

The origin of the anchialine cave fauna – the “deep sea” versus the “shallow water” hypothesis tested against the empirical evidence of the Thaumatoocyprididae (Ostracoda)

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Abstract

Two alternative hypotheses explaining the origin of some of the oceanic anchialine cave faunas, viz. those of Iliffe et al. (1984) and Stock (1986a) are critically reviewed.

Data pertaining to the phylogeny, ecology and biogeography of the mydocopid ostracods belonging to the Thaumatoocyprididae (Halocyprida) show close affinities between the cavernicolous and the marine shallow water dwelling representatives.

Résumé

Deux hypothèses alternatives qui expliquent l'origine de certains éléments faunistiques des grottes anchialines océaniques, c'est-à-dire celles d'Iliffe et al. (1984) et celle de Stock (1986a), sont revues d'une manière critique.

Des données concernant la phylogénie, l'écologie et la biogéographie des Ostracodes Mydocopides appartenant aux Thaumatoocyprididae (Halocyprida) indiquent des affinités étroites entre les Thaumatoocyprididés cavernicoles et les représentants marins vivants dans des eaux peu profondes en dehors des grottes.

Introduction

In the last twenty years there was a tremendous increase in knowledge of the diversity of the subterranean fauna (see Botosaneanu, 1986, for a review).

It was a surprise to discover the rich marine fauna which lives in anchialine caves (sensu Stock et al., 1986: 9) of oceanic islands. But not only new taxa have been described, also new biogeographical patterns and hypotheses explaining the origin and the distribution of the subterranean fauna emerged.

For the historical biogeography a very intriguing problem arose concerning the fauna of these anchialine caves of oceanic islands. As Iliffe et al. (1984) noted, many ancient and/or primitive taxonomic groups (e.g. the crustacean Remipedia or Thermosbaenacea) absent from epigeal marine habitats occur on both old land masses and young oceanic islands. It is difficult to explain how such “living fossils” dispersed to oceanic islands, like Bermuda or the Galápagos Islands, which were never connected to continental land masses and which are separated from the continental coasts through deep oceans. Different hypotheses have been proposed for such biogeographic patterns.

Iliffe et al. (1984) when analyzing the fauna of the Jameos del Agua cave, on Lanzarote, Canary Islands, proposed that some of the troglodytes occurring on oceanic islands of volcanic origin could originate by immigration of deep sea elements living below 200 m depth through crevicular systems (sensu Hart et al., 1985: 291). Stock (1986a, 1986b) challenged the hypothesis of the “deep sea” and suggested that the fauna of anchialine marine caves originates from benthic, shallow water, animals whose colonization of the oceanic islands occurred in not so remote times (e.g. from the Atlantic islands in the last 30–40 million years). Both hypotheses are historical-narrative explanations (sensu Bock, 1981) and their validity should be tested against additional empirical observations. Despite the inductive character of statements with low predictive power, these historical-narrative

models offer us scientific explanations for the biogeographical patterns and allow the development of better research programmes.

The halocyprid ostracods of the family Thaumatoocyprididae are recorded from the Permian to Recent. As living representatives they are distributed in deep sea and anchialine cave habitats. The two alternative hypotheses mentioned will be tested against the empirical evidence of the Thaumatoocyprididae.

The alternative hypotheses under test

1. The "deep sea hypothesis"

Iliffe et al. (1984) consider that bathyal and/or abyssal organisms penetrate into the subsurface habitats through crevices. Deep sea biota colonized crevicular systems formed in solid rocks (especially those of volcanic origin) and migrated upwards through the macropores reaching the anchialine caves. Documentation of phylogenetical affinities between deep sea and marine cave taxa exists since more than 100 years (Fuchs, 1894; Racovitza, 1912; Vandell, 1965; Riedl, 1966; Margalef, 1976). Migration of organisms from the deep sea to shallow water anchialine caves is considered possible because of the similarities between these two types of environment like total darkness, low food resources, and thermal stability (Margalef, 1976). Evidences for this hypothesis have been provided by Iliffe and/or his associates in various papers (Iliffe et al., 1983; Hart et al., 1985; Manning et al., 1986; Wilkens et al., 1986; Boxshall, 1989). Because the deep sea fauna is accepted by these authors to be very old, the migrations to anchialine caves could occur since more than 100 million years (Iliffe et al., 1983). Wilkens et al. (1986: 223) consider that the origin of some of the endemic hypogean fauna of the Canary Islands "probably derived from widely spread deep sea ancestors".

The plausibility that the deep sea fauna can expand upwards in habitats with similar ecological conditions can be documented with analogical examples. For instance, Hessler & Thistle (1975) consider that some deep sea isopod Ilyarachnidae (Janiroidea) were able to invade the shallow polar

waters from a deep sea stock, because both environments have the same low temperature conditions. A similar scenario is conceived for the water mites of the genus *Bathyhalacarus* (Bartsch, 1988).

A cladistic phylogenetical analysis of the Mischophrioida, a group of copepods with species occurring either in the deep sea or in marine caves of oceanic islands suggested to Boxshall (1989) that the colonization route of anchialine subterranean habitats on islands took place through crevicular corridors which connect the deep sea with the caves. However, Newman (1985) noted that there is up to today no clear evidence for such direct crevicular connections.

Stock (1986a, 1986b) criticized the "deep sea" scenario. He considered that some of the examples given by Iliffe and his associates (e.g. the amphipods Paradaliscidae) are based on taxa that could not have a long history in the bathyal/abyssal habitats, because an extended anoxia period occurred in the oceans, especially during the Upper Cretaceous and/or the Paleocene (Benson, 1979, 1984; Arthur & Schlanger, 1979). Therefore, their origin should be better searched in a shallow water fauna.

2. The "shallow water hypothesis", Stock's (1986a) scenario

There are faunistical indications pointing to closer phylogenetical relationships between anchialine cave taxa and marine taxa living outside the caves in the shallow water zones. For instance, the representatives of Thermosbaenacea which colonize oceanic anchialine caves have no relatives in the deep sea, but have closer affinities to littoral interstitial species (Stock, 1986c).

Stock (1986a, 1986b) considers that the anchialine cave fauna of the oceanic islands derived from oxiphilous or hypoxic animals which lived during the Neogene on the continental shelf.

Empirical evidence for the Thaumatoocyprididae

1. Ecology and biogeography (Fig. 1)

The first anchialine cave thaumatoocypridid *Thaumatoocypris orghidani* was recorded by Danielopol (1972) from Cuba. This species is now attributed to

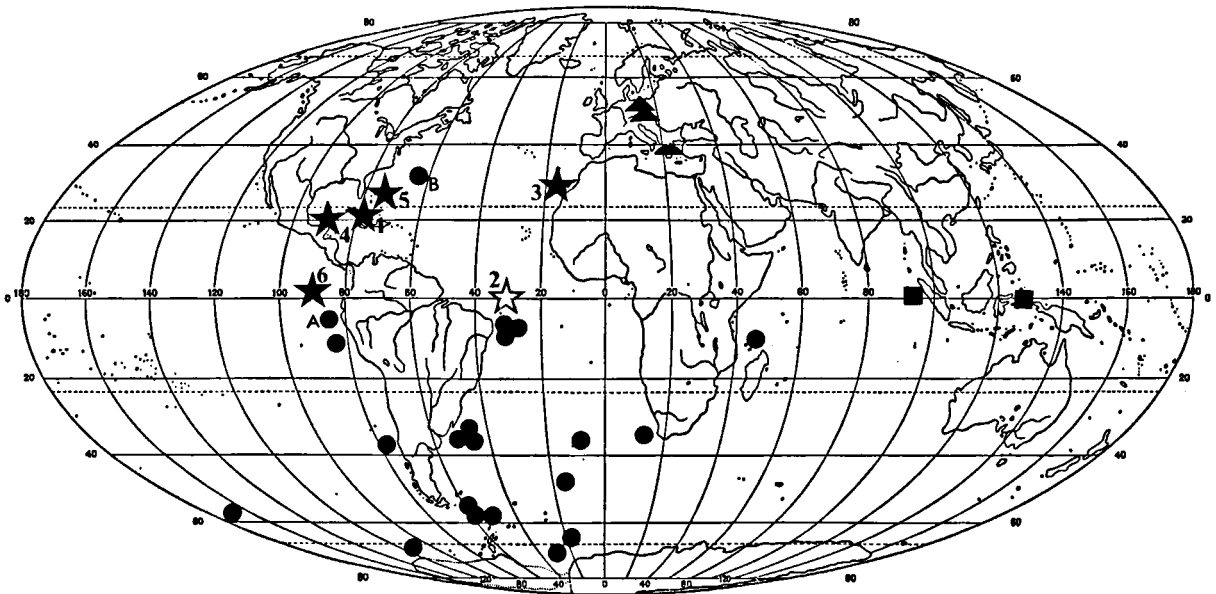


Fig. 1. Distribution of living and fossil Thaumatoocyprididae: Squares = *Thaumatoocypris echinata*; dots = *Thaumatoconcha*, various species (A = *T. elongata*, B = *T. polythrix*); black stars = anchialine cave species, white star = deep sea dwelling species (1 = *Danielopolina orghidani*, 2 = *D. carolinae*, 3 = *D. wilkensi*, 4 = *D. mexicana*, 5 = *D. bahamensis*, 6 = *D. styx*); hemicircle = *Thaumatomma piscifrons*; triangle = *Pokornyopsis*, two fossil species. (Map adapted from Kornicker & Sohn, 1976a; Kornicker & Iliffe, 1989a, c.)

the genus *Danielopolina* Kornicker & Sohn, 1976a. Four other species of *Danielopolina* occur in anchialine caves, viz. in Lanzarote (Jameos del Agua), Canary Islands, *D. wilkensi* Hartmann, 1985; in the Bahamas and the Yucatan Peninsula, Mexico, *D. bahamensis* and *D. mexicana* Kornicker & Iliffe, 1989a; and finally in the Galápagos Islands, *D. styx* Kornicker & Iliffe, 1989c. *D. wilkensi* occurs also in the shallow crevicular system (2 to 8 m below the surface) of Lanzarote, located closely to the coast, and up to 300 m inland (Wilkins et al., 1986). There is one species of *Danielopolina* known, viz. *D. carolinae* Kornicker & Sohn, 1976a, occurring in a benthic deep sea zone off the Brazilian coast in the Atlantic Ocean at 3459 m depth.

The genus *Thaumatoocypris* has only one species, *Thaumatoocypris echinata* Müller, 1906, which was found in the pelagic waters of Indonesia between 1100 and 2000 m depths (Poulsen, 1969). The deep sea thaumatoocypridid species included in the genus *Thaumatoconcha* Kornicker & Sohn, 1976a were collected in the Indian, Atlantic, and Pacific Oceans and have been described by Kornicker & Sohn (1976a) and Kornicker (1985). Hartmann (1985) found one female of *Thaumatoconcha* sp. in 150 m

depth of the Antarctic shelf close to King George Island. All these species are epibenthic dwelling ostracods. *Thaumatoconcha polythrix* Kornicker & Sohn, 1976a, occurs in the deep sea (below 2000 m depth) not far from Bermuda Island and *Th. elongata* Kornicker & Sohn, 1976a, was found at 3750–4125 m depth in the South Pacific off the Peru-Chilean coasts, thus not so far remote from the Galápagos Islands.

Triebel (1941) and Bartenstein (1949) found two thaumatoocypridid species (now attributed to the genus *Pokornyopsis* Kozur) in the lower Jurassic sediments of Germany (Kornicker & Sohn, 1976b). The paleo-environment is a silty sediment deposited in shallow waters not deeper than 200 m of an epicontinental sea and the ostracods, with well-calcified carapaces, are benthic forms (see also Neale, 1983).

The Thaumatoocyprididae have antennae with long natatory setae and a strong furca. The carapace has a rounded shape. With the exception of the pelagic species *Thaumatoocypris echinata* which has on the carapace very long tubular processes, the other Thaumatoocyprididae species have short blunt processes. Considering these morphological features one could hypothesize that the species can bur-

row into the fine sediment and/or live in interstitial spaces of coarse grain sediments or alternatively swim free in water above the bottom.

The *Danielopolina* species in the anchialine caves have been caught swimming in free waters (Danielopol, 1976; Kornicker & Iliffe, 1989a, 1989c). It is interesting to mention the morphological and ecological analogies of this genus with the ostracod Polycopidae. These species have also round carapaces, strong natatory antennae and a strong furca. Most of the recent polycopids live endo- and epibenthically or in interstitial habitats (Neale, 1983). The species of the genus *Metapolycope* occur in anchialine caves (in Bermuda), in the deep sea and in polar shallow waters (Kornicker & Iliffe, 1989b).

Because the anchialine caves are in contact with the marine shallow environment outside the caves one can presume that a continuity of some sandy gravelly or silty sediment habitats existed between the epigeal and hypogean systems. The benthic ostracods could therefore easily colonize the hypogean habitats. Such an example is documented by Maddocks & Iliffe (1986) for *Anchistrocheles hartmanni* Maddocks, 1976 (Bairdiacea) from an anchialine cave in Bermuda. This is an interstitial species initially found living in the sublittoral zone along the coast of Bermuda (Maddocks, 1976). *Danielopolina orghidani* could also be an interstitial species which penetrated from the sandy coast into the Grietas Matansas, Cuba, where such sandy gravelly sediments exist (Juberthie et al., 1977, and Orghidan & Juberthie, pers. comm.).

It is interesting that the more primitive species *Danielopolina mexicana* (see further) occurs on the continent in the Yucatan Peninsula while the other less primitive cave dwelling *Danielopolina* species occur on islands of different ages like Cuba, an old land mass, or Galápagos and Lanzarote, which are young volcanic islands.

2. Phylogeny and evolution

Kornicker & Sohn (1976a) distinguished within the order Halocyprida with a cladistic analysis two main phylogenetical groups: the Cladocopina containing the group of the Polycopacea, and the Halocypridina containing the Thaumatoocypridacea and the Halocypridacea. The latter superfamily has

many pelagic representatives, clustered in several families, while the former has only one family: the Thaumatoocyprididae.

Kornicker & Sohn (1976b) consider that the Thaumatoocyprididae derive from the Devonian ostracod group *Checotonomus* Kesling (Entomoconchidae). The oldest known thaumatoocypridid, *Thaumatomma piscifrons* Kornicker & Sohn, 1976a, was found in Permian sediments in Greece (Kornicker & Sohn, 1976a). Two Jurassic “*Thaumatoocypris*” species, *T. feifeli* Triebel, 1941 and *T. bettenstaedti* Bartenstein, 1949, now assigned to the genus *Pokornyopsis*, have affinities with *Thaumatomma* Kornicker & Sohn and with the Recent cave dwelling thaumatoocypridids of the genus *Danielopolina* (cf. Kornicker & Sohn, 1976b). The genera *Thaumatoocypris* and *Thaumatococcha* form a separate phylogenetical lineage within the Thaumatoocyprididae (Kornicker & Sohn, 1976b). These are benthic species of large size – the carapace has generally more than 1.4 mm length – (the range is between 1.4–2.3 mm) living in the deep sea (Kornicker & Sohn, 1976a; Kornicker, 1985).

Within the genus *Danielopolina*, *D. mexicana* appears more primitive than the other species, i.e. it has a carapace of medium size (0.8 mm length) and a Bellonci organ (most of the halocyprids have this organ). *Pokornyopsis* species which show phylogenetical affinities with *Danielopolina* have carapaces of medium size, viz. *P. bettenstaedti*, 0.8–1 mm length and *P. feifeli*, 1–1.2 mm length (Triebel, 1941; Bartenstein, 1949; Kornicker & Sohn, 1976a). The other *Danielopolina* species devoid of a Bellonci organ can be clustered in two groups, one living in anchialine caves (*D. orghidani*, *D. styx*, *D. wilkensi*, and *D. bahamensis*) with small carapace size (0.4 to 0.6 mm length) and a group with very large carapace size (1.85 mm length) composed of the deep sea dwelling *D. carolinae*.

Kornicker & Sohn (1976a) consider the shallow benthic taxa like *Pokornyopsis* species from the Jurassic to be at the origin of the thaumatoocypridids which gave rise to the *Danielopolina* group. Some of the *Danielopolina* species colonized the subsurface environment of the marine caves, while others migrated into the deep sea. Strangely

enough, no *Danielopolina* species display any adaptation to aphotic environments. All the living Thaumatoocyprididae are blind. But this is not due to a regressive evolution which occurred in the caves or in the deep sea, but a characteristic of the Halocyprida.

Discussion

Following the Iliffe et al. (1984) hypothesis one should expect to find in anchialine caves the *Thaumatoconcha* or *Danielopolina* species of large size (more than 1 mm carapace length) that could have penetrated into the crevicular systems of the oceanic islands from the deep sea. One would expect these especially in Bermuda and the Galápagos Islands (Fig. 1). But this is not the case. The contention of Wilkens et al. (1986) and Boxshall (1989) that *Danielopolina* species from anchialine caves derive from deep sea ancestors which spread through crevicular systems can be questioned in the light of the morphology and ecology of these species. Why should a deep sea thaumatoocypridid with large carapace size evolve miniaturized (small) carapaces as we see in the anchialine cave dwelling *Danielopolina*? The crevicular corridors are macroporous systems which enables the life of many large Crustacea. Such an example is, e.g., the remipedian *Lasionectes entrichoma* Yager & Schram, 1986; it has 22 mm length and the cephalon is more than 2 mm large! A more parsimonious explanation is that the anchialine caves have been colonized by shallow water dwelling *Danielopolina* with medium or small carapace sizes which live either in surface or interstitial habitats. Ecological difficulties with the “deep sea” hypothesis applied to the Thaumatoocyprididae occur when one considers the specialization to low temperature in the oceanic deep sea waters of the benthic ostracods. Benson (1975) showed that during the Late Eocene / Early Oligocene the thermospheric deep sea ostracod fauna, especially in the Atlantic, changed drastically its composition. During the last 40 million years the deep sea benthic ostracod fauna, mainly in the Atlantic, is characterized by psychrophilic species. These do not colonize the shallow warm waters of the shelf

habitats, because of their inaptitude to cross the thermocline zone of the oceanic layered waters (Benson et al., 1984, 1985). The genus *Thaumatoconcha*, for instance, has ten species living in the deep sea and one species occurs in antarctic cold waters at less than 200 m depth, but none in the shallow warm water habitats (Hartmann, 1985).

In conclusion the brief review on the evolutionary history, ecology, and biogeography of the Thaumatoocyprididae does not corroborate the “deep sea hypothesis”. The present data suggest that the anchialine caves on oceanic islands derived their *Danielopolina* species from shallow water habitats, either surface or interstitial ones, located along the continental margins or oceanic islands. This scenario is in accordance with the “shallow water hypothesis” of Stock (1986a).

Homage to Jan H. Stock

The present note was stimulated by Stock's ideas (1986a) and by his research on the subterranean fauna of oceanic islands. Incidentally my data corroborate Stock's “shallow water” hypothesis. But I consider that the best homage that I can bring to this scientist is to show him that the research direction within which he worked so successfully (viz. the explanation of the diverse and original subsurface aquatic fauna of oceanic islands) will be further followed using the ostracods. I intend to stimulate people to intensify the search of Thaumatoocyprididae. If my intuition is correct, then one could find representatives of this group along the continental coasts in interstitial habitats. New investigations of the dispersal mechanisms of ostracods to oceanic islands from remote coasts have also to be looked for. Ehlers & Ehlers (1980) pointed out that the interstitial Turbellaria from the Canary Islands could originate independently from continental interstitial taxa. This scenario is discussed also by Danielopol & Bonaduce (in press) for interstitial Xestoleberidae occurring on volcanic islands like Galápagos in the Pacific, and Stromboli in the Mediterranean.

The possibility of a combination of dispersal along the continental margins and short passive dis-

persal by rafting is conceived for marine interstitial polychaetes (Westheide, 1977; Westheide & Rieger, 1987). Such a possibility of dispersal could apply to ostracods as well (Danielopol & Bonaduce, in press). We need certainly more field observations and experimental studies considering subsurface dwelling Ostracoda!

Finally, I want to stress that the investigation of the subterranean fauna of oceanic islands developed in many of us both excitement and wonder. The excitement is produced by acquisition of new knowledge. A sense of wonder “increases ever more with the development of our knowledge”. This has been noted by A. Einstein (quoted by Holton, 1986: 76) when he looked retrospectively to his field of research, but the remark applies to us biologists as well, confronted with the unexpected diverse and interesting subsurface aquatic fauna that we discovered in the last years.

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