDRESS 1988).

SULLIVAN and SOMERO (1980) measuring the enzyme activities (LDH, MDH, PK) in fish skeletal muscle and brain, found that certain deep-sea fishes have only minimal capacities for active locomotion compared to shallow-living species. Within the deep-sea fishes, the benthopelagic rattails (Macrouridae) and sablefish (Anoplopomatidae) have the highest enzyme activities. Active pelagic swimmers have much higher activities of LDH and PK than sit-and-wait predators. CHILDRESS (1995) states that reduced locomotory activity is a common phenomenon in deep-sea animals. This topic will be dealt with when food and feeding strategies are discussed.

Food and feeding activities

Here, the situation in caves will be compared with the sunless bathypelagic and bathybenthic zone, which is the largest and most deserted of all major living spaces in the ocean. In both habitats, food must be brought in from outside the system: cave animals depend on material which comes in by floods or via other animals like bats leaving guano, and deep-sea animals depend on the rain of organic material.

An exception - excluded in this paper - in both systems are chemoautotrophic communities around hydrothermal vents in either the deep sea or in caves with sulfurous waters like the Cueva del Azufre in Tabasco, Mexico (PETERS et al. 1973) or the recently discovered Movile cave near the Black Sea in Romania (SARBU and POPA 1992).

Omitting these chemoautotrophic systems, one can state that food in general is abundant neither in caves nor in the bathyal. The occurrence of food is mostly aperiodic and unpredictable, except where it occurs seasonally and predictably under the migration routes of certain fish species (TYLER 1988) in the deep sea or in connection with rainy seasons in tropical cave regions. Two main trends concerning feeding strategies are apparent in the deep sea. The first is that most abyssal taxa are deposit feeders: suspension feeders decrease with increasing depth. The second trend is that carnivore specialists become scarce with increasing depth and omnivorus scavengers become more important (GAGE and TYLER 1991). Stomach analyses show an apparent lack in selectivity of predatory species, especially fishes (MAUCHLINE and GORDON 1984, 1985). The benthopelagic macrourid fishes seem to feed on multi-species patches, and four types of feeding strategies may be distinguished (MAUCHLINE and GORDON 1986). One should expect the development of special mechanisms to find the scarce food in the darkness and to survive changing food quantities.

In cave dwellers we have more data about such adaptation mechanisms: cave fishes are better prey detectors than their above-ground relatives, as demonstrated by POULSON (1963) in amblyopsid fishes: the blind *Amblyopsis* *spelea* found a prey hours before the partial troglobyte *Chologaster agassizi* did. In contrast, *C. agassizi* ate all ten *Daphnia* in an aquarium before *A. spelea* had eaten half this amount (POULSON and WHITE 1969). In addition, the maximal prey detection distance is greater in the cave species. In the characid *Astyanax fasciatus,* competition experiments led to similiar results: in a limited time, the cave specimens found 80 % of the food, the epigean only 20 % (HÜPPOP 1987). The cave fish are able to built up enormous fat reserves. One-year-old cave fish fed ad libidum had a mean fat content of 37 % fresh body mass compared to 9 % in epigean fish under the same conditions (HÜPPOP 1989). Cave animals are able to survive for long periods without food - nearly one year in invertebrates up to several years in cave fishes and salamanders (VANDEL 1964). These findings are in accordance with the reduced metabolic rates in cave dwellers versus epigean relatives (HÜPPOP 1985). Keeping in mind the comparable situation for the metabolism in deep-sea animals (CHILDRESS 1995), we can suggest similar behavioural adaptations in the deep sea.

Reproductive behaviour

Sucessfull reproduction in lightless habitats is based mainly on chemical communication. First, males have to find the females, and then they need behaviour patterns to provide effective fertilisation in the absence of any visual orientation. The galatheid crab *Munidopsis polymorpha* of the marine lava cave on Lanzarote receives a chemical signal by moulting females ready for reproduction. Arriving near the female, the male has to prevent flight reaction by rhythmic movements of his chelipeds at a distance of a few centimetres (Fig. 12). On the basis of such movements and contacts of the long antennae, the female accepts the copulation or escapes. The female has to choose the fittest male for reproduction without any optical signal (PARZEFALL and WILKENS 1975). In the characid fish *Astyanax fasciatus,* a similar situation has been found: the female produces a chemical substance in the genital region and restricts her movements to a small area. There is evidence that the female also marks the substrate by contact with the genital region. The swimming activity of the male increases after contact with such a female. He then swims parallel and tries to achieve contact using fine hooks on his anal fin in order to spawn in the free water (WILKENS 1972). In cave-living salamanders like *Proteus anguinus,* chemical signals on the substrate and in the free water are very important for intraspecific communication and reproduction. All the cave dwellers studied already brought such a system from their epigean ancestors. There is no known case up to now in which the reproductive behaviour in the epigean form is based on optical releasers being reduced in the cave form (PARZEFALL 1992).

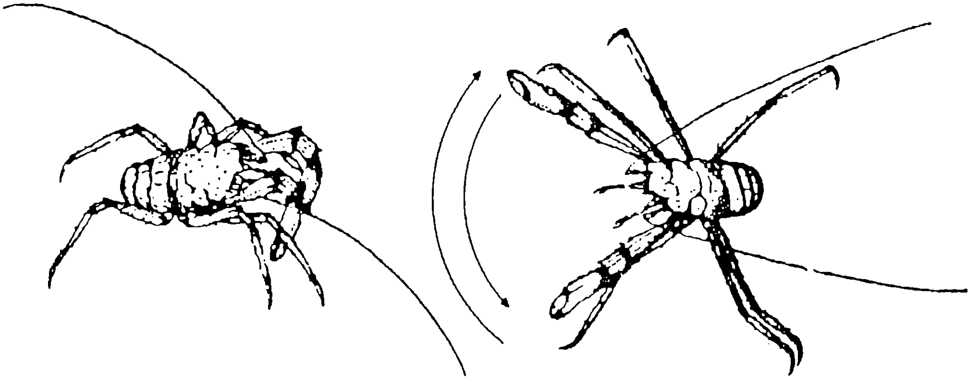

Fig. 12: Sexual behaviour in *Munidopsis polymorpha* from the marine lava cave Jameos del Agua, Lanzarote, Canary Islands. The male (right) shows cheliped shaking in front of the female (PARZEFALL and WILKENS 1975).

From the distribution data of individual species in the deep sea, we know that the population density of many species is low and therefore chemical communication must be an important factor for finding the sexual partner. The fact that the posterior nostril becomes enlarged in breeding males of halosaurs, i.e., the genus *Aldrovandia,* is an indication for the importance of female chemical signals. In addition, light signals may help to bring the sexual partners of some species together (MARSHALL 1979). In such a habitat one may expect a higher number of hermaphroditic species, but, like in shallow water, most deep-sea invertebrates have separate sexes with external fertilisation (GAGE and TYLER 1991). The chance for a successful fertilisation may also increase by living in aggregations, seasonal breeding, or long-term storage of ripe sexual products.

Aggressive Behaviour

Intraspecific aggression is a basic pattern of social behaviour to defend resources like food, space for reproduction, and sexual partners. The behavioural repertoire consists of threatening, attack, and submission. The most effective visual system cannot be used by animals living in the darkness. Nevertheless, most of the cave dwellers studied seem to exhibit aggressive behavour as well in darkness: the galatheid crab *Munidopsis polymorpha,* for example, which has already been described in the section on reproductive behaviour, is aggressive year round. While resting or feeding, the animals maintain a minimal distance from one another depending on the length of their second antennae. Within this distance, *Munidopsis* attacks with extended chelipeds (Fig. 13). Using dummies, we were able to demonstrate that this behaviour depends not on optical releasers but on water movement (PARZE-

FALL and WILKENS 1975). All the cave fishes studied apparently also exhibit agonistic behaviour consisting of biting, chasing, and tailbeating. In those species we could compare with epigean relatives, however, differences were found: in general the fishes fight in close body contact or send waterwaves at a short distance to the opponent. In the epigean *Astyanax fasciatus*, for example, both sexes defend small size-dependent food territories. They school only briefly when disturbed by a predator. The blind cave populations cease schooling and the single fish swim normally throughout the cave pool without aggressive contact. The cave fish become territorial only after a longer period without food. Then, small territories measuring a few centimeters will be defended by biting and tailbeating in close body-contact (HAUSBERG 1995). Thus, the aggression seems to have changed in adaptation to the new habitat.

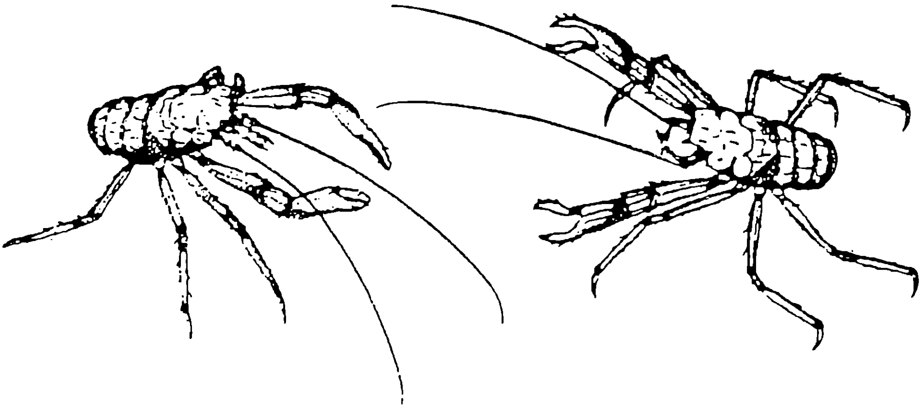

Fig. 13: Aggressive behaviour in *Munidopsis polymorpha*, threatening with chelipeds (PARZEFALL and WILKENS 1975).

Aggression probably also exists in the deep sea. The galatheid crab *Munida sarsi,* caught in 240 m depth near Bergen (Norway), showed the same aggressive pattern as described above for *Munidopsis*. Models triggered this behaviour only when they were made to move (BERRILL 1970). The galatheids identified on the videoclips of thermal vents present their extended chelipeds to neighbouring conspecifics, comparable to the aggressive behaviour described above for *Munidopsis polymorpha* from a shallow-water lava cave on Lanzarote. COHEN and HAEDRICH (1983) who analyzed the fish fauna of the Galapagos thermal vent region based on time-lapse photographs, described the macrourid species *Coryphaenoides bulbiceps* as attracted by bait and feeding aggressively, singly or in groups of 2 to 6 specimens. However, the authors do not report aggressiveness for the other 19 species identified. At 4800 m depth of the Porcupine Abyssal Plain, the movements of several fish species were monitored by inducing them to ingest acoustic pingers or transponders embedded in bait deployed on the sea floor. All fish consuming transponders swam out of range within 12 h and none has ever returned within range of the sonar system. There were no signs of home range or territoriality in the species studied (*Coryphaenoides armatus, Antimora rostrata, Centroscymnus coelolepis).* These fishes are therefore either entirely nomadic or have home ranges greatly exceeding the 1 km diameter zone scanned by the sonar system (BAGLEY et al. 1994).

Dorsal light reaction

With some exceptions, nearly all fishes swim with their back towards the light. This vertical orientation of the dorso-ventral axis is triggered by the direction of light and gravity. If the light direction changes, the fish show a compensatory reaction. This reaction results in a deviation of the normal vertical position and can be experimentally measured as an angle of inclination. The angle is species-specific and genetically controlled. The dorsal light reaction depends on the functioning of the eyes.

In behavioural studies of the characid *Astyanax fasciatus* using cross breedings with functional eyes, LANGECKER (1990, 1993) found that the angle of inclination must have changed in the cave fish. Using a phylogenetically young cave population of the same species (Micos fish) after selection for functional eyes yielded comparable results. This system is - independently from the eyes - almost completely regressed in the cave fish. The regression is genetically based on a system of at least three genetic factors (LANGECKER 1990). To date, no other aquatic cave dwellers or deep-sea fishes have been tested for this behaviour pattern.

Circadian clock

The circadian clock in animals has to be synchronized by external stimuli termed Zeitgeber or forcing signals, which principally involve light and temperature. These stimuli are normally absent in caves. Studies on the locomotory activity of different taxa have shown that cave dwellers in general exhibit no or doubtful locomotory periodicities. In highly adapted cavernicolous animals under constant experimental conditions, no precise daily periodicities could be detected. Thus, circadian oscillations of the metabolism appear to be unnecessary to maintain internal stability (LAMPRECHT and WEBER 1992). One might expect a comparable situation in deep-sea animals living in the permanent darkness, but no data are currently available.

Life history

Life histories in cave animals are characterized by increasing egg size and parental care, increased generation times associated with increased age at first reproduction, and longevity. The blind cave salamander *Proteus anguinus* starts reproduction at about 7 years and reaches an age between 30 and 40 years (BRIEGLEB 1962). Comparing the life-spans of different amblyopsid fishes reveals that with increasing evolutionary time in caves, the times until hatching and attainment of sexual maturity are increased (Fig. 14) and the mean number of ova are becoming smaller and the volume of ova larger. This corresponds to the classic pattern of K-selected species (CULVER 1982). Certain cave amblyopsids do not reproduce every year because of food or mate scarcity (POULSON 1971). This trend has been demonstrated even in the cave populations of the characid *Astyanax fasciatus*. They have a significantly greater yolk content, and this difference has a genetic basis (HÜPPOP and WILKENS 1991). Our field data also indicate an irregular reproduction (PARZEFALL 1983). Most deep-sea organisms support the paradigm given for the cave fish (POULSON 1964). The female of the cave galatheid *Munidopsis polymorpha* carries a few big eggs (1-8) under the abdomen (WILKENS et al. 1990).

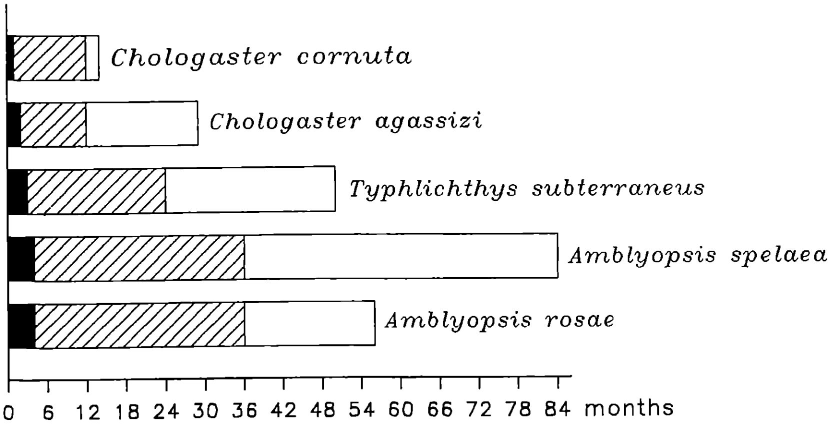

Fig. 14: Lifespans of species of amblyopsid fishes. Black bar is the time to hatching, striped bar is time from hatching to first reproduction, open bar is reproductive lifespan (CULVER 1982, POULSON 1963).

Among bathypelagic and bathybenthic forms there are many species of fishes or molluscs that follow the rules outlined above for cave dwellers. Other taxa, however, i.e., brittlestars do not follow these predictions. The increased data makes it difficult to speak of a typical deep-sea life history: the complexity of the deep sea does not allow such an oversimplification (GAGE and TYLER 1991).

Discussion

How can we explain the demonstrated behavioural and morphological changes and are these explanations congruent for cave and deep-sea dwellers? In discussing regressive traits in cave animals, one cannot neglect the interesting possibility that selection may play a minor role compared with the accumulation of neutral mutations and genetic drift.

It was mainly KOSSWIG (1948, 1963) who demonstrated that eyes and pigmentation show a high variability in many cave animals. His hypothesis was that the absence of stabilizing selection allows an accumulation of selectively neutral mutations, and that variability within a population decreases during cave life due to mutation pressure. This leads, in phylogenetically old cave populations, to genetic homozygosity and diminished variability for the reduced pattern. This hypothesis received support in recent years from the neutral mutation theory of molecular evolution promoted by KIMURA (1987).

Other authors favour selective explanations involving selection for increased metabolic economy (POULSON 1963) or indirect effects of pleiotropy (BARR 1968). There is a general consensus that differentiation of cave populations cannot occur when there is gene exchange with surface populations. The present paper suggests that this condition is also fullfilled in bathybenthic and bathypelagic species.

On this basis, the neutral mutation theory seems to be the most plausible of the above mentioned hypotheses to explain eye and pigment reduction as well as the reduction of the dorsal light reaction and the circadian clock. The different degree of the reduction, for example of the eye, could be due to the different phylogenetic time for the colonisation of the lightless habitat or to an ongoing migration to illuminated zones. In those deep-sea colonizers that use the light signals of the prey or the partner, the eyes should only be reduced to a certain degree.

All the other traits presented seem to be the result of an adaptation process. The selective advantages must be studied for each trait separately. Here, only some possible explanations with regard to cave animals can be offered: these explanations can be similar in deep-sea animals on the basis of the parallel development of the traits presented. Especially for the deep-sea animals, however, experimental work has to prove the adaptive significance for each trait studied.

Summary

Deep-sea and cave dwellers show various degrees of eye reduction in fishes and invertebrates. The degree is positively correlated with the depth range in the deep sea. This paper presents examples in different taxa. In fishes, emphasis is placed mainly on the Ophidiiformes. Correlated to changes in the eye, the melanin pigmentation has been reduced to varying degrees. According to our present state of knowledge, both traits are not genetically linked. These animals also exhibit constructive traits to compensate the disadvantages of life in the dark. Many species in both habitats have developed long body appendages. The lateral-line sense has been improved. Bioluminescence and sound production is restricted to certain deep-sea taxa only. Behavioural changes have been described for the phototactic behaviour, the locomotory activity, food and feeding, reproductive and aggressive behaviour, as well as for the dorsal light reaction and circadian rhythm - mainly in cave dwellers. Comparative data for deep-sea animals are scarce. The life histories of cave and many deep-sea dwellers are characterized by increasing egg size, decreasing egg number, parental care, increased generation times associated with increased age at first reproduction, and longevity. The behavioural and morphological changes presented are discussed on the basis of the neutral mutation theory.

References

ANDRIASHEV, A.P., 1953: Ancient deep-water and secondarily deep-water fishes and their importance in a zoogeographical analysis. - In: Notes on special problems in ichthyology. - Moscow, Leningrad: Akad. Nauk SSSR, Ikhiol. Komm. (Translation from Ichthyol. Lab., Bureau of Comm. Fisheries, Washington DC).

BAGLEY, P. M., SMITH, A., PRIEDE, I. G., 1994: Tracking movements of deep demersal fishes in the Porcupine Seabight, North-East Atlantic Ocean. - J. Mar. Biol. Assoc. U.K. **74**: 473-480.

BALL, E. E., COWAN, A. N., 1977: Ultrastructure of the antennal sensilla of *Acetes* (Crustacea, Decapoda, Natantia, Sergestidae). - Philos. Trans. R. Soc. Lond. B. **277**: 429-457.

BANTA, A. M., 1907: The fauna of Mayfield's cave. - Publ. Carnegie Inst. **67**: 1-114.

BARR, T. C., 1968: Cave ecology and evolution of troglobites. - Evol. Biol. **2**: 35-102.

BERNASCONI, R., RIEDEL, A., 1994: Mollusca. - In JUBERTHIE, Ch., DECU, V., (Eds): Encylop. Biospeleol. **1**: 53-61.

BERRILL, M., 1970: The aggressive behaviour of *Munida sarsi* (Crustacea: Galatheidae). - Sarsia **43**: 1-11.

BIRSTEIN, J. A., ZARENKOV, N. A., 1970: On the bottom decapods (Crustacea, Decapoda) of the Kurile-Kamchatka region. - Tr. Inst. Okeanol. Akad. Nauk SSSR **86**: 420-426.

BOWMAN, T. E., 1994: Mictacea. - In JUBERTHIE, Ch., DECU, V., (Eds): Encyclop. Biospeleol. 1: 121-122.

BREDER, C. M., RASQUIN, P., 1947:Comparative studies in the light sensitivity of blind characins from a series of Mexican caves. - Bull. Am. Mus. Nat. Hist. **89**: 325-351.

BRIEGLEB, W., 1962: Zur Biologie und Ökologie des Grottenolms *Proteus anguinus* LAUR. (1768). - Z. Morphol. Oekol. Tiere **51**: 271-334.

CHILDRESS, J.J., 1995: Are there physiological and biochemical adaptations of metabolism in deep-sea animals? - TREE **10**: 30-36.

CHUN, C., 1914: Cephalopoda from the Michael Sars North Atlantic Deep-Sea Expedition. - Rep. Michael Sars N. Atl. Deep Sea Exped. **3**: 1-28.

CLARKE, G. L., 1970: Light conditions in the sea in relation to the diurnal vertical migrations of animals, pp. 41-50. - Proc. Intern. Symp. Biol. Sound Scattering in Ocean. Maury Center for Ocean Science,Washington DC.

COHEN, D. M., HAEDRICH, R. L., 1983: The fish fauna of the Galapagos thermal vent region. - Deep-Sea Res. **30**: 371-379.

COINEAU, N., HENRY, J. P., MAGNIEZ, G., NEGOESCU, I., 1994: Isopoda aquatica. - In JUBERTHIE, Ch., DECU, V., (Eds): Encyclop. Biospeleol. **1**: 123-140.

COWLES, D. L., CHILDRESS, J. J., 1988: Swimming speed and oxygen consumption in the bathypelagic mysid *Gnathophausia ingens*. - Biol. Bull. Woods Hole Mass. **175**: 111-121.

CULVER, D. C., 1982: Cave life. Evolution and Ecology. - Harvard: Harvard Univ. Pr.

EIGENMANN, C. H., 1909: Cave vertebrates of America. A study in degenerative evolution. - Carnegie Inst. Washington Publ. **104**: 1-241.

ELOFSSON, R., HALLBERG ,E., 1977: Compound eyes of some deep-sea and fjord mysid crustaceans. - Acta Zool. 58: 169-177.

ERCOLINI, A., BERTI, R., 1975: Light sensitivity experiments and morphology studies of the blind phreatic fish *Phreatichthys andruzzii* VINCIGUERRA from Somalia. - Monit Zool. Ital.(NS) Suppl. **6**: 29-43.

ERCOLINI, A., BERTI, R., 1977: Morphology and response to light of *Uegitglanis zammaranoi* GIANFERRARI, anophthalmic phreatic fish from Somalia. - Monit. Zool. Ital. (NS) Suppl. **10**: 183-199.

FONG, D. W., 1989: Morphological evolution in the amphipod *Gammarus minus* in caves: quantitative genetic analysis. - Amer. Midl. Nat. **121**: 361-378.

GAGE, J. D., TYLER, P. A., 1991: Deep-sea biology: a natural history of organisms at the deep-sea floor. - Cambridge: Cambridge Univ. Pr.

GERTYCHOWA, R., 1970: Studies on the ethology and space orientation of the blind cave fish *Anoptichthys jordani* HUBBS and INNES 1936 (Characidae). - Folia Biol. **18**: 9-69.

GINET, R., 1960: Écologie,éthologie et biologie de *Niphargus* (amphipodes, gammaridés hypogés). - Ann. Spéléol. **15**: 127-376.

GUINOT, D., 1994: Decapoda brachyura. - In JUBERHIE, Ch., DECU, V., (Eds): Encyclop. Biospeleol. **1**: 165-179.

HARMS,W., 1921: Das rudimentäre Sehorgan eines Höhlendekapoden *Munidopsis polymorpha* KOELBEL. - Zool. Anz. **52**: 1010-1115.

HART, C. W. Jr., MANNING, R. B., 1981: The cavernicolous caridean shrimps of Bermuda (Alpheidae, Hippolythidae and Atyidae). - J. Crust. Biol. **1**: 441-456.

HARTMANN-SCHRÖDER, G., 1974: Die Unterfamilie Macellicephalinae HARTMANN-SCHRÖDER 1971 (Polynoidae, Polychaeta). Mit Beschreibung einer neuen Art, *Macellicephala jameensis,* n.sp. aus einem Höhlengewässer von Lanzarote (Kanarische Inseln). - Mitt. hamb. Zool. Mus. Inst. **71**: 75-85.

HASSAN, El. S., 1985: Mathematical analysis of the stimulus for the lateral line organ. - Biol. Cybern. **52**: 23-36.

HAUSBERG, C., 1994: Das Aggressionsverhalten von *Astyanax fasciatus* (Characidae, Teleostei): Zur Ontogenie, Genetik und Evolution der epigäischen und hypogäischen Form. - Ph. D. Thesis Univ. Hamburg.

HERRING, P. J., 1974: New observations on the bioluminescence of echinoderms. - J. Zool. Lond. **172**: 401-418.

HERRING, P. J., 1977: Bioluminescence of marine organisms. - Nature **267**: 788-793.

HOLSINGER, J., 1994: Amphipoda. - In JUBERHTIE, Ch., DECU, V., (Eds): Encylop. Biospeleol. **1**: 147-163.

HORRIDGE, G. A., BULTON, P. S., 1977: Prey detection by Chaetognatha via a vibration sense. - Proc. R. Soc. London B. **168**: 413-419.

HÜPPOP, K., 1985: The role of metabolism in the evolution of cave animals. - NSS Bull. **47**: 136 -146.

HÜPPOP, K., 1987: Food finding ability in cave fish (*Astyanax fasciatus)*. - Int. J. Speleol. **16**: 59-66.

HÜPPOP, K., 1989: Genetic analysis of oxygen consumption rate in cave and surface fish of *Astyanx fasciatus* (Characidae, Pisces). - Mém. Biospéol. **16**: 169-176.

HÜPPOP, K., WILKENS, H., 1991: Bigger eggs in subterranean *Astyanax fasciatus* (Characidae, Pisces). Their significance and genetics. - Z. zool. Syst. Evolutionsforsch. **29**: 280-288.

ILIFFE, T. M., WILKENS, H., PARZEFALL, J., WILLIAMS, D., 1984: Marine lava cave fauna: composition, biogeography and origins. - Science **225**: 309-311.

KIMURA, J. E., 1987: Die Neutralitätstheorie der molekularen Evolution. - Berlin: Paul Parey.

KOSSWIG, C., 1948: Genetische Beiträge zur Präadaptationtheorie. - Istanbul. Univ. Fen. Fak. Mecm. Seri. B. **13**: 176-209.

KOSSWIG, C., 1963: Genetische Analyse konstruktiver und degenerativer Evolutionsprozesse. - Z. zool. Syst. Evolutionsforsch. **1**: 205-239.

LAGARDÈRE, J.P., 1985: Biogéographie et composition taxonomique du peuplement abyssal de Mysidacés. - In LAUBIER, L., MONNIOT, C., (Eds): Peuplements profonds du golfe de Gascogne, pp. 425-428. - Brest: Institut francais de recherche pour éxploitation de la mer.

LAMPRECHT, G., WEBER, F., 1992: Spontaneous locomotion behaviour in cavernicolous animals: the regression of the endogenous circadian system. - In CAMACHO, A. I., (Ed.): The natural history of biospeleology, pp. 225-262. Madrid: Monogr. Mus. Nac. Cienc. Nat.

LANGECKER, T. G., 1990: Der Einfluß des Lichtes bei der Evolution von Höhlenfischen. - Ph. D. Thesis Univ. Hamburg.

LANGECKER, T. G., 1992: Light sensitivity of cave vertebrates. Behavioural and morphological aspects. In CAMACHO, A. I., (Ed.): The natural history of biospeleology, pp. 295-326. - Madrid: Monogr. Mus. Nac. Cienc. Nat.

LANGECKER, T. G., 1993: Genetic analysis of the dorsal light reaction in epigean and cave dwelling *Astyanax fasciatus* (Teleostei, Characidae). - Ethol. Ecol. Evol. **3**: 357-364

LANGECKER, T. G., LONGLEY, G., 1993: Blind catfish (*Trogloglanis pattersoni* and *Satan eurystomus)* from deep artesian waters: a study on convergent adaptation to cave and deep sea biota. - In SCHRÖDER, J., BAUER, J., SCHARTL, M., (Eds): Trends in Ichthyology. GSF-Bericht, pp. 239-257. Blackwell Scient. Publ.

LANGECKER, T. G., SCHMALE, H., WILKENS, H., 1993: Transcription of the opsin gene in degenerate eyes of cave dwelling *Astyanax fasciatus* (Teleostei, Characidae) and of its conspecific epigean ancestor during early ontogeny. - Cell Tissue Res. **273**: 183-192.

LEMCHE, H., HANSEN, B., MADSEN, F. J., TENDAL, O. S., WOLFF, T., 1976: Hadal life as analyzed from photographs. - Widenskablige Meddelelser fra Dansk. - Naturhistorik Forening **139:** 263-336.

LONGLEY, G., KARNEI, H., 1979: Status of *Trogloglanis pattersoni* EIGENMANN, the toothless blindcat, and status of *Satan eurystomus* HUBBS and BAILEY, the wide mouth blindcat. - U.S. Wildlife Service, Albuquerque NM, Endangered Species Report **5**: 1-45.

LÜLING, K. H., 1954: Untersuchungen am Blindfisch *Anoptichthys jordani* HUBBS and INNES (Characidae). - Zool. Jahrb. Abt. Zool. Phys. **65**: 9-42.

MARSHALL, N. B., 1962: The biology of sound producing fishes. - Symp. Zool. Soc. London **7**: 45-60.

MARSHALL, N. B., 1964: Bathypelagic macrourid fishes. - Copeia **1964**: 86 -93.

MARSHALL, N. B. 1971: Exploration in the life of fishes. - Cambridge MA: Harvard Univ. Pr.

MARSHALL, N. B., 1979: Developments in deep-sea biology. Poole Dorset: Blandfort Pr.

MARSHALL, N. B., THINÈS, G., 1958: Studies of the brain, sense organs and light sensitivity of a blind cave fish (*Typhlogarra widowsoni*) from Iraq. - Proc. Zool. Soc. London **131**: 441-456.

MAUCHLINE, J., GORDON, J. D. M., 1984: Diets and bathmetric distribution of the macourid fish of the Rockall Trough, northeastern Atlantic. - Mar. Biol. **81:** 107 -121.

MAUCHLINE, J., GORDON, J. D. M., 1985: Trophic diversity in deep-sea fish. - J. Fish Biol. **26**: 527-535.

MAUCHLINE, J., GORDON, J. D. M., 1986: Foraging strategies in deep-sea fish. - Mar. Ecol. Prog. Ser. **27**: 227-238.

MENZIES, R. J., GEORGE, R. Y., ROWE, G. T., 1973: Abyssal environment and ecology of the world oceans. - New York, London: John Wiley.

PARZEFALL, J., 1983: Field observation in epigean and cave population of the Mexican characid *Astyanax mexicanus* (Pisces, Characidae). - Mém. Biospéol. **10**: 171-176.

PARZEFALL, J., 1986: Behavioural preadaption of marine species for the colonisation of caves. - Stygologia **2**: 144-155.

PARZEFALL, J., 1992: Behavioural aspects in animals living in caves. - In CAMACHO, A.., (Ed.): The natural history of biospeleogy. - Madrid: Monogr. Mus. Nac. Scien. Nat. 327-376.

PARZEFALL, J., WILKENS, H., 1975: Zur Ethologie augenreduzierter Tiere: Untersuchungen an *Munidopsis polymorpha* KOELBEL (Anomura, Galatheidae). - Ann. Spéléol. **30**: 325-335.

PAYNE, F., 1907: The reaction of the blind fish *Amblyopsis spelaeus* to light. - Biol. Bull. Woods Hole Mass. **13**: 317-323.

PESCE, G., JUBERTHIE-JUPEAU, L., PASSELAIGUE, F., 1994: Mysidacea. In JUBERTHIE, Ch., DECU, V., (Eds): Encyclop. Biospeleol. **1**: 111-113.

PETERS, N., PETERS, G., PARZEFALL, J., WILKENS, H., 1973: Über degenerative und konstruktive Merkmale einer phylogenetisch jungen Höhlenform von *Poecilia sphenops* (Pisces, Poeciliidae). - Int. Rev. gesamten Hydrobiol. **58:** 417- 443.

POULSON, T. L., 1963: Cave adaptation in amblyopsid fishes. - Amer. Midl. Nat. **70:** 257- 290.

POULSON, T. L., 1964: Animals in aquatic environments: animals in caves. - In DILL, D. B., (Ed.): Adaptation to the environment. Handbook of Physiol. **4,** pp. 749-771. - Baltimore: Williams & Wilkins.

POULSON, T. L., 1971: Biology of cave and deep sea organisms: a comparison. - Nat. Speleol. Soc. Bull. **33:** 51-61.

POULSON, T. L., WHITE, W. B., 1969: The cave environment. - Science **165:** 971-981.

REX, M. A., 1976: Biological acccomodation in the deep sea benthos: comparative evidence on the importance of predation and productivity. - Deep-Sea Res. **23**: 975-988.

REX, M. A., 1977: Zonation in deep-sea gastropods: The importance of biological interactions to rates of zonation. - In KEEGAN, B. F., CEIDIG, P. O., BOADEN, P. J. S., (Eds): Biology of benthic organisms, pp. 521-530. - Oxford, New York: Pergamon Pr.

RIEDL, R., 1966: Biologie der Meereshöhlen. - Hamburg, Berlin: Paul Parey.

RODRIGUEZ, E., 1996: Light-reaction and eye-regression of cavernicolous animals from the Jameos del Aqua (Lanzarote, Canary Islands). - In UIBLEIN, F., OTT, J., STACHOWITSCH, M., (Eds): Deep-sea and extreme shallow-water habitats: affinities and adaptations. - Biosyst. Ecol. Ser. **11**: 145-150.

SANDERS, H. L., HESSLER, R. R., GARNER, S. P., 1985: *Hirsutia bathyalis*, a new unusal deep-sea benthic peracaridian crustacean from the tropical Atlantic. - J. Crust. Biol. **5**: 30-37.

SCHEMMEL, C., 1977: Zur Morphologie und Funktion der Sinnesorgane von *Typhliasina pearsei* (Hubbs). - Zoomorph. **87**: 191-202.

SARBU, S., POPA, R., 1992: A unique chemoautotrophically based cave ecosystem. - In CAMACHO, A. I., (Ed.): The natural history of biospeleology. - Madrid: Monogr. Mus. Nac. Cienc. Nat., pp. 637 - 663.

SULLIVAN, K. M., SOMERO, G. N., 1980: Enzyme activities of fish skeletal muscles and brain as influenced by depth of occurrence and habits of feeding and locomotion. - Mar. Biol. **60**: 91-99.

THINÈS, G., 1954: Etude comparative de la photosensibilité de poisson aveugle *Caecobarbus gertsii* BLGR et *Anophtichthys jordani* HUBBS et INNES. - Ann. Soc. R. Zool. Belg. **85**: 35-58.

THINÈS, G., 1958: Beobachtungen über die Phototaxis und die Thermotaxis des blinden Höhlenfisches *Caecobarbus gertsii* (Cyprinidae). - Experientia **14**: 381.

THINÈS, G., 1969: L'évolution régressive des poissons cavernicoles et abyssaux. - Paris: Masson et Cie.

TRAJANO, E., 1987: Biologia do bagre cavernicola *Pimelodella kronei* e de seu provavel ancestral, *Pimelodella transitoria* (Siluriformes, Pimelodidae). - Ph. D. Thesis Univ. Sao Paulo.

TSURNAMAL, M., 1978: The biology and ecology of the blind prawn, *Typhlocaris galilea* CALMAN. - Crustaceana **34:** 195-213.

TYLER, P. A.. 1988: Seasonality in the deep sea. - Oceanogr. Mar. Biol. Annu. Rev. **26**: 227 -258.

VANDEL, A., 1964: Biospéologie. La biologie des animaux cavernicoles. - Paris: Gauthier-Villars.

VAN MOL, J. J. C., 1967: Ecologie comparée de deux espèces de Brotulidae (Pisces) des îlles Galapagos: *Caecogilbia deroyi* POLL et VAN MOL 1967 et *C. galapagosensis* POLL et LELEUP 1965 . - Bull. Acad. R. Belg. Ser. **53**: 232-248.

WÄGELE, J. W., 1989: Evolution und phylogentisches System der Isopoda. Stand der Forschung und neue Erkenntnisse. - Zoologica **140**: 1-262.

WALD, G., RAYPORT, S., 1977: Vision in annelid worms. - Science **196**: 1434-1439.

WILKENS, H., 1970: Beiträge zur Degeneration des Melaninpigmentes bei cavernicolen Sippen des *Astyanax mexicanus* (FILIPPI). - Z. zool. Syst. Evolutionsforsch. **8**: 173-199.

WILKENS, H., 1972: Über Präadaptation für das Höhlenleben, untersucht am Laichverhalten ober- und unterirdischer Populationen des *Astyanax mexicanus*. - Zool. Anz. **188**: 1-11.

WILKENS,H., 1976: Genotypic and phenotypic variability in cave animals. Studies on a phylogentically young cave population of *Astyanax mexicanus* (FILIPPI). - Ann. Spéléol. **31**: 137-148.

WILKENS, H., 1988: Evolution and genetics of epigean and cave *Astyanax fasciatus* (Characidae, Pisces). - Evol. Biol. **23**: 271-367.

WILKENS, H., PARZEFALL, J., 1974: Die Ökologie der Jameos del Agua (Lanzarote). Zur Entwicklung limnischer Höhlentiere aus marinen Vorfahren. - Ann. Spéléol. **29**: 419-434.

WILKENS, H., JUNGE, P., LANGECKER, T. G., 1991: Speciation of troglobites: studies in the San Antonio cave (Oaxaca, Mexico). - Int. J. Speleol. **20**: 1-13.

WILKENS, H., PARZEFALL, J., RIBOWSKI, A., 1990: Population biology and larvae of the anchialine crab *Munidopsis polymorpha* (Galatheidae) from Lanzarote (Canary Islands). - J. Crust. Biol. **10**: 667-675.

Address of the author:

Jakob PARZEFALL, Zoologisches Institut und Zoologisches Museum der Universität Hamburg, Martin-Luther-King-Platz 3, D-20146 Hamburg, Germany.
E-mail: fb5a004@zoologie.uni-hamburg.de

Zeitschrift/Journal: Biosystematics and Ecology

Jahr/Year: 1996

Band/Volume: 11

Autor(en)/Author(s): Parzefall Jakob

Artikel/Article: I. Light. Behavioural and morphological changes caused by light conditions in deep-sea and shallow-water habitats. In: Deep Sea and Extreme Shallow-water Habitats: Affinities and Adaptations. 91-122