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# Evolution of cavernicolous planthoppers (Homoptera, Fulgoroidea) on oceanic islands : A comparison between Hawaii and the Canary Islands

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Until recently, the apparent impoverishment of terrestrial obligate cavernicolous arthropods in the tropics was regarded to be due to the lack of unfavorable ecological conditions which in temperate regions have left troglophilic organisms "trapped", e.g., during glaciation ("relict hypothesis" : e.g.)[2]. Howarth[8] however, provided an alternative model to explain the evolution of terrestrial troglobites in the tropics, postulating that troglobite evolution followed the pattern of adaptive radiation, with the existence of adequate habitats in a given area as a mandatory pre-requisite ("adaptive shift model"). This bioclimatic model allowed predictions on the occurrence of terrestrial troglobites. Subsequent faunal inventories of limestone caves and lava tubes in many parts of the tropics (e.g., Australia[10]) and on oceanic islands complied with these predictions, revealing extraordina-rily rich terrestrial cave faunas.

In regard to the planthoppers, Hawaii and the Canary Islands have in particular proven rich in obligate cavernicolous species. On both oceanic archipelagoes lava tubes with adequate cave-planthopper habitat (roots of surface-vegetation as the energy-source for rhizophages). On both island groups, cave-adapted species have evolved independently, but with astonishing similarity in external morphology which is characterized by the usually strong reduction of compound eyes, wings, and body pigment.

**Cavernicolous species**

*Hawaii*: In the surface fauna of Hawaii, two primary colonizations within the family Cixiidae have occurred, represented by the genera *Iolania* and *Oliarus*. Of these, only *Oliarus* has undergone intensive speciation (adaptive radiation?) on all major islands (ca. 80 epigean species)[13]. A total of six evolutionary lines have colonized underground habitats on Molokai (1), Maui (3) and Hawaii Island (at least 2)[7]. Biosystematic studies concentrated on one of the evolutionary lines on Hawaii Island, the apparently widespread species *Oliarus polyphemus*. The analysis of intraspecific communication signals of several populations from different lava tubes on Mauna Loa, Kilauea, and Hualalai volcanoes revealed that all populations tested are apparently reproductively isolated. Thus, the formerly widely distributed *Oliarus "polyphemus"* is rather a species-complex comprising at least 7 separate species.

*Canary Islands:* In the cavernicolous species have evolved within two planthopper families : the Cixiidae and the Meenoplidae. In the Cixiidae, at least 11 species have colonized underground habitats : 4 *Cixius*-species on La Palma, 2 *Cixius*-species on El Hierro, and at least 5 *Tachycixius*-species on Tenerife. These species presumably represent at least 8 separate evollutionary lines. In the Meenoplidae, we now know of 3 cave-adapted *Meenoplus*-species: one of La Palma, and two on El Hierro. The 3 *Meenoplus*-species presumably represent at least two evolutionary lines[4].

Interestingly, a case parallel to the *Oliarus polyphemus* species-complex on Hawaii has been discovered on Tenerife : populations of *Tachycixius lavatubus* from 3 lava tubes in different regions of the island display a high degree of divergence in their communication signals and are most likely reproductively isolated[5].

**Epigean relatives and hypothetical ancestral species.**

*Hawaii*: On the islands, where cavernicolous *Oliarus*-species are found today, closely related surface species are still extant. Thus it is plausible, that the troglobitic *Oliarus*-species on Hawaii arose through parapatric spe-ciation, i.e., an adaptive shift to underground habitats is likely to have occurred without prior extinction or extirpation of their epigean ancestral species.

*Canary islands:* For the majority of the cavernicolous planthopper species of the Canary Islands no close relatives are found in the recent epigean fauna. This present-day "relict situation" however, does not necessarily imply the evolution of cave-adaptation subsequent to the disappearance of the ancestral surface species. Extinction of the surface populations could have occurred after the cavernicolous species had evolved.

**Faunal diversity and origin of divergence.**

Compared to Hawaii, the Canary Islands show a higher degree of diversity in cave planthopper species on a higher taxonomic level : at least 8 evolutionary lines within 2 genera in the Cixiidae, and at least two evolutionary lines within one genus in the Meenoplidae (total : 14 species). In Hawaii, a total of 13 cavernicolous species belong to 6 separate evolutionary lines within one genus (*Oliarus*) of one family (Cixiidae). This is apparently due to the differences in the composition of the surface fauna which depends on geological age and distance to the nearest continent. Those islands of the Hawaiian chain, which today reach above sea level, are comparatively young (0.5 - ca. 5 myr[3]). They are situated in a distance of ca. 3,850 km from the nearest continent, and have apparently been reached by comparatively few initial colonizing species. Based on a maximum age of 5 myr (Kauai) and their recent insect fauna, it has been calculated[11] that there has been only one successful colonization in 12,750 years. According to morphological criteria, all 80 epigean *Oliarus*-species are likely to have originated from a single primary colonization[13]. In contrast, the Canary Islands are substantially older : e.g., for the oldest parts of La Gomera, Arana & Carracedo[1] assume ca. 20 myr. The islands in a distance of only 150 km (Fuerteventura) to 500 km (El Hierro, La Palma) to continental Africa. Accordingly, a higher number of primary colonizers has reached the islands.

In Hawaii as well as in the Canary Islands, the discovery of apparently closely related yet reproducti-vely isolated populations of obligate cavernicolous species on one and the same island (*Oliarus polyphemus* species-complex on Hawaii Island, *Tachycixius lavatubus* species-complex on Tenerife) fosters considerations on the origin of the observed differentiation. On one hand, it is conceivable that a single species adapted to caves and subsequently underwent speciation processes. On the other hand, one or several (closely related) species could have given rise to (temporally and geographically) separate cave colonizations.

The geological conditions on volcanically active islands seem to favour the assumption of speciation subsequent to the cave-adaptation of a single species. Recent radiocarbon-dating of lava flows and ash layers on Hawaii Island[12] show that the surface of active volcanoes is renewed at a rate of 40%/1000 years (Mauna Loa), and 90%/1000 years (Kilauea) respectively. This renewal causes changes in surface vegetation, which in turn have impact on the underground environment (e.g., distribution of roots). Thus it is conceivable that a cave-adapted rhizophagous species inhabits a continuous area in a lava flow which is loosely vegetated by pioneer plants. Field observations revealed that the abundance of roots inside the caves is highest in only loosely vegetated flows.

This is due to the fact, that soil formation is not (yet) well progressed on the surface. Xeric surface conditions force the plants to produce immense root masses to guarantee sufficient water supply. Depending on the climatic conditions (windward or leeward side of the island) such a successional stage (= loosely vegetated lava flow) can persists for variable amounts of time (from a few decades to several centuries)[6]. Conversely, there are almost no roots in caves within old lava flows where rain forest cover has developed, along with progressed formation of a soil layer which now contains the majority of roots. The original area of a hypothetical rhizophage may be divided up by new lava flows which destroy vegetation on the surface and roots in subterranean habitats. Differentiations acquired during separation may become established quickly (e.g., due to founder effects, small population size of K-selected organisms) eventually leading to reproductive isolation.

It is amazing that in Hawaii as well as in the Canaries the highest number of cavernicolous planthopper species is found on the volcanically most active islands (Hawaii Island, Tenerife, La Palma) whereas no cave-adapted planthopper species apparently occur on the older (and volcanically inactive) islands (Oahu, Kauai, La Gomera, Gran Canaria). this may indicate that the existence of a cave-adapted community with planthoppers as rhizophagous primary consumers is highly dependent on active volcanism : lava flows continuously create new habitats which then gradually disappear as vegetational succession and erosion progress.

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