

BIOGEOGRAPHY AND EVOLUTIONARY SCENARIO OF AQUATIC ORGANISMS IN MACARONESIA

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With 1 table and 4 figures

Biogeographers and geologists disagree about the origin and age of the Macaronesian islands.

The prevalent geological opinion nowadays is that all islands were built up by volcanic activity from deeper waters and broke independently through the sea surface (consequently are not underlain by sialic, continental crust). The K/Ar dating of lava rocks on the islands rank from early Miocene to Present, but has been done almost without exception from lavas presently exposed at the islands' surface, thus reflecting only the age of more recent eruptions and not necessarily the age of the underlying base rock.

SCHMINCKE (1989), in a treatise on Gran Canaria, summarized a number of geological questions which are valid for all Macaronesian islands. From his treatment, most of the following points are taken (Table I):

TABLE I - Some main geological questions concerning the Macaronesian islands

1. Were the islands once a continuous landmass or did they originate as independent islands?
2. Was any of the islands ever in contact with the African continent?
3. Is any of the islands underlain by continental (sialic) crust?
4. Were the islands formed over a "hot spot"?
5. When did volcanic events on the islands start?
6. (and most important for biogeographers): When did the islands break through the sea surface to continue their existence as subaerial edifices?

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Biogeographers have stressed that certain islands must have been in contact with or close to the Eurafrikan continents, because otherwise it would be hard to explain the presence of Eurafrikan animals with poor dispersal capacities on the islands. One of the most striking examples is the presence of fossils of flightless birds and land-turtles on some of the Canary Islands, but in the sequel I will extend these examples to quite a number of Recent aquatic invertebrates. On the basis of evolutionary arguments, biogeographers rate the subaerial age of several of the Macaronesian islands much older than most geologists (STOCK, 1990).

In this paper, we will consider the controversial points in some detail.

First the geological questions, as enumerated in Table I. None of them is completely solved, but some tendencies are clear.

Question 1 (see ROTHE & SCHMINCKE, 1968): Several authors have assumed that at least the Canary Islands were at first one large volcanic platform, which subsequently fell apart and eroded to the present islands (it was even speculated that ALL islands formed once a contiguous land mass, the famous Atlantis; MUCK, 1979). Biogeographically, the view that the Canarias formed once a single land mass is in so far attractive, in that it explains the striking similarities in the biotas (see EVERS, 1964; EVERS et al., 1970). Most geologists agree nowadays, however, that every island arose independently from the ocean floor; for aquatic organisms I have peace with this conclusion, because although it is clear that many aquatic organisms have one common ancestor, the degree of island endemism is so evident that a rather long period of isolation of each island is not unlikely. Modern geological data confirm that the islands have neither been in contact with one another nor with the African continent, although biogeographers, supported by some geologists, have pointed out that at least the eastern islands of the Canary group might be fragments of the African continental plate, thus explaining the faunistic similarities. However, it seems settled nowadays (ROESER, 1982; HINZ et al., 1982) that all islands of the Canarias are located immediately to the west of the magnetic anomaly marking the boundary between the continental and oceanic lithosphere (question 3 of table I).

According to the hot spot theory (table I, question 4), the oceanic crust moved by sea floor spreading away from the Mid-Atlantic Ridge, and passed during the move over a hot spot where a consecutive series of islands was formed. The theory is supported by two observations: (1) the islands, closest to the Mid-Atlantic Ridge, often produce younger K/Ar datings for the lavas than the more remote islands; and (2) the degree of erosion is greater in the more remote, older, islands than in the younger islands.

Although this general idea holds true reasonably well (but not absolutely) within the

islands of a given archipelago, comparisons between the distance to the Mid-Atlantic Ridge (sea floor spreading rate) and K/Ar datings of different archipelagoes show no good agreement (MITCHELL-THOMÉ, 1982). The hot spot origin (question 4 of table I) is not yet settled, but seems unlikely.

Questions 5 and 6 are obviously related, but at least question 6 is rarely touched by geologists. Here, however, biologists come in the picture, because it is evident that terrestrial and freshwater biotas can only develop after emergence of an island.

Our own biological studies centred around aquatic Crustacea Malacostraca, mainly Amphipoda, both from surface and subterranean (ground) waters. The subterranean representatives are typically K-strategists: they produce a very limited offspring (only 1 to 4 young at the time), lack any larval (pelagic) stages, the young hatch in the shape of small adults, all stages are very sensitive to changes in environmental conditions, dying almost at once when temperature, salinity, etc. change. Consequently any transport on rafting tree trunks, coconuts, wind, in bird feathers, or by humans, is excluded in the case of these crustaceans (STOCK, 1990; HOLSINGER, 1991). But of course there were and are many other animals that disperse more readily. These good-dispersers, like terrestrial isopods or millipedes, are, however, of little use for historical biogeography.

One can safely say that the dispersal capacities of the crustaceans are extremely limited. In good agreement with these poor dispersal capacities are the great number of taxa on species and subspecies level, each endemic to a single island, or even (in the case of larger islands) to one hydrological system.

Let me first dwell upon some of the examples of Eurafican or other affinities of Macaronesian Amphipoda, pertaining to question 2 of table I:

(1) The genus *Metacrangonyx* contains blind, subterranean species: 35 in Morocco, two in the near-east (Sinai and Dead Sea region), one in the Balearic islands, and -- the most interesting case -- one in the higher regions of Fuerteventura, one of the eastern Canary Islands (Boutin, 1993; STOCK & RONDÉ-BROEKHUIZEN, 1986).

(2) The *Chaetogammarus simoni*-group is a small group of epigeal freshwater species distributed in North Africa (from Libya to Algeria), but having also one species in the highest parts of La Gomera in the western Canary Islands (BEYER & STOCK, 1994).

(3) The genus *Rhipidogammarus* contains both epigeal and hypogean species; it has 4 species around the western and central Mediterranean basin, but also 2 species on Tenerife and 1 on La Gomera (Canary Islands). Several of these species can tolerate high salinities (STOCK, 1988b; STOCK & SÁNCHEZ, 1990; BEYER & STOCK, in press).

(4) The genus *Pseudoniphargus* consists exclusively of blind species: some 40 subterranean species in the Iberian peninsula and the Balearic Islands, one on Sicily, some 10 species on the western Canary Islands (but non on the eastern!), 1 on the Azores, and 2 on

Bermuda (!). Recently 3 new species have been discovered in the Madeira archipelago (fig. 1). All species live in fresh ground waters, but for 2 that are marine interstitial/intertidal (1 in Madeira, 1 in the northern Mediterranean belt) (STOCK, 1980, 1988a; STOCK et al., 1986; NOTENBOOM, 1988; STOCK & ABREU, 1994).

Pseudoniphargus (Amphipoda)

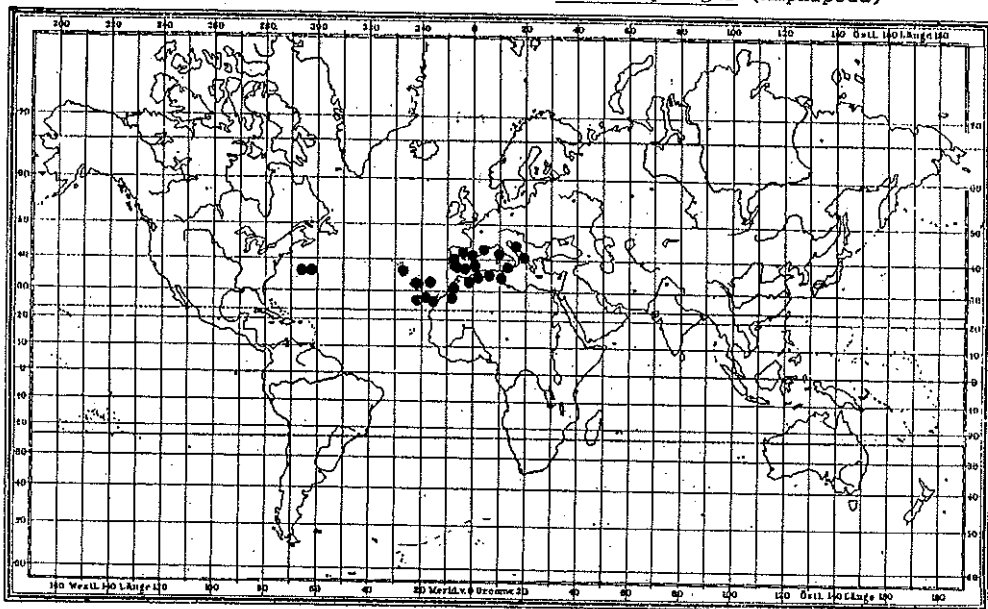


Fig. 1 - Actual Amphi-Atlantic distribution pattern of 56 species of the amphipod genus *Pseudoniphargus*. One dot may represent more than one species, or more than one locality, in particular on the Iberian peninsula (after STOCK, 1993).

Bermuda does not seem to fit readily in this distribution pattern, since the island is considered of oceanic origin, is located west (not east) of the Mid-Atlantic Ridge, and is often dated as late-Tertiary. However, a deep drill core in the Bermuda Seamount date the lamprophyric sheets at about 33 million years (My) ago, and the pre-existing tholeiitic lava at 110 My ago (REYNOLDS & AUMENTO, 1974). Moreover, Bermuda has recently yielded a fossil tortoise, probably related to *Hesperotestudo* (W. STERRER, pers. comm., 19 Nov. 1993). The presence of a tortoise and of the predominantly East-Atlantic/Mediterranean genus *Pseudoniphargus*, on a so-called oceanic island seems to indicate that the primordials of Bermuda were once located in the Tethyan littoral belt.

(5) The genus *Sarothrogammarus* consists of 8 freshwater species, the distribution of which corresponds to the extension of the Tethys sea in the Sarmatian period: from Afghanistan and Turkestan in the east to Sicily; but in addition 2 species occur on Madeira, of which one in the intertidal zone (STOCK, 1995).

It should be stressed that in some of these genera, we know extant species still living in or near the sea, always intertidal or in river mouths.

Nowadays, almost all students agree that the ancestors of these amphipods once were marine (a so-called thalassoid origin) and lived in a sea now disappeared, the Tethys, which ended to exist as such in the Miocene.

There is also wide agreement about the idea that these amphipods did not *actively* invade the freshwater or subterranean environment, but that they 'stranded' *passively* during periods of regression (i.e., periods in which the sea-level dropped or the land was tectonically uplifted). After 'stranding', the animals gradually adapted to lower salinities and eventually evolved into inland species we know to-day. Especially NOTENBOOM (1988, 1991), BOUTIN & COINEAU (1990), and BOUTIN (1993) have recently analyzed in great detail the relation between sea-level regressions and the evolution of these amphipods. This evolution model, the stranding of marine populations, was for obvious reasons baptized Regression Model (STOCK, 1977, 1980).

If it is true that the evolution of these thalassoid crustaceans was dependent on sea-level lowering and/or land uplift, it is clear that the Regression Model can be tested by the following criteria:

- (1) the animals occur only in areas once inundated by sea-water, now dry;
- (2) they never occur in areas that were always above sea-level;
- (3) they do not occur in areas dry in the past, from which they could have dispersed to areas falling dry during regressions;
- (4) they occur always in areas that underwent regressions, never in areas that underwent transgressions.

In every case seriously studied these criteria have been affirmed, giving support to the validity of the Regression Model. An example is for instance the rich fauna of inland groundwater crustaceans on the islands of the Antillean arc (a regression area), and the near-absence of such forms on the Bahamas, which, though at the nearest point only some 50 km away from the Antilles, are in a transgression zone (STOCK, 1990).

Where geologists propose still controversial data as to the era in which the Mid-Atlantic islands arose first above the surface of the sea, biogeographers can contribute additional information.

In the case of Fuerteventura in the Canary archipelago, published records on the date when the most ancient rocks (the so-called Basal Complex) first emerged, range from the late-Cretaceous to the Neogene (!). Giraud (in BOUTIN, 1993: 230) postulated that the island underwent 4 uplifting stages, the first in the late-Cretaceous, and then in the early-Eocene, then again around the Eocene/Oligocene boundary, and finally from the mid-Miocene to Present. In an elegant phylogenetic, phenetic and area-cladistic analysis of 39 species of genus *Metacrangonyx*, BOUTIN (1993) arrived at the conclusion that *M. repens* (the only insular species, endemic to Fuerteventura) and 15 species belonging to the same clade distributed on the Moroccan mainland, evolved during the recede of the sea of the late-Senonian gulfs. Since evolution of these species is only possible in emerged areas, this places the earliest emergence of Fuerteventura in the late-Senonian (65-70 My B.P., at the end of the Cretaceous). It cannot be accidental, in the light of the very intensive sampling carried out in Fuerteventura, that *Metacrangonyx* is limited on this island to the oldest part. It did not disperse from the Basal Complex to the more recently formed parts of the island.

Along other ways, again using historical biogeography, the age of islands like Fuerteventura and Madeira can be assessed as well. On each of these two islands, a member of the subgenus *Antilleella* of the genus *Ingolfiella* is found; the remaining 4 species of *Antilleella* occur in a part of the Lesser Antillean arc, more precisely on the island chain off Venezuela (Aruba through Margarita). Similar cases of Amphi-Atlantic occurrence of groundwater organisms are rather numerous, e.g. *Curassanthura* (Isopoda), *Speleonicippe* (Amphipoda), *Namanereis* (Polychaeta) (fig. 2), top, *Speleonectes* (Remipedia), *Monodella* and *Halosbaena* (Thermosbaenacea), etc. (STOCK, 1993). WILKENS et al. (1986), Iliffe et al. (1983), HART et al. (1985), RONDÉ-BROEKHUIZEN & STOCK (1987) and STOCK (1990, 1993) have pointed out that the distance between the Antilles and Macaronesia in the Tertiary and Quaternary is too large to allow dispersal of such feeble dispersers as groundwater animals over a wide stretch of open ocean. The only way to explain these similar distribution patterns ('generalized tracks' according to Croizat's terminology) is to assume that they were already in place when the Atlantic was not yet widely open (fig. 2, bottom). Again, this places the emergent phase of the Macaronesian islands in the Cretaceous.

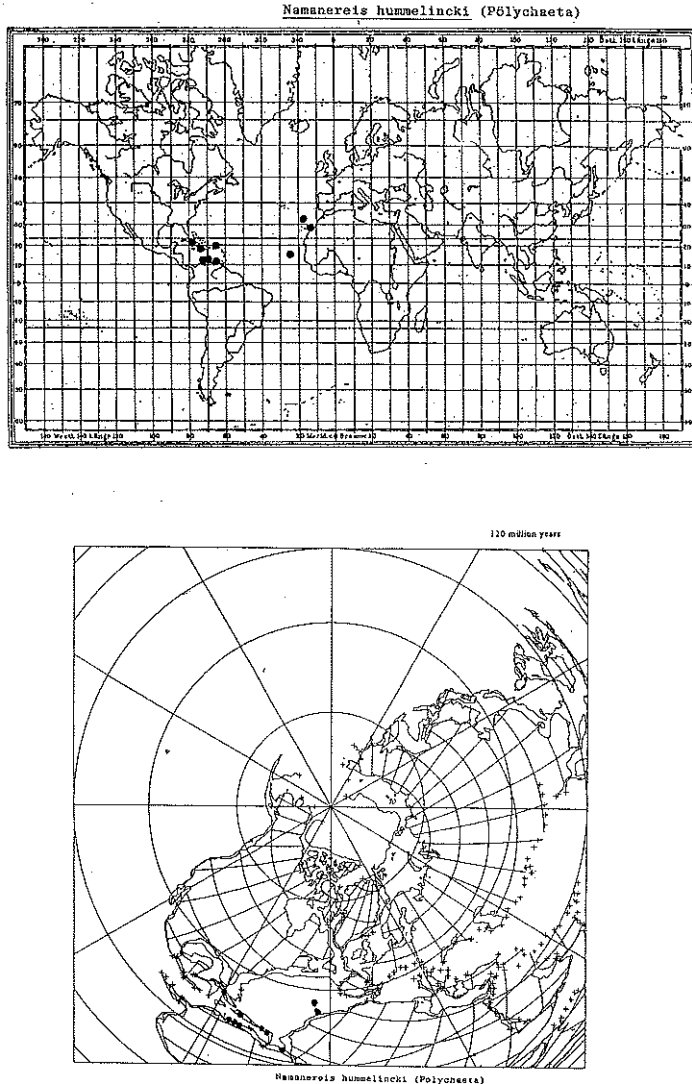


Fig. 2 - Actual Amphi-Atlantic distribution pattern of the subterranean polychaete *Namanereis hummelincki* (top) and the actual localities plotted on a map of the positions of the land masses in the Cretaceous (120 My BP) (bottom). Note that in the Cretaceous the localities lie much closer together than their present-day remoteness indicates. The explanation is, that the polychaete was already present at its localities before the Atlantic opened up. Basis map of the Cretaceous situation after SMITH et al., 1981.

Still another, indirect proof is provided by the biogeography of a considerable number of congeneric subterranean crustaceans that are found both on Pacific and on Atlantic islands. These animals must have been present in both oceans before the sea-way between the Pacific and the Atlantic closed. The Isthmus of Panama, which nowadays prevents any direct marine contact between the two oceans, arose in the Miocene. Therefore, the presence of closely related taxa in the two areas can be explained only when two conditions are fulfilled: (1) these taxa were already present in both oceans, thus before the Miocene, and (2) primordials of the islands on which they occur must have been present at that time (STOCK, 1993).

The conclusion must be that the primordials of several mid-Atlantic islands are very much older than most geologists admit. Biological evidence, based both on phylogeny (the *Metacrangonyx* case) and biogeography (Amphiatlantic occurrence of several, taxonomically diverse, stygobionts; distribution both in the Atlantic and the Pacific (see also HOLSINGER, 1991) leads to the notion that certain islands existed either as very shallow submarine platforms or as low subaerial edifices ¹, located at the very boundary of the continental plates, as early as in the Cretaceous. Of course, volcanic activity has changed the surface of these islands considerably during the Tertiary and even during the Quaternary, but the eruptions affected only part of the pre-existing islands and left other parts temporarily untouched. The untouched parts acted as pockets or refugia for the old Mesozoic faunal ancestors.

If we accept this conclusion about the age of certain (if not all) Macaronesian islands (question 6 of table I), also question 2 is solved: the Atlantic Ocean was in the Cretaceous still closed, or at best starting to open, making the exchange of biotas between the proto-islands and the Eurafrikan continents possible. Note that biogeographical indications point in the direction that not only the Macaronesian islands, but also Ascension (the case of the shrimps *Procaris* and *Typhlatya*) and Bermuda (the case of *Pseudoniphargus*) are of approximately the same, viz. late-Mesozoic, age.

One of the biological assumptions on which our conclusions are based is that many freshwater taxa, especially groundwater Crustacea Malacostraca, evolved passively as a result of regression of the land/sea boundary. Small scale events, like regional tectonic uplift, are easily understood and often registered by geologists on the Macaronesian islands. Remains the question what caused large-scale eustatic sea-level changes. This question is not only relevant to evolutionists, but is actual nowadays in relation to a general heating of the atmosphere (the greenhouse effect) and presumably resulting sea-level rise of some 40-50

¹The very shallow or even surface origin of many lava samples has been confirmed by Professor L.N. KOGARKO, during her lecture at the 1st Symposium on the Atlantic Islands (Funchal, 1993). Based on chemical analyses of the rocks, KOGARKO concludes that the lavas of the Cape Verde islands, and as a matter of fact of most Macaronesian islands, were formed under low pressure (thus not in the deep-sea).

cm in the next century due to the melting of polar ice caps (STOCK, 1992).

Temperature fluctuations were common in the geological past. In the marine environment, such fluctuations can be determined by the ratio O^{16}/O^{18} in calcium carbonate skeletons of fossils (this ratio is temperature dependent). From such data it is shown for instance that the temperature in the Miocene dropped by some 5 to 9° C, causing large scale extinction of Caribbean reef corals. Another clue is provided by the deposition of black shales on the sea floor. Since black shales are important in oil industry, we have a fair knowledge on the world-wide occurrence of these deposits (ARTHUR et al., 1987). They are formed under anoxic or at best oligoxic conditions, as a decomposition product of dead organisms. Formation of black shales is thus connected with low to zero oxygen concentrations and with mass extinction. The chain of events is presumed to be as follows: heating up of the sea water → lower oxygen saturation → melting of ice and sea-level rise → inundation of coastal plains → mass extinction of terrestrial coastal flora, which is washed into the sea → large amount of decomposing debris in the sea and further lowering of the oxygen concentrations → mass extinction of marine animals (STOCK, 1990).

Such series of catastrophic events happened with a certain regularity in the geological past. Some authors even believe that anoxic events are cyclic, with a periodicity of some 32 My (FISCHER & ARTHUR, 1977). The last anoxic event took place at the Oligocene/Miocene boundary, some 30 My BP, the next-last at the Mesozoic/Tertiary boundary, some 62 My BP. In the earlier Mesozoic similar events have been demonstrated (SCHLANGER & JENKINS, 1976; SCHLANGER et al., 1987). Professor P. HUT, of Princeton University, tentatively related the periodicity of such events with solar effects. According to Hut, the sun is not a simple star, but half of a double star, of which the other half is no longer active (a black dwarf). The revolution time of the sister-star, indicated by the name Nemesis, is computed as approximately 32 My. This means that it comes once every 32 My close to the Earth, causing a comet storm, lasting perhaps 1.5 My. The comet Chicxulub, that crashed in the Gulf of Mexico about 65 My ago, could have been a fragment of the comet storm (PRIESTER, 1993).

If the 32 My cycle is true, we have to expect the next crisis within the next 2 My. So, not only a short-term heating of the Earth (the greenhouse effect) is threatening our biotas, but also a long-term, secular event.

During the last two anoxia stages in the Atlantic, almost the entire water mass, with the exception of the upper 100-200 m, was affected. In the uppermost layer, phytoplankton development and atmospheric contact increased the oxygen content. This implies that below some 200 m no animal life was possible and that just above the anoxic layer only those animals survived that were resistant to low oxygen contents. Any still living Tethyan deepwater animals died (figs. 3-4).

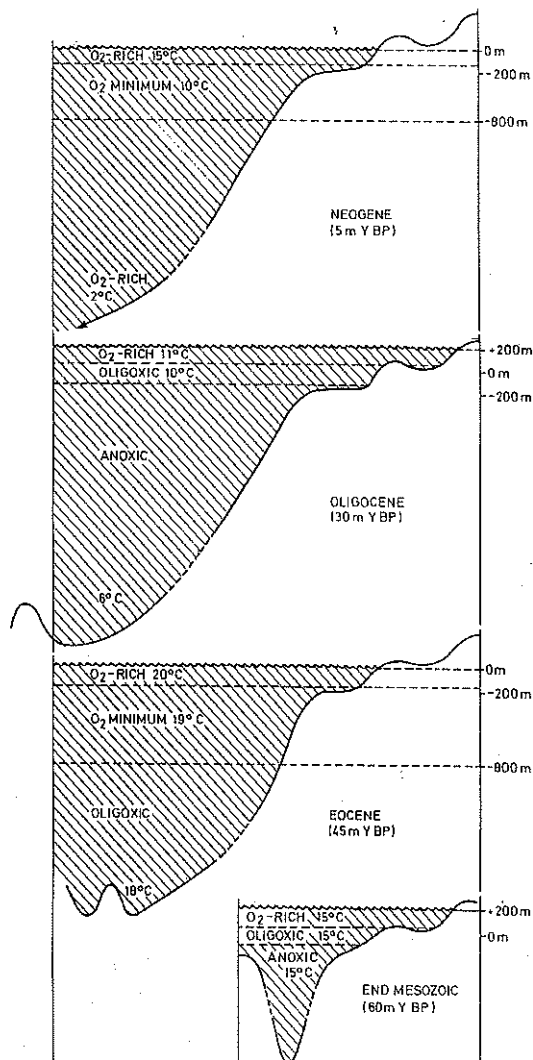


Fig. 3 - Various stages in the development of the Atlantic Ocean at *ca.* 30° N (several data according to FISCHER & ARTHUR, 1977; paleotemperatures based on O¹⁸/O¹⁶ data). Periodic anoxia stages coincide with eustatic sea-level transgressions. Cooling, especially of the bottom waters, is correlated with the reventilation of the Atlantic after the opening to the North Pole in the Oligocene/Miocene, enhancing the flow of Arctic and Antarctic, cool and oxygenated deep-water currents. Note that periods of extended anoxia existed *ca.* 30 and 62 My BP; during this period bathyal and abyssal macroscopical life was impossible. (After STOCK, 1990.)

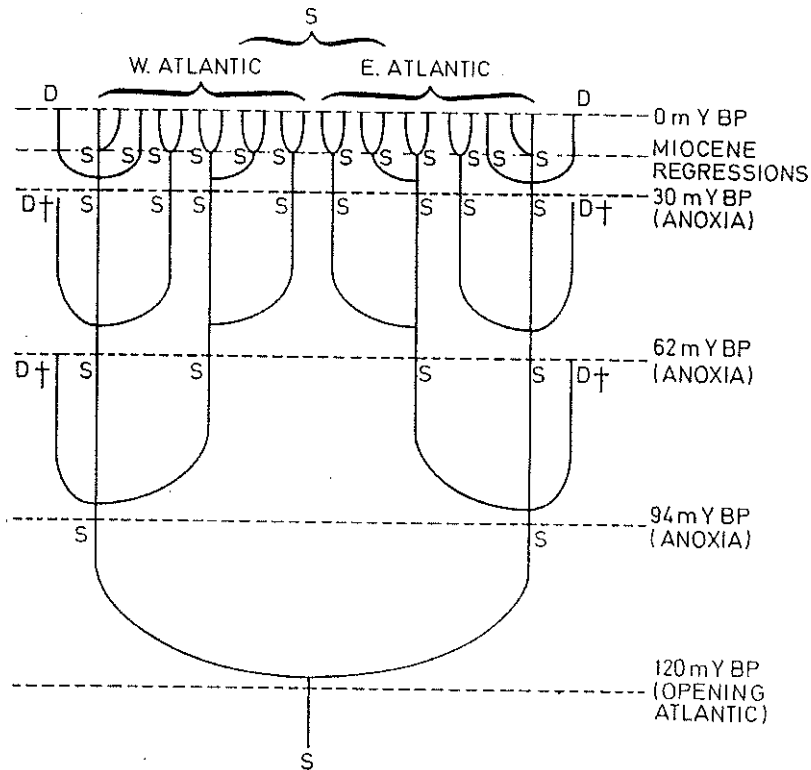


Fig. 4 - Diagrammatic evolution tree of stygobionts, both marine crevicular/interstitial and continental/insular (S) and evolution and extinction of deep-sea taxa (D) in the Atlantic Ocean at ca. 30°N. At each of the periodic anoxia stages, extinction of deep-water taxa (†) took place (the extinction is corroborated by paleontological evidence at the Eocene/Oligocene boundary and the Mesozoic/Tertiary boundary). In the oligoxic, aphotic intermediate watermasses, the best possibilities for stygofaunal evolution existed.

The marine transgressions (causing anoxia) alternate with marine regressions, resulting, according to the Regression Model, in stranding of marine stygofaunal elements, from which in turn the insular and continental (*i.e.* inland) stygobionts evolved.

The diagram explains the evolution of numerous stygobiont taxa, and the low number of deep-water taxa, due to periodic extinction. No doubt, several stygobionts have been subjected to extinction as well, but because of lack of paleontological evidence, these extinction moments have not been indicated in the diagram. (After STOCK, 1990.)

When, still in the Atlantic, oxygen conditions improved during the Miocene, animal life evolved rapidly. The improvement was due to sea-floor spreading: the gap between Greenland and Europe widened and deepened to an extent enabling oxygen-rich Arctic surface water to reach the central Atlantic. In the earlier Tertiary, and in the Mesozoic, surface and bottom temperatures in the ocean were still high (FISCHER & ARTHUR, 1977, fig. 4). Differentiation between cold bottom waters and warm surface waters started only after the gradual opening of the North Atlantic, in the Tertiary, when cold polar waters got access to the Atlantic.

After every anoxia crisis, the animals surviving the crisis, were competitively forced to live in places where such low oxygen levels still prevailed. Such places are for instances deep rock crevices, meiobenthic and interstitial habitats, sea caves, etc. From these animals evolved the numerous Recent stygobionts: they were already preadapted to low oxygen levels and crevicular or interstitial life, thus ready to inhabit successfully caves and other types of underground habitats on land, the type of habitats in which they occur to-day.

The cooling during the Miocene, and subsequent ice-cap formation, resulted in a eustatic sea-level regression which had several biological effects: stranding of the ancestors of the stygobionts, extinction of important parts of thermophilous coastal habitats, like coral reefs and mangrove forests, evolution of a cold-loving deep-sea fauna.

The process of evolution of marine organisms under low oxygen conditions in cryptic habitats is called the pre-adaptation phase in the Regression Model. A somewhat similar process, however with a more active, dispersing, role of the organisms was envisaged by BOUTIN & COINEAU (1990) and NOTENBOOM (1991) and called the first phase of a Two-Phase Model.

CONCLUSIONS

I postulate the following events for the Mid-Atlantic islands:

- (1) The epigeal and groundwater Malacostraca evolved from marine ancestors.
- (2) This evolution started when the primordials of the islands were close to, or above, sea-level (water depth less than 200 m, as deeper waters were uninhabitable during periods of anoxia).
- (3) These animals are poor dispersers (lack of free-living larval stages, low egg numbers, etc.), leading to high degree of endemism.
- (4) The ancestors of these Malacostraca must have been widely distributed in the former Tethys Sea, judging from their present-day amphi-Atlantic or even pan-tropical

distribution patterns.

(5) Point 4 indicates that their origin must be placed in the Mesozoic; Boutin's study (1993) of the Canary Islands points to the Cretaceous (late Senonian) as the subaerial age for Fuerteventura.

(6) All biological evidence points to a similar age for most Mid-Atlantic islands (Macaronesia, Ascension, Bermuda). Because the North Atlantic was still closed in the Cretaceous, all islands were at that time closely associated with the Eurafrikan continental plates.

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