

## The darkness syndrome in subsurface-shallow and deep-sea dwelling Ostracoda (Crustacea)

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**Abstract:** Animals that permanently live either within subsurface habitats in shallow marine environments of consolidated and/or loosely packed sediments or on the bottom of the deep sea commonly display a complex of morphological and biological traits that is here termed the **darkness syndrome**. Classic examples are regressed ocular structures and body pigments, combined with the compensatory development of extra-optic sensorial traits. It is largely accepted that animals which adapt to the aphotic subsurface and deep-sea habitats become prisoners of their constraining environment. The Austrian zoologist Th. FUCHS, using examples from the Atlantic Ocean, was the first (1894) to propose a deep-sea origin for the shallow marine cave fauna. Modern biological literature offers additional arguments for this hypothesis. Here, evidence is presented for an alternative and/or additional scenario: shelf-dwelling animals, which are not strongly specialized for life in the photic environment, easily colonize deep-sea and/or shallow subsurface habitats. Examples from two major groups of ostracods, Podocopida and Halocyprida, are used in support of this latter evolutionary model.

### Introduction

The high biological richness of our planet Earth is partly due to photosynthesizing organisms, which efficiently capture and use solar energy. Much of the scientific effort in the past was dedicated to describing diversity of life, which evolved at the surface of the planet in well-illuminated habitats. Since antiquity, however, man has recognised that life also exists in darkness. The quest for answers as to why organisms have chosen to live in environments deprived of light and how such organisms adapted to living conditions perceived by man as very constraining, represents, what G. HOLTON (1986) would call a persistent cultural thema.

It is now fully realised that life in darkness is widespread. Both Earth's subsurface waters and large parts (more than two thirds) of the oceans are devoid of light. HUTCHINSON (1965) coined the term **allobiosphere** for the large domain where life exists without the participation of solar energy and the primary photosynthesizing producers.

The aquatic allobiosphere, in addition to the two characteristics mentioned above (extraordinary wide distribution and lack of light), was generally

viewed by several generations of naturalists as a more or less homogeneous, stable, and energetically poor environment (for review see *inter alia* EDWARDS 1988, GAGE and TYLER 1991, GINET and DECOU 1977). For many scientists one of the exciting queries was why do organisms which live in photic environments colonize and even adapt closely to the ecological conditions of the allobiosphere. Again, this question is of eminent interest from an evolutionary biology point of view because of the wide distribution of life in darkness. Unfortunately, none of the explanatory models proposed to date has gained wide acceptance.

Here, after a brief enumeration of some of the convergent morphological and biological specialisations displayed by animals inhabiting the aquatic allobiosphere, and which can metaphorically be termed the **darkness syndrome**, we shall contrast two evolutionary scenarios. They explain the causes and the pathways of the colonisation of the main environments of the allobiosphere, the deep sea (the bathial and hadal domains, where solar light no longer penetrates) and the shallow-marine subsurface habitats (the microporous habitats in loosely packed sediments, and/or the macroporous ones, such as coastal caves, which develop in solid rocks of various origins). The examples presented and/or discussed below are mainly chosen from carcinological studies, especially those dealing with Ostracoda. This is due to our long experience with this crustacean group and its wide documentation in both zoological and palaeontological literature.

## **The darkness syndrome, some peculiarities**

Animals which live in darkness display, in many cases, similar suits of traits. Generally, the optical structures, the vision capacities, and the body pigments are regressed or completely lacking; on the other hand, there may be a compensatory development of other sensorial structures (e.g., VANDEL 1965, MARGALEF 1976, GAGE and TYLER 1991, PARZEFALL 1996).

In many animal groups there is a reduction in limb strength. Such a condition has been described for the Crustacea Ostracoda, where there is a reduction of the carapace strength in many deep-sea species (BENSON 1975, 1984). The reduction in limb strength is probably related to the lower metabolic activity in both deep-sea and subterranean animals (CHILDRESS 1995, POULSEN 1971, CULVER 1982). Such traits are due either to the process of adaptation to the allobiospheric environment or they can originate from factors outside the allobiosphere; one speaks in the latter case of exaptations, or preadaptations, as discussed by DANIELOPOL and ROUCH (1991). The regression of ocular structures, at least in the case of the crustacean *Gammarus minus*

(Amphipoda), which lives in cave systems, is considered by CULVER et al. (1995) as an adaptive feature. It is produced by natural selection in order to economize the energy expenditure of those animals, which commonly live in darkness and oligotrophic habitats.

CHRISTIANSEN (1992) coined the term **troglomorphy** for cave-dwelling animals exhibiting the above-mentioned suit of traits. The striking convergence between troglomorphic traits and those occurring in deep-sea animals led us to propose here the more general concept of the **darkness syndrome**.

The shape of many aquatic allobiospheric animals seems to have a non-functional adaptive design. The monstrous appearance of deep-sea fishes was often emphasized (MARSHALL 1979). Similar strange creatures are also known to inhabit the subterranean environment, as recently (1992) discussed by ALBERCH (for the ostracod carapace shape, see discussion in DANIELOPOL 1980).

Animals that have acquired the **darkness syndrome** are sometimes considered to be prisoners of their environment because of their hyperspecialisation (see GINET and DECOU 1977 for such a discussion on the troglobite fauna). Therefore, many researchers consider that allobiospheric animals are unable to recolonize photic environments, where the struggle for life is much harder than in the quiet and stable deep-sea or groundwater environments. On the other hand, they can successfully extend their distribution into other dark habitats. For instance, deep-sea specialized species are able to colonize shallow marine caves if an ecological continuity between them exists. This plausible evolutionary model was first (1894) proposed by the Austrian naturalist Theodor FUCHS and will be discussed below.

## **Theodor FUCHS and the idea of a deep-sea origin for the marine cave fauna**

The Austrian naturalist Th. FUCHS was one of the personalities actively involved in the Austro-Hungarian deep-sea expeditions (SCHEFBECK 1991). In a short note (1894), FUCHS suggested that the marine cave fauna originates from deep-sea animals already adapted to life in darkness. His contention was based on two clear examples, i.e. the close phylogenetic relationships of the decapod *Munidopsis polymorpha*, from the shallow marine cave Jameos del Agua (Canary Islands), to other deep-sea Galatheidae species and the close relationships between the cavernicolous fish *Lucifuga dentata* from Cuba and deep-sea Ophidiidae. RACOVITZA (1907) extensively discussed FUCHS' scenario and concluded that a colonisation of shallow marine caves directly

from the deep sea is implausible. RACOVITZA (op. cit.) considered that there was too little convincing evidence supporting FUCHS' hypothesis. Moreover, he believed that the deep-sea fauna, which is closely adapted to a cold water environment, could not survive in the warmer water of the subtropical shallow marine caves. Several years later, however, RACOVITZA (1912) added an additional example to FUCHS' hypothesis based on the Cirolanidae Isopoda: the cavernicolous species described by him were considered related to deep-sea species. After this short period of interest for the deep-sea origin of the marine cave fauna, the FUCHS scenario was abandoned until recent times. From the early 1970s on, intensive exploration of marine caves in Southern Europe, Caribbean Islands, Bermuda, Canary Islands, Galapagos, Western Australia, etc. was carried out by various research groups (review *inter alia* in ILIFFE et al. 1984, HARMELIN 1986, MANING et al. 1986, WILKENS et al. 1986, HUMPHREYS and ADAMS 1991, ILIFFE 1992, VACELET 1996). They led to the discovery of several other cavernicolous animals displaying close affinities to deep-sea fauna. Especially interesting was the crustacean groups belonging to the Ostracoda Thaumatoctyprididae (Halocyprida), the Copepoda Misophrioida, and those of the order Mictacea (BOWMAN et al. 1985, BOXSHALL 1989, ILIFFE 1992).

DANIELOPOL (1972) emphasized, for the first time, that a thaumatoctypridid ostracod from an anchialine cave in Cuba was related to a deep-sea species, *Thaumatoctypris echinata*. Additional information was subsequently published by KORNICKER and his co-authors during the last twenty years (KORNICKER and SOHN 1976a, 1976b, KORNICKER and ILIFFE 1989a, 1989b, KORNICKER and YAGER 1996). Following the revision of the Thaumatoctyprididae ostracods by KORNICKER and SOHN (1976b), the troglobite thaumatoctypridids were assigned to the genus *Danielopolina* which also included a new deep-sea species, *D. carolinae*, collected in the South Atlantic off the Brazilian coast at 3459 m. Until recently, most of the cavernicolous *Danielopolina* were found in shallow marine caves located on both sides of the Central Atlantic, i.e., four species occur in the Caribbean region and two species on the Canary Islands (review in BALTANÁS and DANIELOPOL 1995). Two other species were found in the Pacific, i.e. on the Galapagos Islands (KORNICKER and ILIFFE 1989b) and in Western Australia (BALTANÁS, DANIELOPOL, HUMPHREYS unpubl.). Considering especially the Atlantic *Danielopolina* species, BOXSHALL (1989) suggested that the deep-sea species *D. carolinae* is morphologically the most primitive member of the genus compared with the anchialine species and therefore concluded that this ostracod group was a convincing example of deep-sea animal group which colonized shallow marine caves. KORNICKER and ILIFFE (1985) suggested that deep-sea halocypridids like *Danielopolina* and *Deeveya* species could penetrate into

deep crevicular channels at bathial or abyssal depths and spread up to the shallow anchialine caves due to the continuity in ecological conditions (darkness, temperature) between both environments. Their data represent an interesting revival of the FUCHS' scenario. However, one of the intriguing problems for both marine biologists and speleologists was why animals colonise the allobiosphere? On various occasions biologists suggested that some of the shelf marine animals are forced by various environmental pressures to retire into refugial territories like the deep sea and the marine caves, which offer less stressful and more stable ecological conditions (review in ROUCH and DANIELOPOL 1987, GAGE and TYLER 1991). Such an argument was used by KORNICKER and ILIFFE (1989b) to explain the migration of Thaumatoocyprididae into both habitats. These authors suggested (op. cit.) that *Danielopolina* species took refuge in the allobiospheric habitats, most probably during the Mesozoic, under the pressure of the more aggressive shelf competitors.

The deep-sea origin of the marine cave animals, especially Crustacea, was strongly challenged by STOCK (1986), who considered that during the late Mesozoic and early Tertiary the deep-sea fauna was decimated by long-term anoxic events and therefore the origin of the anchialine fauna should be better sought in shelf euryoxic forms. DANIELOPOL (1990), and more recently BALTANAS and DANIELOPOL (1995), forwarded morphological and phylogenetic arguments for an implausible deep-sea origin of the cavernicolous ostracod species of the Thaumatoocyprididae. Especially these latter authors showed, using a cladistic analysis of the living Thaumatoocyprididae, that the most primitive *Danielopolina* species is a shallow-dwelling form from Western Australia and not the deep-sea species *D. carolinae*. These data cast doubt on the validity of the deep-sea hypothesis, at least for the Thaumatoocyprididae group as argued by ILIFFE, BOXSHALL, and others (see above). Hence, we looked for an alternative scenario to better explain the origin of the subsurface shallow- and deep-sea ostracods (see below).

## **An alternative view on the origin of subsurface shallow- and deep-sea dwelling ostracod fauna**

### **A. The shallow-benthic origin scenario**

Free-living benthic animals are generally capable of actively selecting their habitat, i.e., they permanently explore their immediate environmental space in order to find appropriate energy resources; they are therefore able to expand, in time, their spatial distribution depending on the location of new propitious

habitats and under the premise that they do not encounter strong environmental constraints.

Generalists, i.e., those species which display ecological flexibility or broader ecological tolerances to the environmental conditions, have good chances to actively colonise new habitats.

Those shelf species that acquired traits which fit the **darkness syndrome** in shallow depths will more easily spread into the subsurface and/or deep-sea habitats. Marine benthic animals adapted to poorly illuminated shelf habitats, e.g., at the surface and/or within fine-grained sediments, generally display either negative or neutral phototactic reactions. Such habitats include flocculent superficial benthic sediments and/or sandy-silt sediments loaded with fine particulate organic matter. In both environments the penetration of light is reduced and oxygen concentrations are typically low.

The colonisation of new deep-sea habitats by benthic animals displaying the above-mentioned characteristics is facilitated in thermospheric marine systems with a reduced or poorly defined thermocline. Classic examples are the Tethys Ocean during the Mesozoic and the Paleogene time and/or the present-day Mediterranean and the Red Sea (MCKENZIE 1986, TÜRKAY 1986).

An additional factor which increases the success of stable faunal settlements within allobiospheric habitats is the capacity of such animals to develop or improve traits characteristic to the **darkness syndrome**.

The necessity for preadaptations for successful colonisation of allobiospheric habitats, like the subterranean ones, by epigeal animals was stressed by KOSSWIG and his students (e.g., KOSSWIG 1977, PARZEFALL 1986).

Finally, it should be mentioned that organisms highly specialized to live in photic environments have a theoretically lower chance of effectively colonising subsurface shallow- and deep-sea habitats.

The present colonisation scenario could be interpreted as a special case of the "active colonisation model" of ROUCH and DANIELOPOL (1987); it can also be interpreted as displaying analogies with the "zonation model" of ILIFFE (1986) and the "niche expansion scenario" of UIBLEIN (1995).

In the following we present several ostracod examples which support the shallow-benthic colonisation scenario.

## B. The Ostracoda evidence

The marine environment is dominated by two ostracod groups, the exclusively benthic Podocopida Cytheracea and the Myodocopa, which have both planktonic and benthic representatives. This latter group can be further divided in two groups relevant to our present topic: the Myodocopida and the Halocyprida. While the Podocopida have a medial naupliar eye and the Myodocopida have medial and lateral eyes (which can regress in allobiospheric species), the whole Halocyprida order is eyeless (KORNICKER and SOHN 1976b).

The Cytheracea, which appeared during the Paleozoic, strongly diversified, especially on the shelf, during the Middle and Upper Jurassic (WHATLEY and STEPHENS 1976) and still dominate the marine environment (HARTMANN 1989). One group, the Xestoleberididae, known since the Cretaceous, is particularly relevant to our present topic.

There are about 200 Recent and fossil Xestoleberididae species, classified within seven genera. Most xestoleberidids inhabit well-illuminated shallow-water habitats; a few species are adapted to interstitial sandy systems and deep-sea habitats (BONADUCE and DANIELOPOL 1988, DANIELOPOL and BONADUCE 1990, DANIELOPOL et al. 1995). One of the peculiarities of the Xestoleberididae group is the strong development of the ocular structures. The medial eye dissociates into three ocelli, and dioptric structures develop on the carapace of most of the species living in the photic environment. BONADUCE and DANIELOPOL (1988) stressed that shallow-dwelling xestoleberidids develop four types of dioptric lenses on the antero-dorsal carapace.

The exclusively subsurface dwelling Xestoleberididae, i.e., species belonging to *Microxestoleberis* and *Xestoleberis* group *X. arcturi*, live interstitially. They have a reduced carapace size, thin valves, elongated thoracopod claws, and display traits characteristic for the darkness syndrome, i.e., the medial eye and the carapace lenses are reduced, and the body pigment has disappeared (BONADUCE and DANIELOPOL 1988, DANIELOPOL and BONADUCE 1990). The deep-sea *Platyleberis* species, known since the Upper Cretaceous (DANIELOPOL et al. 1995), have regressed ocular structures too (BONADUCE and DANIELOPOL 1988).

The phylogenetic affinities of the allobiospheric Xestoleberididae were established only for the *Xestoleberis* belonging to the group *X. arcturi* (BONADUCE and DANIELOPOL 1988, DANIELOPOL and BONADUCE 1990). There are two surface-dwelling *Xestoleberis* species, related to the four interstitial taxa, which live on algae and *Posidonia* in sublittoral habitats, i.e., *X. rubrimaris* and *X. chilensis*. The former species, first discovered on the Red Sea coast at Hurghada (HARTMANN 1964), were also collected on the

West Australian coast (HARTMANN-SCHRÖDER and HARTMANN 1978). The latter species also has a wide distribution, being known at many sites along the Chilean and the Western Australian coasts (HARTMANN-SCHRÖDER and HARTMANN 1962, 1978). Both species have reduced carapace size with a thin wall, reduced pigmented eyes in which the three ocelli are not dissociated, no carapace lenses, and slightly bent distal thoracopod claws (DANIELOPOL and BONADUCE 1990). Therefore, one can assume that the surface-dwelling *Xestoleberis* of the group *arcturi* were preadapted to live within interstitial sandy systems. The slightly bent distal thoracopod claws also allows phytophilous species to creep easily on/within sandy substrates.

One of us (D.L.D.) observed living *X. delamarei* specimens from a sandy beach near Banyuls, France. These interstitial ostracods did not react negatively to the microscope light. They actively explored the sandy substrate in the aquarium, creeping in and out the sediment; a similar behavior was also observed in polycopids (see below).

Once surface-dwelling xestoleberidids extended their niche into the interstitial habitats, they continued to adapt to the new environment, e.g., the eye structures regressed in the case of the exclusively interstitial species *X. delamarei*, *X. costatata*, and *X. galapagoensis* (DANIELOPOL and BONADUCE 1990).

Those Xestoleberididae such as *X. broomensis* (HARTMANN-SCHRÖDER 1978), *X. duemaculata* (HARTMANN 1979), and *Ornatoleberis parva* (HARTMANN 1981), which display strongly developed eyes, a thick carapace with dioptric lenses, and short, hook-shaped distal claws on the thoracopods, were unable to adapt to allobiospheric habitats. They are specialised for life in the photic shelf zone with high energetic resources, i.e., well-oxygenated water and a high quality food supply from the Aufwuchs of various organic substrates. *O. parva* which live on algae, were also found within sandy coarse sediments (HARTMANN 1981). In this latter case, animals apparently do not display any of the **darkness syndrome** traits mentioned for the exclusively interstitial taxa of the *X. arcturi* group.

The Halocyprida ostracods offer additional support for the shallow-benthic colonisation scenario. HARTMANN and HARTMANN-SCHRÖDER (1988) recorded 187 deep-sea halocyprids, while the number of the Myodocopida species is much lower (n=88). The number of shallow subsurface marine halocyprids is also higher than that of the myodocopids. There are 61 interstitial Cladocopina species (DANIELOPOL and HARTMANN 1986) and 27 halocyprid species living in anchialine caves (KORNICKER and ILIFFE 1995),



while the Myodocopina only seldom exclusively colonize marine cave habitats (7 species are recorded by KORNICKER and ILIFFE 1995).

In their study on the planktonic myodocopids from the Atlantic Ocean off Bermuda, KORNICKER et al. (1976) noted that the Halocyprida, which lack eyes, are less negatively phototactic than the Myodocopida. The same applies for benthic Myodocopa, i.e., the present authors observed that the Cladocopina halocyprids respond indifferently to light under laboratory conditions, while myodocopines such as *Vargula hilgendorfii* are negatively phototactic (VANNIER and ABE 1993).

KORNICKER (1975, 1989) noted that the deep-sea planktonic Myodocopa feed more commonly on fine dead organic particles. This author remarks (op. cit.) that the number of predatory Myodocopa species in shallow-water habitats is substantially higher; they belong mainly to Myodocopina, with well-developed eye structures. It is worth noting that the subsurface halocyprids, both Cladocopina and Halocypridina feed on small algae, organic detritus, fine sediment, and/or dead organisms (HARTMANN 1955, KORNICKER and ILIFFE 1989a, 1989b). Like their surface-dwelling relatives they are not specialized to feed on living organisms.

Some Halocyprida ostracods are apparently tolerant to low oxygen conditions and live on/in a wide range of substrates. *Polycope reticulata* (Cladocopina), for example, occurs in the Gulf of Naples on/in "black mud", silty sand mixed with dead *Posidonia* detritus, coralligenous sand, etc. (BONADUCE et al. 1982, Tab. 1). The same applies for *Pontopolycope rostrata* in the Mediterranean (BONADUCE et al. op. cit.). These two cladocopines have a wide bathymetric range in the thermospheric seas. Beyond inhabiting the photic shelf zone, they also colonize bathyal habitats in the Mediterranean and the Red Sea (BONADUCE et al. 1982, 1983). One *Pontopolycope* species (*P. mylax*) even lives in an anchialine cave in Jamaica (KORNICKER and ILIFFE 1992).

Fossil halocyprids of the suborder Cladocopina lived on fine-grained sediments during the Lower Jurassic in Western and Northern Europe along the Tethys Ocean margins (NEALE 1983). This latter author compared the Lower Jurassic polycopids with Recent benthic species (described by ROME 1964) and concluded that the former were benthic surface dwellers. Like certain Recent polycopids, the Lower Jurassic species were most probably euryoxibionts, able to live in both well-oxygenated and dysaerobic habitats which were common in the warm epicontinental domain of the Western Tethys during Lower and Middle Jurassic (HALLAM 1975). Such benthic habitats were rich in flocculent organogenic sediment and formed an epibenthic turbid water layer, a soupy ground, as described by TYSZKA (1994) and

also known from the **Posidonienschiefer** facies in many parts of Western Europe (HALLAM 1975).

Representatives of the genus *Metapolycope* (Cladocopina) occur in photic shelf habitats, like *M. compressa* in the Mediterranean (BONADUCE et al. 1982), in the deep sea, e.g., *M. hartmanni* and *M. microthrix* in the Atlantic Ocean between 600 and 2200 m (KORNICKER and VAN MORKHOVEN 1976), *M. echinata* at 5240 m in the Kuril-Kamchatka Trench (CHAVTUR 1981), and in anchialine caves, e.g., *M. duplex* in Bermuda (KORNICKER and ILIFFE 1989a).

Various authors (HARTMANN 1955, BONADUCE, VANNIER unpubl.) observed living Cladocopina ostracods in the laboratory. They swim rapidly with their strong antennae and steadily explore the subsurface spaces of the coarse sandy sediments offered. They can propel themselves in bursts of up to 20 cm through the water column using the strong furca. These capabilities suggest that representatives of the Halocyprida Cladocopina actively colonized allo-biospheric habitats during various times, beginning in the Lower Jurassic when the group first significantly diversified (NEALE 1983).

A very similar pattern can be deduced for the Halocypridina Thaumatocypri-  
ridacea. The genus *Danielopolina*, which now has living representatives in both the anchialine caves (eight species) and in the Atlantic deep sea (one species) is closely related to the genus *Pokornyopsis*, whose representatives occurred in the Western Tethys realm during the Jurassic and possibly Triassic times (KORNICKER and SOHN 1976a, 1976b, AUBRECHT and KOZUR 1995). The two surface-dwelling species of *Pokornyopsis*, *P. bettenstaedti* and *P. feifeli*, for which we have enough paleoecological information (TRIEBEL 1941, BARTENSTEIN 1949), occurred in benthic shelf facies with various oxygen concentrations. While the former species, known from the Lower Jurassic in Northern Germany, lived in very fine silty sediments and poorly oxygenated habitats (BARTENSTEIN 1949), *P. feifeli* occurred in the Upper Jurassic (Swabian Malm, in Southern Germany) in well-oxygenated carbonate facies (TRIEBEL 1941). The latter species has also been described from Central Europe (Czorsztn, Slovakia) from an Upper Jurassic paleoenvironment resembling the modern anchialine caves of oceanic islands (AUBRECHT and KOZUR 1995). These authors showed that *P. feifeli*, at Czorsztn, migrated from a shelf benthic habitat (no deeper than 200 m) through surface crevices into anchialine karstic systems.

The close phylogenetic relationships between *Pokornyopsis* and *Danielopolina* taxa (AUBRECHT and KOZUR op. cit.) lead one to assume that the Recent cave-dwelling *Danielopolina* originated from a shelf-dwelling

species. This hypothesis is partly corroborated by a cladistic analysis (BAL-TANÁS and DANIELOPOL 1995). The most primitive *Danielopolina* species is an undescribed taxon from an anchialine cave in Western Australia, i.e., a shallow environment. The other stygobiont *Danielopolina* species inhabit caves along the paleocoasts of the Tethys Ocean during the Upper Jurassic (BAL-TANAS, DANIELOPOL, HUMPHREYS unpubl.).

The morphological similarities between the Thaumatoocyprididae (Halocypridina) and the Polycopacea (Cladocopina), as discussed by KOR-NICKER and SOHN (1976b), suggest that the former group actively extended its niche into the allobiosphere in a manner similar to that described above for the polycopids. Hence, it is very likely that already the Mesozoic *Danielopolina* migrated directly from a shelf environment into either shallow marine caves or the deep sea without being physically or biologically constrained. The migration into the latter environment was facilitated by the thermospheric conditions of the Tethys during the Mesozoic, as was noted for other ostracod groups as well (BOOMER et al. 1995).

The Myodocopina which are strongly specialized for life in photic environments with high energetic resources, adapted less well to the allobiosphere. Only two species (*Pseudophilomedes kylix* and *Skogsbergia galapagensis*) from Bermuda and/or Galapagos marine caves display traits related to the **darkness syndrome** (KORNICKER and ILIFFE 1989a, 1989b). These species have a reduced and unpigmented medial eye and fewer ommatidia in the lateral eyes. Finally, one should mention that several deep-sea myodocopines are completely blind (KORNICKER 1975).

## Discussion and conclusions

1. In addition to the contribution of Th. FUCHS, two other Austrian scientists, involved with the "Pola" Austro-Hungarian deep-sea expeditions to the Red Sea, Eduard SUESS and Carl CLAUS, indirectly played an active role in developing modern ideas related to the colonisation of deep-sea and subsurface habitats.

Eduard SUESS (1893), discussing the dynamic evolution of the Tethys Ocean during the geologic epochs, showed that one can reconstruct the palaeodepths using the degree of development of the ocular structures, still visible in the fossils. This idea is now widely applied by palaeontologists and even neontologists (e.g., BENSON 1984, BONADUCE and DANIELOPOL 1988).

Carl CLAUS (1874, 1891) described sensorial setae of pelagic halocyprid ostracods, i.e., the frontal organ and the sensory tubes of the antennule, which are now known to be chemosensory limbs that help to compensate for the lack of visual organs (ANDERSON 1977, HEIMANN 1979).

2. The darkness syndrome represents a complex of traits visible in both deep-sea and shallow subsurface animals. Reduced ocular structures probably represent the most common aspect of the **darkness syndrome**. In ostracods, the reduced ocular structures represent either adaptations to the allobiospheric environment (i.e., the case of the interstitial *Xestoleberis* belonging to the species group *arcturi*) or are preadaptations (e.g., the Halocyprida groups).

3. The alternative scenarios presented above should be understood as an exploratory search for more inclusive views on the origin of deep-sea and shallow subsurface marine animals. Such alternative scenarios should stimulate biologists to look for additional ecological, phylogenetic, and palaeontological evidence in order to corroborate or falsify the hypothetical models. The scenarios presented here are not exhaustive. One should also recall the passive dispersal models either through floating objects (see STEINECK et al. 1990, for deep-sea xylophile ostracods; DANIELOPOL and BONADUCE 1990, DANIELOPOL et al. 1995, for marine interstitial ostracods on oceanic islands) or through continental shelf and/or seamount subsidence (WHATLEY et al. 1983, LARWOOD and WHATLEY 1993, for Pacific deep-sea ostracods). In our opinion, the shallow-benthic colonisation model, as expressed in the second scenario, is based on firmer evidence, i.e., it uses ecological, morphological, phylogenetic, and palaeo/biogeographic data, while the alternative model, originally proposed by FUCHS, largely relies on phylogenetic data from a restricted number of animal groups.

4. One should consider the colonisation of shallow subsurface habitats (like marine caves) and the deep sea not as a maladaptive or constraining evolutionary pathway but as a normal evolutionary process in which some animal groups, like the Halocyprida and/or the *Xestoleberis arcturi* complex, were better able to **adopt** the allobiospheric environment and further to **adapt** to new habitats; in other words, they had a better capacity to expand their niche (for similar examples from the deep-sea fish fauna, see UIBLEIN 1995).

5. The anthropomorphic idea that animals which have lost their sight capacities poorly succeed in photic environments, being outcompeted by their oculate congeners or easily eliminated by stronger predators (for example, see GRASSÉ 1973, p. 258), is certainly contradicted by the adaptive success of the Halocyprida. More than 150 species of pelagic halocypridids, despite their lack of eyes, successfully inhabit the photic zone of oceanic waters (DEEVEY

1974, POULSEN 1977, ANGEL 1983, and M. ANGEL pers. comm. to D.L.D.). Apparently, the reduced light sensitivity and reduced morphological specialisation (e.g., the ocular structures), as we showed in the case of the *Xestoleberis* of the group *arcturi* and of the various Halocyprida groups, was an advantage for the successful colonisation of new allobiospheric habitats.

6. Shelf organisms like phytophilous *Xestoleberis* species or the voracious benthic and/or pelagic Myodocopina, closely adapted to a specific habitat and/or to high energetic food types, less successfully colonized the marine allobiosphere.

7. The here discussed analogy between the evolutionary pathways for the colonisation of subsurface habitats of certain marine Ostracoda, with those of two podocopid limnic ostracod groups (Candoninae and Notodromadinae) is striking. Most of the limnic subterranean ostracods belong to the Cypridacea Candoninae (DANIELOPOL 1978). This group has a very high capacity to adapt to new environments both in the photic and allobiospheric zone. All representative are benthic and lack ocular and body pigments. The epigeic species are insensitive to light, are not specialized for a particular food type (they feed mainly on fine sediment and organic detritus), and actively explore the superficial sediment layers. They are thus morphologically and ecologically preadapted to colonize and further adapt to the aquatic subterranean environment. The opposite is true in the Notodromadinae, a small group ubiquitous in inland waters (HARTMANN 1989). This taxon is rare in subterranean waters and evolved no stygobiont species (DANIELOPOL 1978). The Notodromadinae have strongly developed medial eyes with dissociated ocelli and dioptric carapace lenses. The latter structures are more strongly developed in the male, serving in mate recognition (see data in BONADUCE and DANIELOPOL 1988). The Notodromadinae are specialized for a hyponeustonic life and feed on the fine organic particles bound to the surface of lentic water bodies.

8. Finally, we firmly believe that new explorations of the deep sea and shallow subsurface habitats, e.g., the marine caves, combined with the description of newly discovered organisms and careful ecological observations, will provide the same excitement to future generations of naturalists as those experienced by the researchers who participated in the "Pola" deep-sea expeditions.

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