Explorations of the systematics and deep history of stygobiont amphipods

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Summary

This thesis consists of 13 articles that deal with aspects of zoogeography and evolution of cryptic crustaceans in transition between seabottom and freshwater subterranean ecosystems.
The late Professor J. H. Stock around 1976 initiated the research at the University of Amsterdam concerning the zoogeography of groundwater fauna, when he began to report on thermosbaenaceans and ingolfiellids from the West Indies. These groups of crustaceans complete their life cycle under strict underground conditions and thus posed a subject for studying vicariance biogeography: how did supposedly unconnected populations of stygofauna evolve and does this evolution reflect the geological history of the places where they are found today?

Apart from the purely academic interest in stygobiont crustaceans just as they are - inconspicuous, silent, and sometimes beautifully adapted remnants of bygone eras, hidden from the eye in the underground - there is the wider perspective of trying to find relations between animal evolution and geological history.

Within this framework the articles were written. A division in four themes is evident: (A) general mechanisms and patterns of evolution in stygobiont amphipods, (B) Caribbean anchialine and littoral sediment habitats, (C) mid-Atlantic sea mount relicts and beach inhabitants of the Canary Islands, and (D) Mediterranean freshwater ingolfiellids from wells and caves.

The **first article**, and the most elaborate one, benefits from the cladistic methods adopted in later years by most workers in our Institute under Prof. F. R. Schram. A truly cosmopolitan, but rarely encountered, group of underground crustaceans belonging to the amphipod suborder Ingolfiellidea is studied and an overview of this group is presented. More data on type material were collected and we constructed a phylogenetic character matrix upon which cladistic and biogeographic analyses could be performed. As has been commented upon by earlier workers, some groups have much older patterns of distribution than the (supposedly derived) morphology of their bodies bespeaks. Subterranean amphipods are thought to have limited dispersal capacities in comparison with marine and freshwater benthic relatives and therefore a much older origin is suspected than the fossil record of 40 My now shows. In the first article, in which a world wide ingolfiellid distribution is discussed, we propose that even if dispersal is `slow' it can be nevertheless active and perhaps fast, or rather persistent, enough to move animals along in connection with a spreading sea-floor. Since some ingolfiellids are reported from opposite sides of oceans as well as on the deep-sea floor this opens the possibility of dispersal via the geological process of sea-floor spreading and the stable presence over eons of time of a suitable habitat for this type of animal.

A pattern emerges from the cladistic analysis of the Ingolfiellidea in which the oldest forms are the large African cave types, and one south Italian species. This fact may reflect the haphazard nature of every discovery of cavernicolous and ground water animals, but it definitely means something more too. Stable continental biotas may well have acted as sources for dispersal into other niches such as the small interstitial spaces of river alluvia and, still later, the brackish and marine sands along the continental coasts. Perhaps not coincidentally such a land-to-sea route is also proposed for a group distantly related to the amphipods, the gnathostenetroidoidean isopods (article IX). The usual track postulated in the past by most workers is an `einwanderung' of marine species, via brackish conditions, towards freshwater systems. So now we stand with alternative contending hypotheses concerning the evolution of the ancient groundwater biota.

This focus on elucidating colonization routes also occurs in the study of bogidiellids seen in the **second article**. This large group (110 species, 33 genera) of strictly subterranean amphipods have been extensively sampled in southwest Turkey on a Dutch-Turkish expedition. Collections from littoral submarine springs to inland wells and riverbeds were investigated and comparisons made between several individuals of different populations. The matter of dispersal versus vicariant events is raised here too: can there be thalassoid lineages regularly invading coastal ground waters, arising out of ancient freshwater clades already present in the area? A prediction is made that purely marine bogidiellids will be encountered before long in the Mediterranean. The role of `missing' taxa is

explored as these might explain striking similarities in character states between Caribbean and Turkish species.

An actual case of mingling of morphological characters in populations of adjacent species is described in the **third article** based on fieldwork in France. In this paper, a correlation between the area history and the distribution of ground water crustaceans is worked out in detail. Large rivers such as the Dordogne and the Lot provide for quick dispersal through an area. The transgressions of the Atlantic Ocean in the Aquitanian Basin have had obvious effects on the distribution of several species of *Niphargus*. The value of extensive sampling is made clear through this article.

Part B contains those articles that are based on material from the Caribbean and Hawaii. The **fourth article** describes a new species of *Psammogammarus* from an anchialine cave pool on the northwest side of the Dutch Antilles island of Bonaire. It is noteworthy that the large natatory third uropod of this new species resembles the one in a species on a Red Sea island in a similar environment, while the other members of the genus are geographically much closer to the new species: it is a well known phenomenon that comparable habitat requirements call for convergent adaptations in unrelated species. Furthermore, the absence on Bonaire of what is a common genus on the nearby island of Curaçao, *Metaniphargus*, is remarkable and recalls to memory that rare study on competition between stygobionts [Stock, 1982. The influence of hadziid Amphipoda on the occurrence and distribution of Thermosbaenacea and cyclopoid Copepoda in the West Indies. Polskie Arch. Hydrobiol. 29: 275-282].

The **fifth, sixth** and **seventh article** describes the new genus *Psammomelita*, new species of *Nuuanu* and *Melita*, and another new genus *Thalassostygius*. *Psammomelita uncinata* has peculiar apomorphic structures – ventral hooks between the pleopods and a curved keel on the male maxilliped. All of the species in these publications have underdeveloped eyes. With their appearance in littoral, moving, sands it would appear that they are not only preadapted for lightless environments, but that they also constitute a structural `type' in the interstitial corridor: those with small and compressed bodies and short appendages that are not found inland.

The **eighth article** describes two species of *Metaniphargus* with representatives in the Atlantic and Pacific Ocean. Like *Pseudoniphargus*, this genus with members in marine littoral sands, brackish pools, and inland freshwater wells has a more extended distribution in at least one marine species than in their inland congeners.

Part C begins with the **ninth article** about *Caecostenetroides ascensionis*, an isopod from a genus with only four species, all found in insterstitial habitats in the intertidal zone ranging from Japan through the Mediterranean and Canary Islands to Ascension Island, that lonely peak rising up from the South Atlantic Ocean floor halfway between West Africa and Brazil. Although this isopod from Ascension Island appears to be the odd man out in contrast with the amphipod story on evolutionary tracks, this is not so. We could postulate benthic marine isopod ancestors that invaded empty niches on the continent, we could equally propose an ancient freshwater Tethyan lineage that `crawled down' to the marine interstitial in the case of *Caecostenetroides*.

The **tenth** and **eleventh article** emerged from collections made on the Canary Islands, especially the main island of Tenerife, where the newly described species of *Psammogammarus* and *Ingolfiella* occurred. Both species are accompanied by other interesting fauna such as bogidiellids, other psammogammarids, and several microphthalmous amphipods. They reveal the rich but irregularly populated rubble in tide pools that can only be investigated by long term sampling programs. One must be persistent, returning to at-first-unyielding stations in order to receive one's reward.

Part D, finally, is reserved for two Mediterranean species, described in the **twelfth** and **thirteenth article**. *Ingolfiella cf catalanensis* from a freshwater well close to the sea on the Spanish East Coast, and *Ingolfiella beatricis* from a cave in Slovenia, not far from the Adriatic Sea. This last species stands out in the *Ingolfiella* clade as it is a true freshwater species but with the cephalic lobes between

the first and second antennae well developed, a phenomenon usually reserved for the deep sea and interstitial marine dwellers.

The research on cryptic crustaceans will go on. We now have alternative hypotheses to investigate. Previously, the Regression Model of Stock placed the stygobiont biota in a context of fluctuating sea levels. Others have described many other possible ways of colonization of coastal and continental groundwater as well as deep-sea sediment. We now realize that an incredibly ancient continental biota linked to archaic landmasses may have populated islands at early stages of their formation and may even subsequently provided elements of the deep-sea faunas.