

Biogeographic synthesis of the insular groundwater faunas of the (sub)tropical Atlantic *

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Abstract

Anchihaline habitats occur most frequently in subsiding areas. Typically, they are populated by ancestors of marine origin. These ancestral forms have a much wider distribution in the open sea, thus their hypogean descendents occur in phenetically similar populations on various islands. On the contrary, on rising islands, marine ancestors stranded during the uplift and got isolated in brackish or fresh ground waters, giving rise to phenetic and genetic isolates in very restricted areas. They belong to old genera with a large distribution (amphi-Atlantic or Tethyan). The stygofaunas of both rising and subsiding areas thus originated in the sea, but contrary to the often uttered suggestions, not in the deep-sea. Phenetic resemblance between deep-sea and anchihaline taxa may indicate common ancestry, but then it must be shallow-water ancestry for both, simply because no deep-sea species survived the two oxygen-crises in the early and mid-Tertiary.

It is completely impossible of course to summarize in one short lecture the results of some 20 years (1973–1992) of studies on the groundwater fauna of the islands in the tropical and subtropical Atlantic Ocean. During these studies 2678 faunal samples were taken at 59 islands (Table 1), thus they provide a sound empirical basis for generalizations. The presence of certain animals in certain areas is no doubt of the greatest importance in biogeographic analyses, but the absence of certain taxa can hardly be explained by undersampling, and thus must have some significance as well.

As has been stressed by various authors, groundwater organisms (stygobionts) form excellent objects for historical biogeographic studies, since they mostly have poor dispersal capacities (low number, <6, of eggs, no free-swimming larval stages, substrate-bound life cycles, poor competitive capacities with surface animals...), causing strong local endemism, with not only endemics per island (Fig. 1), but also with geographic isolates within an island (Fig. 2).

Given the combination of limited dispersal and strong local endemism in stygobionts, vicariance models should have a much greater probability of providing satisfactory explanations for present distribution patterns than scenarios based on dispersal (Holsinger, 1991). Dispersal is not eliminated totally as a cause, but it occurs mainly in groups which are more easily dispersed, e.g. wind-borne, such as Ostracoda. Such groups show uncorrelated, random patterns of distribution (Wiley, 1988; my Fig. 3). The general principle of vicariance biogeography holds that different groups of animals show similar (covariant) distribution patterns, the so-called generalized tracks in the sense of Croizat, which are very common in many different groups of stygobionts especially at generic and higher levels. Elsewhere, I have exposed at some length such covariant distribution patterns in Polychaeta, Mysidacea, microparasellid Isopoda, cyathurid Isopoda, cirrolanid Isopoda, prawns, Thermosbaenacea, Remipedia, hadziid Amphipoda, the *Pseudoniphargus* group (Amphipoda), nicippid Amphipoda... I will show here only a few of these examples. One can distinguish a small number of basic patterns, viz. (1) an amphi-Atlantic distribution (Fig. 4), (2) an amphi-

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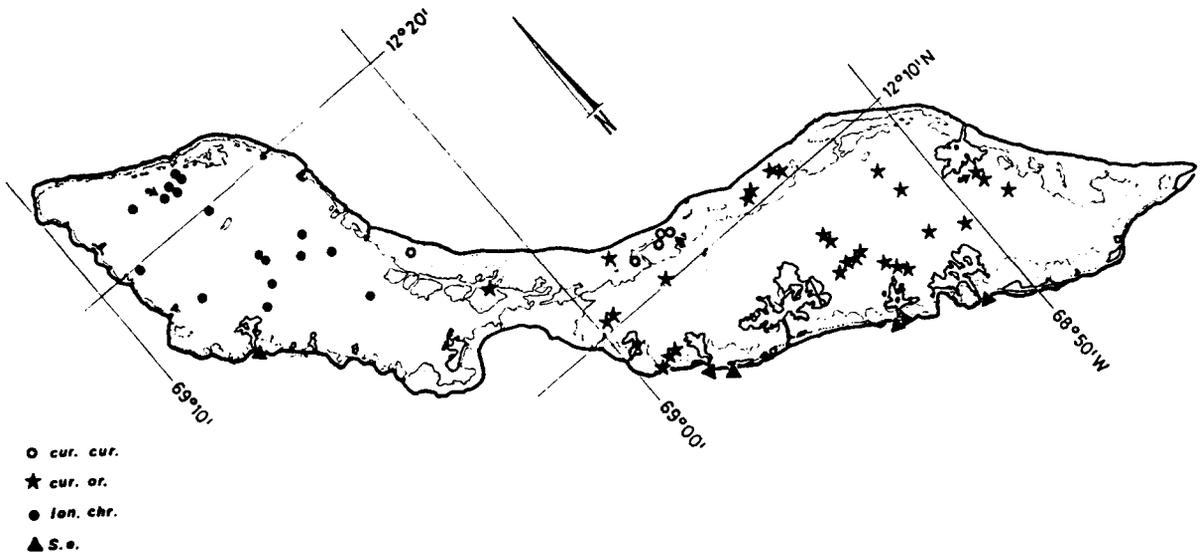


Fig. 2. Distribution of the members of a family of Amphipoda (Hadziidae) on Curaçao. Each symbol represents a different taxon. Note that the 4 taxa are allopatric to a large extent: one on the eastern, Miocene part of the island; one on the western, Miocene part; one on the holo-/pleistocene North coast; and one on the holo-/pleistocene South coast. (After Stock, 1977.)

Table 1. Amsterdam insular ground water survey on the islands in the tropical and subtropical Atlantic, 1973–1992.

| |
|---|
| (1) West Indian region |
| (1.1) Antilles, 44 major islands, of which 32 sampled (in total 1387 samples) |
| (1.2) Bahamas, 19 major islands, of which 9 sampled (in total 117 samples) |
| (1.3) Bermuda, 1 major island, sampled (in total 81 samples) |
| (2) Ascension, 1 island, sampled (in total 50 samples) |
| (3) Cape Verde Islands, 10 major islands, of which 6 sampled (in total 227 samples) |
| (4) Canary Islands, 9 major islands, of which 8 sampled (in total 699 samples) |
| (5) Madeira archipelago, 2 major islands, both sampled (in total 115 samples) |

Atlantic+Mediterranean distribution (Fig. 5), and (3) a Tethyan distribution (Fig. 6).

Such covariant patterns are generally believed to reflect a similar evolutionary history, in the case of stygobionts no doubt the opening of the Atlantic and the disruption of the formerly circumtropical Tethys Sea (Miocene). Taking into consideration the poor dispersal capacities of the stygobiont species, as well as their restricted distributions, we can arrive at one conclusion only: they must have reached their actual locations already before both events took place, *i.e.* before the Miocene events, and in most cases even before the beginning of the Tertiary. This poses at once a major problem: many geological data point to the fact that

the islands on which the stygobionts occur nowadays arose (for the last time) above sea level only in the late Miocene, or even later in the Tertiary. In other words: how can old animals exist on young islands? The answer to this question is not an easy one to give, and may be different from island to island, depending on the geological history of the island.

In several cases, the geological data are not as sound as they seem to be, being mostly based on the K-Ar dating of subaerial lavas and not on samples obtained by deep-drilling. It is unlikely therefore that older islands were, not all at once, but during successive stages in their geological life-time, subject to volcanic eruptions which covered partially the surface we see at present.

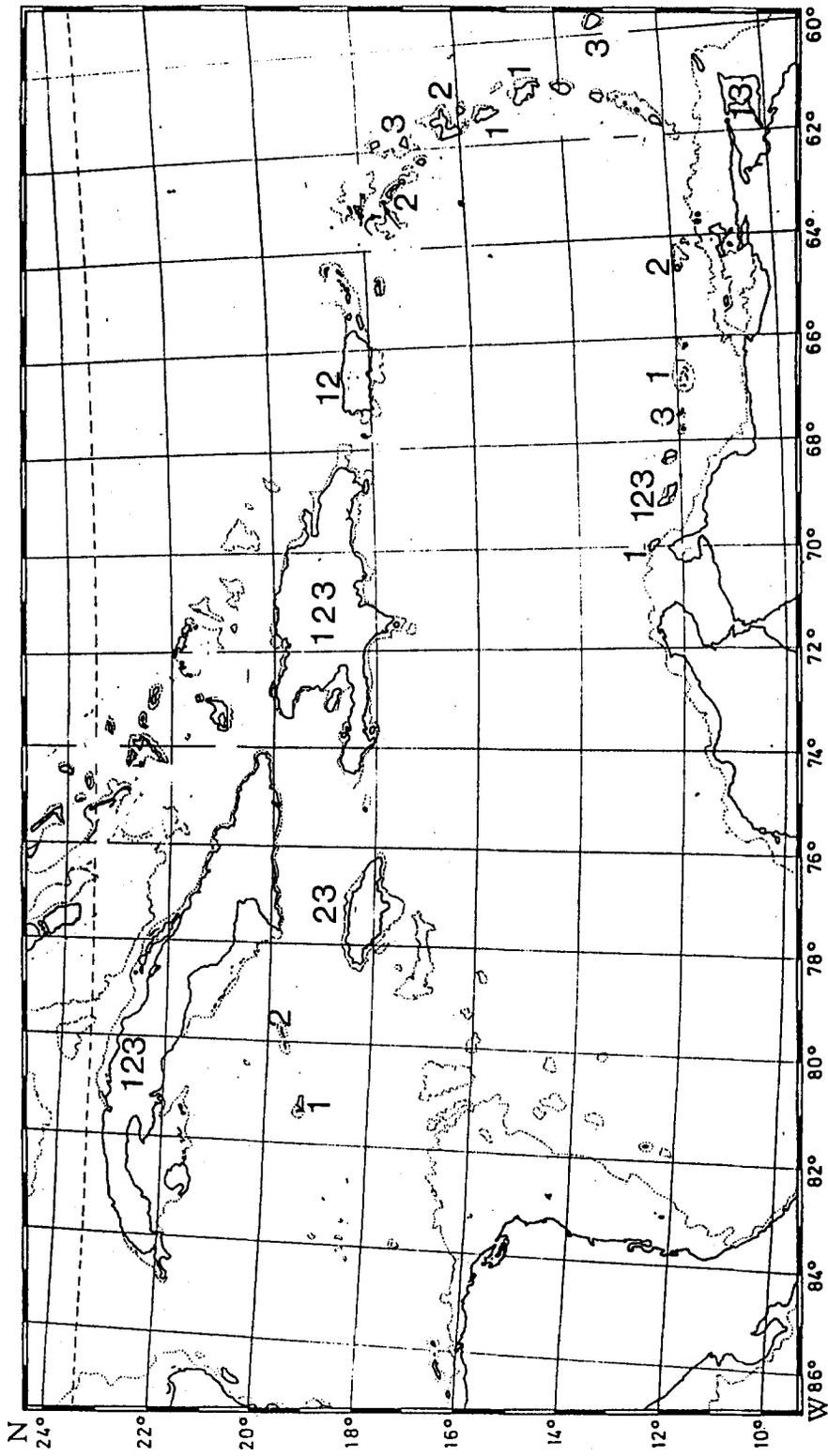


Fig. 3. Typical dispersal pattern in West Indian groundwater ostracods: few species, distribution criss-cross. Three different species indicated by 1, 2, and 3.

Table 2. Stygobiont taxa very often have marine relatives, however (because of isolation and poor dispersal capacities) the number of stygobiont taxa is always much higher than the number of marine taxa of the same genus.

| AMPHIPODA | |
|--|---|
| Bogidiellidae | 5 marine (none bathyal), 60 stygobiont |
| Ingolfiellidae | 10 marine (3 bathyal), 40 stygobiont |
| Hadziidae | 8 marine (1 bathyal), 40 stygobiont |
| Nicippe-cluster (3 genera, Pardaliscidae) | 1 marine (sublittoral to bathyal), 3 stygobiont |
| Salentinellidae | 1 marine/anchihaline (none bathyal), 8 stygobiont |
| Pseudoniphargus-cluster (3 genera, Melitidae) | 3 marine/anchihaline, 48 stygobiont |

Curassanthura (Isópoda)

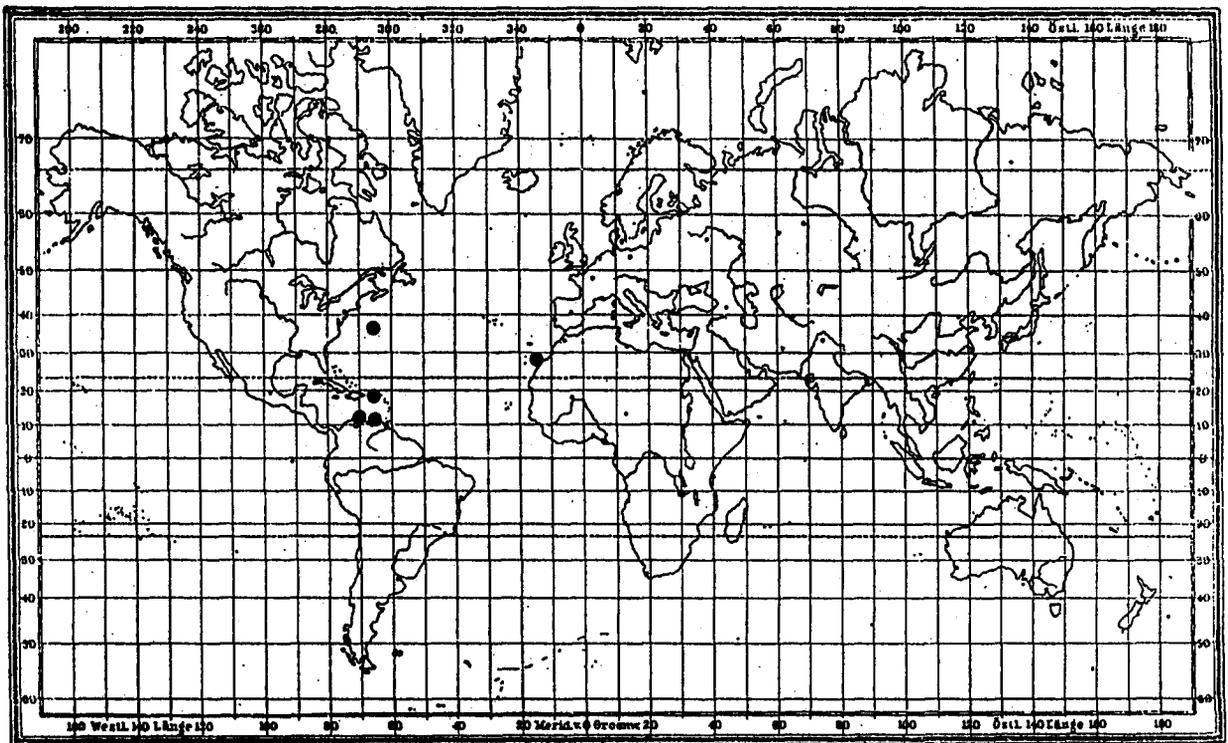


Fig. 4. Amphi-Atlantic covariant distribution pattern in the isopod *Curassanthura*.

A good example is the island of Lanzarote, which was subjected to an enormous volcanic outburst in historical times, recent lavas covering almost one-third of the island but leaving the remaining part intact. If a subsequent eruption were to touch the remaining part, the entire island would be covered by young lavas and the dating of the island would be wrong. However 'old' animals could survive in the part not touched by

eruptions. In my opinion, Ascension, in the Central Atlantic, is one such island on which surface dating under-estimates the real age of the older island underneath.

Another possibility lies in the fact that most, if not all, insular stygobionts evolved from marine ancestors; in fact many stygobionts genera still have congeners in the sea (Table 2). Every taxonomic and phylogenetic

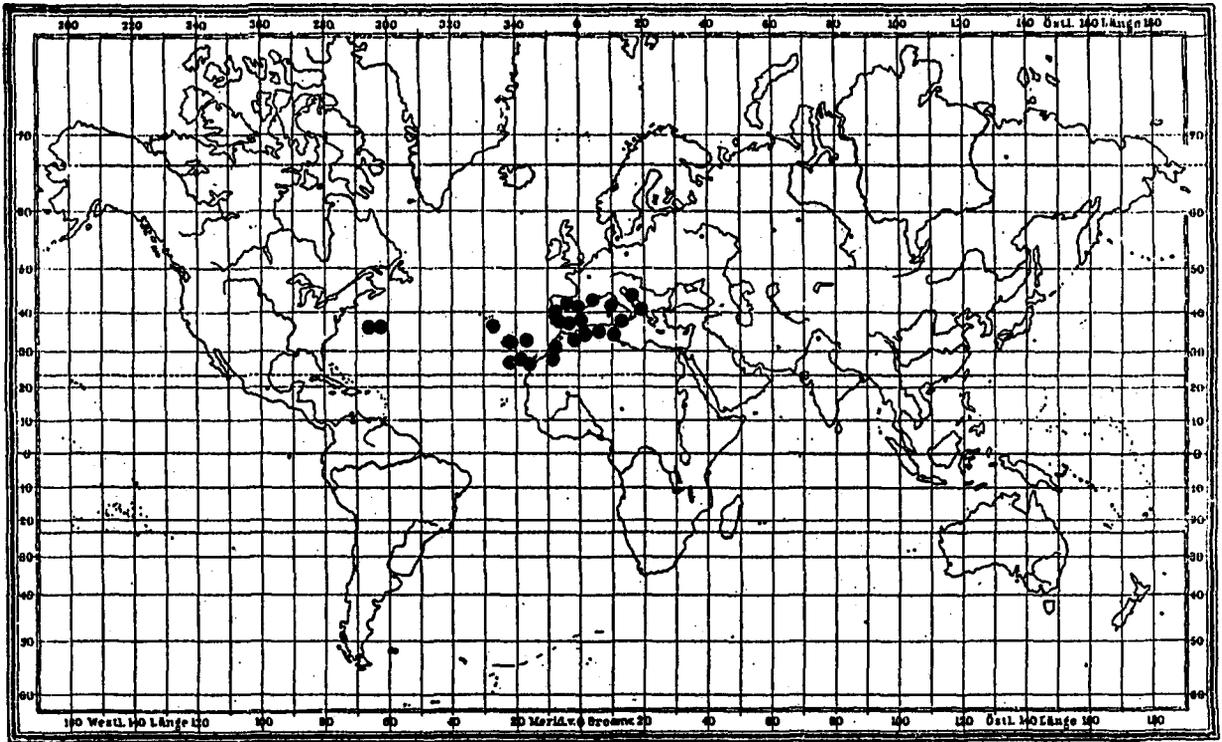
Pseudoniphargus (Amphipoda)

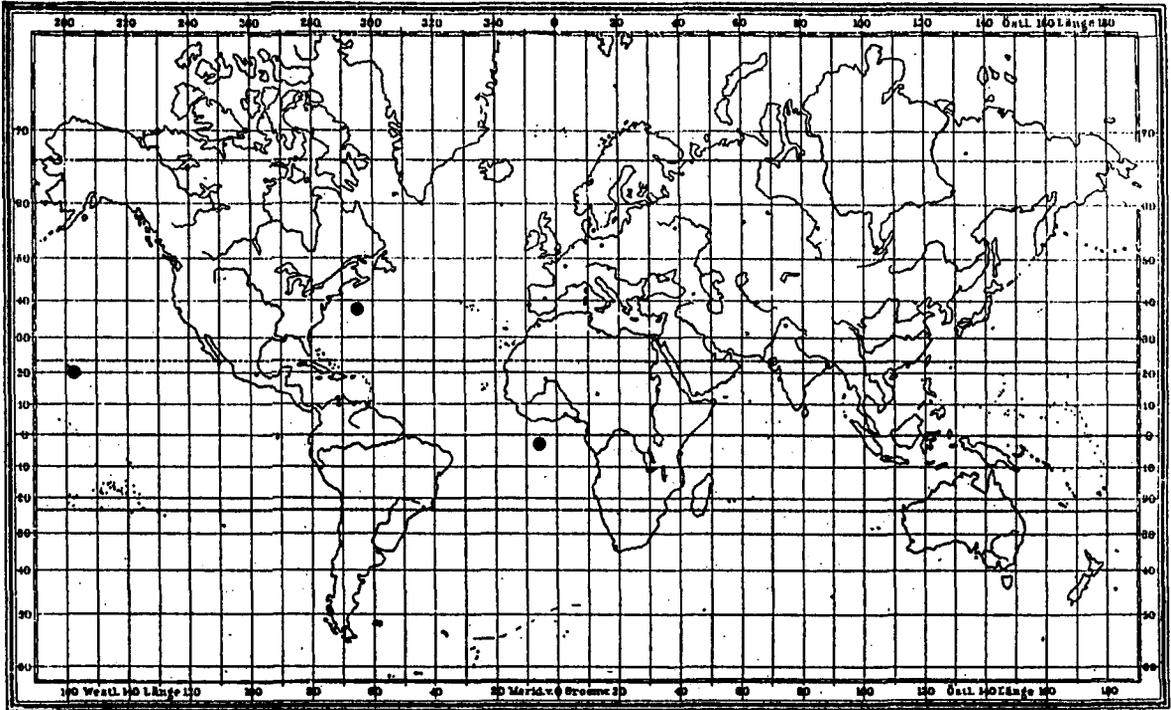
Fig. 5. Amphi-Atlantic plus Mediterranean distribution pattern in *Pseudoniphargus* (Amphipoda).

study confirms this view. This means that these stygobionts did not need subaerial edifices to evolve, but that their marine ancestors could have lived on shallow submerged banks and then adapted to subaerial conditions after such banks arose above sea-level. This idea forms the basis for the much-discussed Regression Model of evolution for stygobionts, where the word 'regression' alludes to a negative movement of the sea-level in relation to the land or a positive movement of the land in relation to the sea. Recent summaries of the subject (Notenboom, 1991; Boutin & Coineau, 1990) place great reliance on this model. In the preceding lines, I have stressed the word 'shallow banks', and not for nothing. Without going into details here (but see Stock, 1986) paleo-oceanography makes it very likely that deeper waters (>200 m) of the Atlantic were depleted of oxygen at the Mesozoic/Tertiary boundary as well as at the Oligocene/Miocene boundary. The anoxia resulted of course in extinction of animal life in waters deeper than some 200 m. If the marine ancestors of the stygobionts were deep-water species (as certain authors suppose, see e.g. Iliffe *et al.*, 1983,

1984), they cannot have at the same time a Tethyan and an amphi-Atlantic distribution pattern, because no old deep-water species could have survived in the Atlantic. Every deep-water taxon we encounter there today must have descended from shallow-water ancestors (a view held already by a former generation of biogeographers, but without support of paleo-oceanography).

On shallow submarine banks, or sea-mounts, marine animal life could survive, especially those animals capable of coping with reduced oxygen tensions. When these sea-mounts arose above sea-level, this group was especially pre-adapted to evolve into stygobionts because oligoxia dominates both in the interstitial habitat (Frenchel & Riedl, 1970) fringing the sea coasts, in the crevicular habitats of the infra-littoral, and in anchihaline habitats more inland on emerging islands. The abundance of stygobionts in habitats with reduced oxygen tension is shown in Figs. 8–10. In such habitats the stygobionts can survive, not only because they were already pre-adapted to these conditions, but also because they can withstand there the competition

Procaris (Macrura)



Metaniphargus (Amphipoda)

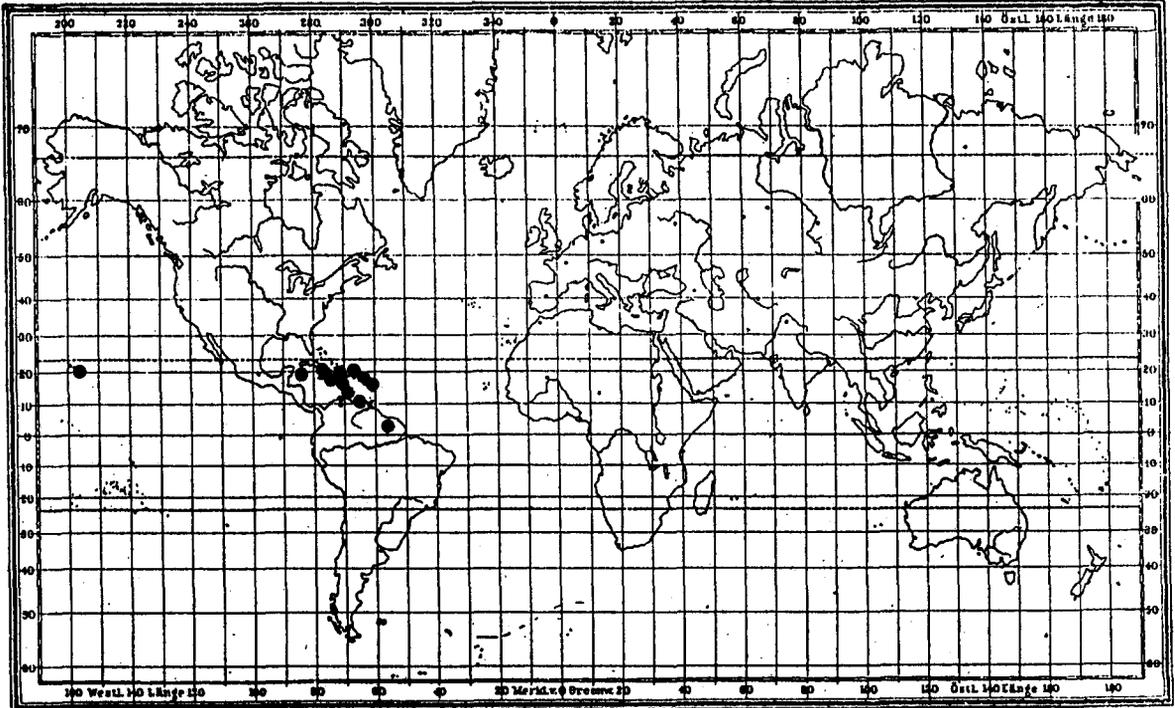
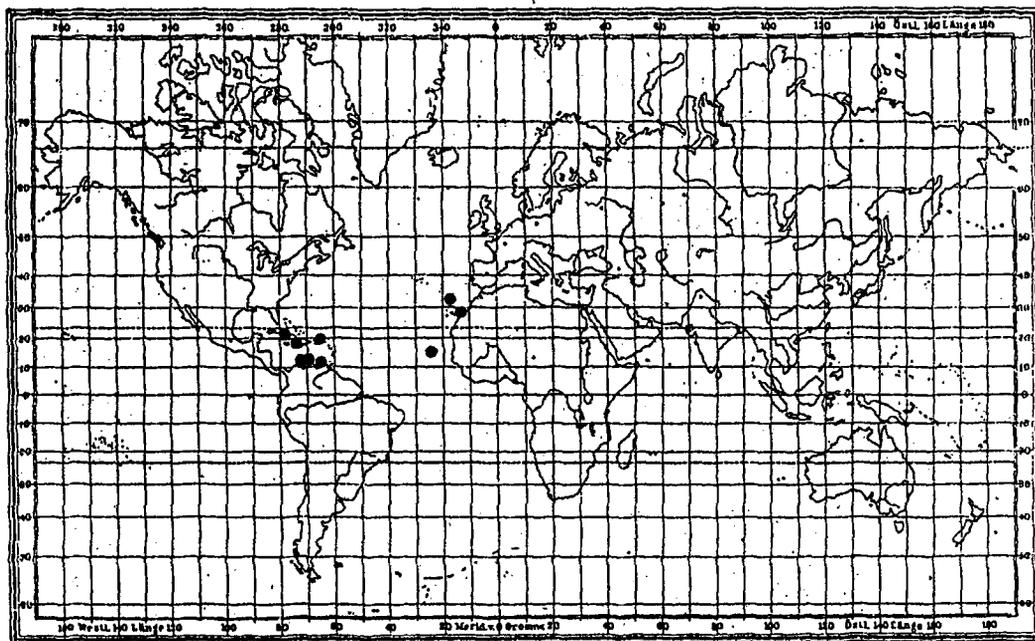


Fig. 6. Tethyan distribution pattern in the prawn *Procaris* (top) and in the amphipod *Metaniphargus* (bottom).

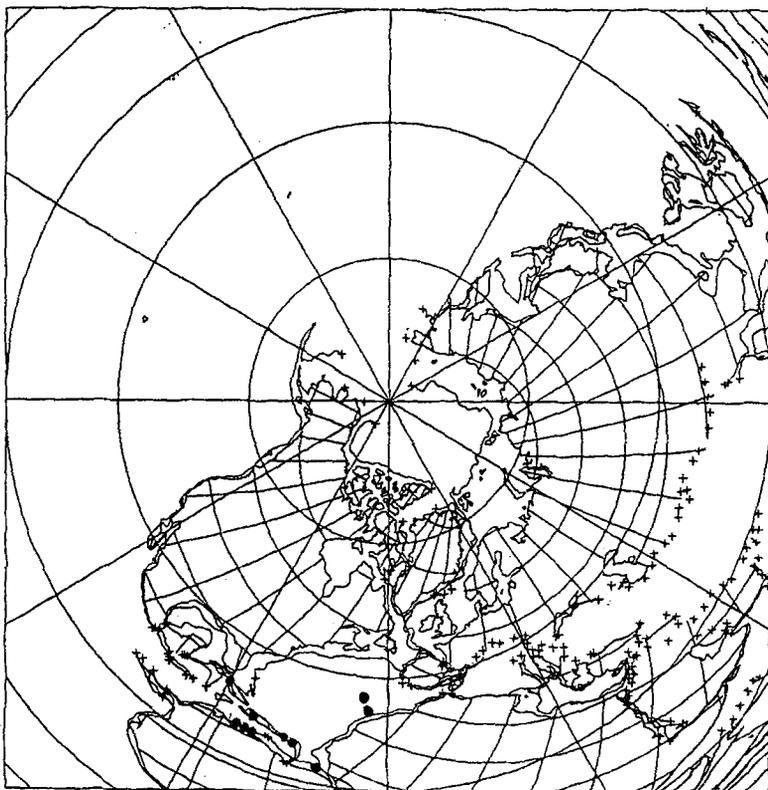
Namanereis hummelincki (Polychaeta)

112



120 million years
Hauterivian (early Cretaceous)

North polar Lambert equal-area
 $N = 44$ $\alpha = 95 = 5.7$



Namanereis hummelincki (Polychaeta)

Fig. 7. The generalized Amphi-Atlantic (and Mediterranean) distribution tracks presumably go back to a period before the opening of the Atlantic when the present-day localities were much nearer to one another. Shown is the stygobiont polychaete species *Namanereis hummelincki* [Basic map of early Cretaceous situation after Smith *et al.*, 1981.]

Table 3. Two groupings of stygobionts based on non-morphological characters. There are no taxa on specific and infraspecific levels occurring in both groups 1 and 2, but there are several identical genera in both groups.

| Group 1 | Group 2 |
|---|--|
| Living in fresh, oligo- and mesohaline waters | Living in polyhaline, marine or hyperhaline near-coastal (anchihaline) ground waters |
| Found at all oxygen tensions | Definitely oligoxic |
| Found in regressing (= rising) areas | Found in transgressing (= subsiding) areas |
| Biogeographically restricted (at species level) to 1 island only; within 1 island often restricted to 1 stream system | At species level not restricted to 1 island or 1 stream system (but often known from type-loc. only) |
| Usually in groundwater systems confined to Tertiary formations | Usually in Holocene/Pleistocene formations |
| Sister species in marine or anchihaline waters | Same species sometimes known from open sea |
| Always blind & unpigmented | Not always blind & unpigmented |
| Always benthic | Benthic or pelagic |
| Never with free-living (pelagic) stages | Sometimes with free-living (pelagic) stages |
| Low number of large eggs | Sometimes with large number of small eggs |

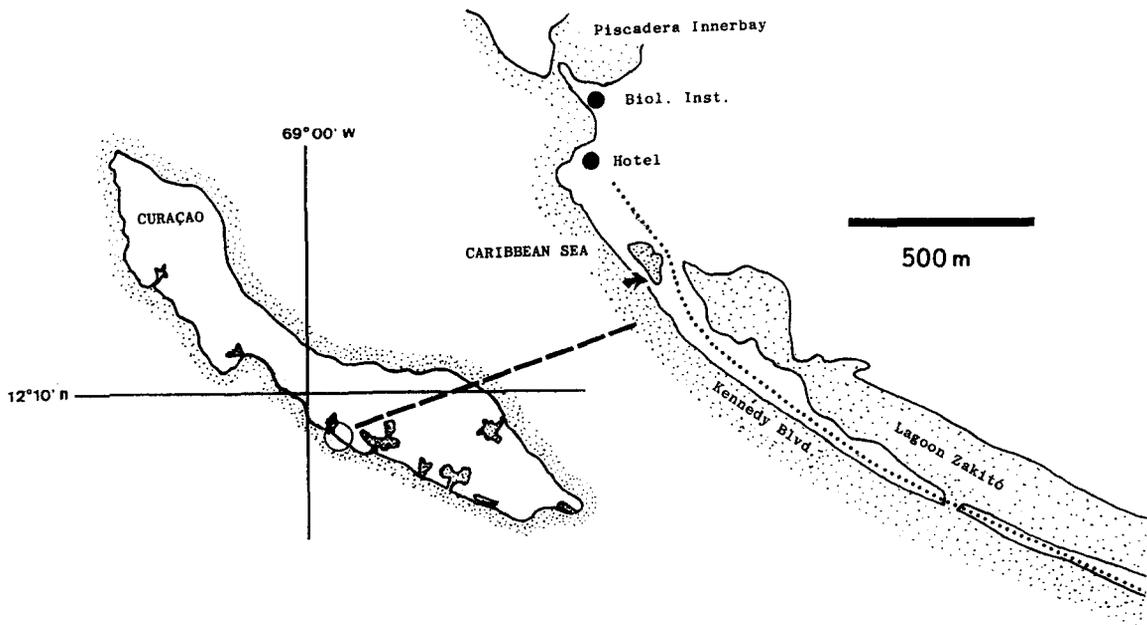


Fig. 8. The location of the area in Curaçao used for sampling stygobionts and corresponding oxygen levels in Figs. 9 and 10. Sea water dotted.

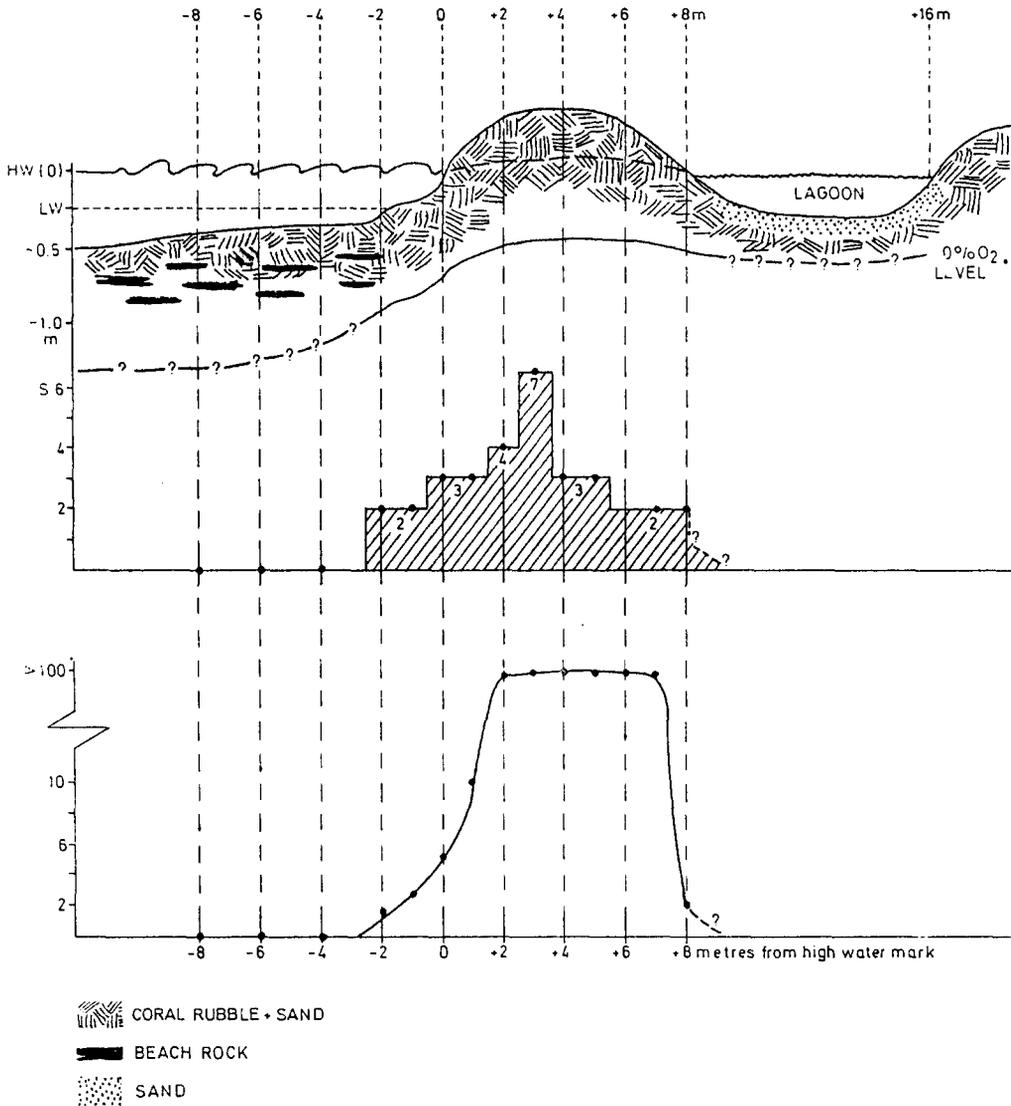


Fig. 9. Number of stygobiont species (top: hatched); and (bottom) number of stygobiont specimens in a coral rubble on Curaçao.

with 'normal', burrowing and other infaunal marine elements.

From both the interstitial and anchihaline habitats, stygobionts can gradually get adapted to lower salinities and finally to fully inland hypogean habitats. No doubt rising or falling sea levels, and rising or sinking islands, have played a mayor role in the mostly vicariant speciation processes (vicariance is the most probable process, since the dispersal capacities of most stygobionts are extremely limited).

In Table 3 we have analyzed a number of non-morphological features in anchihaline animals in comparison with those of truly-inland stygobionts (the term

'continental' stygobionts, coined by Delamare Deboutteville (1960), is a rather queer name for inland, insular stygobionts). The two categories have different features, but it should be borne in mind that the limits between the categories tend to be bridged. The evolution of stygobionts is continuous and not restricted to a single well-delimited geological period but they keep on evolving all the time. We can encounter (though rarely) stygobionts that, so to say, 'just crawled out of the sea', and others that evolved since the Miocene or even earlier. The alternation of rise and fall of sea level relative to the land, or better yet of regressions and transgressions, causes that a mixture of the 2 groups

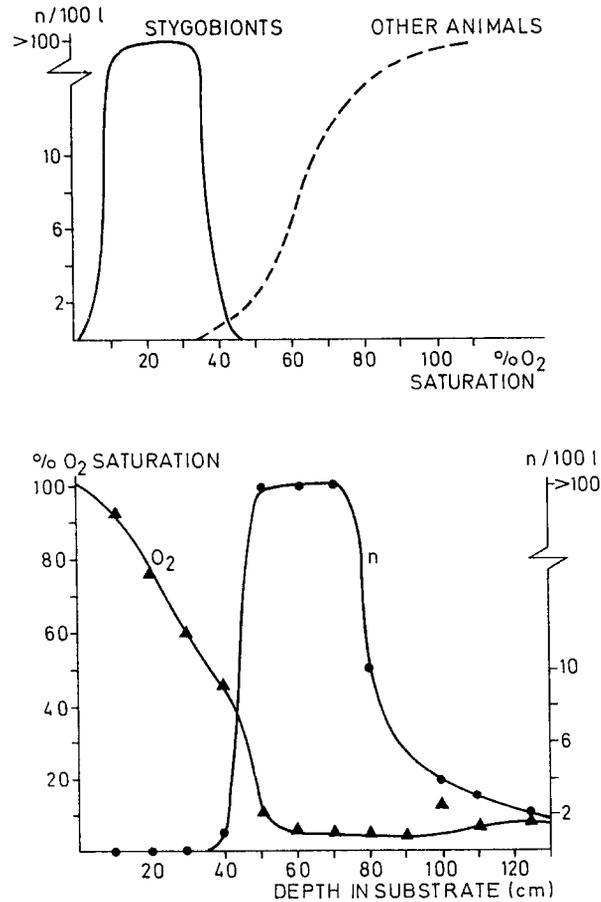


Fig. 10. Number of stygobiont specimens and of 'normal' marine animals in relation to oxygen saturation (top). Relation between oxygen saturation (triangles) and number of stygobiont specimens (dots) (bottom).

animals is present in several areas. The present-day stygofauna is the resultant of the constant changes in the environment. The alternating regressive and transgressive movements along sea coasts can be demonstrated nicely in the Leeward group of the Antilles, where we can recognize in the geomorphology of the islands up to 9 now subaerial (uplifted) tidal erosion flats, and at the same time 3 drowned tidal flats now under sea-level. In the faunas of another island, viz. Bermuda, we find a clear mixture of both groups: drowned karstic caves now filled with salty waters of marine origin having mostly animals of group 2, next to surface layers of fresh water overlying the salty deeper cave waters in which animals of group 1 proliferate.

Almost all animals of group 2 belong to the so-called anchihaline fauna, and are in my opinion more recent intruders into the hypogean realm. Almost all animals of group 1 are 'continental' stygobionts, and

populated the subterranean domain during the Tertiary or even earlier.

Since in some islands transgressive movements (sinking of the islands) is by far the dominant tectonic process, the ground waters of these islands are inhabited almost completely by animals of group 2. This is the case in the Bahamas and in the Turks & Caicos islands. Islands in which regressive movements (tectonic uplift or active vocalism) are predominant, but transgressions (in particular sea level rise) occurred as well, faunal elements of group 1 predominate, but some animals of group 2 also occur as well. This is the case in the Lesser Antilles and the Canary Islands.

In some truly marine habitats, viz. in deep submarine caves and in cracks and crevices, low oxygen tensions have been recorded as well. It is in these habitats that the closest relatives to group II (anchihaline) fauna are to be found (and have been found in some

instances, e.g. *Halosbaena*). Sampling there is complicated, however, so at present these habitats are subject to clear undersampling. They deserve close attention in the next decade.

Some cases are still difficult to understand. The distribution of Ingolfiellidea on the Atlantic islands is such a case. These animals have been found only at the margins of the area under consideration (Fig. 11), viz. on Bermuda, various islands off the coast of Venezuela, the Canary Islands, and Madeira, but are apparently absent from the Greater Antilles, the Volcanic Antilles, Cabo Verde, and Ascension. I have no explanation to offer for this absence.

Acknowledgements

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