Hidden from the light of day: planthoppers in subterranean habitats (Hemiptera: Auchenorrhyncha: Fulgoromorpha)

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Abstract

The vast majority of Auchenorrhyncha species is associated with the green parts of plants in grasslands and forests. A number of species, however, has abandonned environments brimming with abundance in food and light, and in the course of evolutionary change, adapted to the underground realm where darkness and other seemingly adverse conditions prevail. This contribution gives an overview on these species, their way of life, their habits, their evolution and their strategies of survival in unusual habitats.

Introduction

As phytophageous insects, most Auchenorrhyncha species feed on the green parts of living plants. Thus they appear unlikely candidates for a permanent life underground. However, more than 50 subterranean Auchenorrhyncha species are now known in 5 families of the Fulgoromorpha (planthoppers):

Cixiidae, Delphacidae, Kinnaridae, Meenoplidae, and Hypochthonellidae (HOCH 1994). So far no cavernicolous Cicadomorpha have been reported.

All cavernicolous Fulgoromorpha species belong to taxa with immature stages living close to the soil, e.g., under the dead bark of rotting logs, in leaf littoor moss, or even within the soil, feeding on roots or perhaps on fungi (REMANE & HOCH 1988). From this plateau of ecological preadaptation, it seems to be a small evolutionary step to switch completely to a life underground. In epigean (surface-dwelling) species of these taxa, adults leave the nymphal habitat to feed and reproduce above ground. During the process of evolutionary change, the adults of cavernicolous species have acquired behavioral and physiological adaptations which allow for their survival in the nymphal habitat. The ecological conditions of subterranean biota include permanent darkness, constant temperature, a (usually) high relative humidity (HOWARTH 1983), and occasionally, abnormally high carbon dioxide concentrations (HOWARTH & STONE 1990). Much like other obligately cavernicolous (troglobitic) arthropods, cave-dwelling Auchenorrhyncha species display characteristic morphological alterations: e.g., reduction and loss of compound eyes, ocelli, tegmina, wings and bodily pigmentation (HOCH 1994).

Emerging to light: history of exploration

The first cave-dwelling Auchenorrhyncha species was apparently discovered by RACOVITZA at the beginning of last century (RACOVITZA 1907). In this paper, he mentions completely unpigmented nymphs and adults of a „*Cixius*" species from the Cuevas del Drach on the Balearic Island Mallorca. Unfortunately, this species was never described as a new species. Consequently, it is not mentioned in VANDEL (1965). The author has not been able to track down the original material. 45 years later, a remarkable new fulgoroid species was described from Zimbabwe, *Hypochthonella caeca*, for which CHINA & FENNAH (1952) established not only a new genus, but erected even a new family, the Hypochthonellidae. It

displays the characteristic troglomorphies of cave-dwelling insects such as reduction of eyes, wings, and bodily pigment. Adult and immature specimens were found in the soil feeding on roots of tobacco, maize and groundnut. *H. caeca* is the only known true endogean (interstitial soil organism) fulgoroid taxon.

The first valid description of a true cave-dwelling fulgoroid species was published by SYNAVE (1953): a troglobitic cixiid from caves in Madagascar, forming a new genus, *Typhlobrixia*.

VANDEL (1965) considered it a soil form accidental in caves, but HOWARTH (1972) interpreted it as a morphological intermediate between epigean species and strongly troglomorphic species such as the troglobitic cixiids he had discovered in Hawaiian lava tubes: the blind, flight- and pigmentless *Oliarus polyphemus* from Hawaii Island and *Oliarus priola* from Maui (FENNAH 1973a). HOWARTH (1972, 1973, 1983) gave notes on their biology and ecology.

Prompted by these early findings, awareness among speleologists increased and consequently, since then cavernicolous Fulgoroidea were discovered and described from many parts of the world: Mexico, Jamaica, Australia (W.A., Queensland), New Caledonia, New Zealand, Hawaii, Western Samoa, Galápagos, Canary Islands, Azores, Cape Verde Islands (see table 1).

Evolution of cave-adaptation: changing views

The fact that close epigean relatives of obligately cavernicolous *Oliarus* species were found to exist on the same islands and in close vicinity to the lava tubes, was interpreted by HOWARTH (1986) to be the result of parapatric speciation, i.e., quintessentially, adaptive radiation. Exploitation of a novel, i.e., unutilized food resource, roots of native trees, was hypothesized to be the driving force in the adaptation to a permanent life underground. This „adaptive shift hypothesis" based on the discovery of troglobitic terrestrial organisms on young oceanic islands in the tropics challenged the then widely accepted theory on

troglobite evolution. Prior to these findings, observations in temperate climates had suggested that changing ecological conditions on the surface had presumably caused extinction or extirpation of surface populations, leaving troglophilic populations „trapped" underground which subsequently evolved adaptations to the new environment („relict hypothesis", see BARR 1968, VANDEL 1965).

Fig. 3:
Root curtains (*Metrosideros polymorpha*) in Hawaiian lava tube (Photo: H. Hoch)

Based on his discoveries in Hawaii, HOWARTH (1980) developed a bioclimatic model to explain and predict geographic distribution of terrestrial troglobites. According to this model the evolution of troglobites is favored by the bioclimatological and physical characteristics of the cave rather than by those of the surface environment. The model allows to predict the possible existence of terrestrial troglobites wherever caves provide sufficient moisture, food supply, and where they are old enough to allow sufficient evolutionary

Hypochthonellidae	Zimbabwe	CHINA & FENNAH 1952
Delphacidae	New Caledonia	FENNAH 1980a
Kinnaridae	Mexico	FENNAH 1973 b
	Jamaica	FENNAH 1980 b
Meenoplidae	Australia	FENNAH 1973 b, HOCH 1990, 1993
	New Caledonia	HOCH 1996
	Western Samoa	HOCH & ASCHE 1988
	Canary Islands	REMANE & HOCH 1988, HOCH & ASCHE 1993
	Cape Verde Islands	HOCH et al. 1999
Cixiidae	Madagascar	SYNAVE 1953
	Canary Islands	REMANE & HOCH 1988, HOCH & ASCHE 1993
	Azores	HOCH 1991
	Mexico	FENNAH 1973a, 1973b, HOCH 1988
	Argentina	REMES LENICOV 1992
	Hawaii	FENNAH 1973a, HOCH & HOWARTH 1999
	Galápagos	HOCH & IZQUIERDO 1996
	Australia	HOCH & HOWARTH 1989a, 1989b
	New Zealand	FENNAH 1975
	[Baleares]	RACOVITZA 1907 (unconfirmed record)
	[Southern France, New Guinea, Reunion]	unpublished data

Tab. 1:
Geographic distribution of cavernicolous Auchenorrhyncha

Fig. 4:
Entrance of Hawaiian lava tube (Photo: H. Hoch)

time for acquiring cave adaptations. Discoveries of diverse troglobitic arthropod faunas in the tropics, e.g., Australia (Queensland) confirm the predictions, however, vast areas known to contain caves, both in Karst and volcanic regions, remain to be explored (e.g., South America, SE Asia, Africa).

Blind and pale, yet quick and nimble: the morphology of cavernicolous Fulgoromorpha

Reductive trends

The most striking features of cavernicolous Fulgoromorpha are due to reductive evolutionary trends characteristic for cave insects: reduction of eyes, wings and pigmentation. The factors responsible for regressive evolution have been controversially discussed (see discussion in CULVER 1982).

The stepwise reduction of these characters and correlated morphological alterations have been observed in taxa containing epigean, troglophilic and troglobitic species with varying degrees of troglomorphy, e.g., the cixiid genera *Solonaima* from Australia (HOCH & HOWARTH 1989b) and *Oliarus* from Hawaii (HOCH & HOWARTH 1999). In *Solonaima*, for example, the gradual reduction of compound eyes in cave-dwelling species is correlated with the broadening of the vertex and frons and the eventual loss of head carination. As tegmina and wings cease to function, the venation pattern shows increased variation and mesothoracic muscular apodemes degenerate, resulting in a planate and weakly carinate mesonotum. The pronotum also becomes more planate, thus enhancing the depressed body form which may favor moving along smaller cracks and voids.

Generally, adaptation to similar environments has led to amazingly similar evolutio-

nary outcomes in separate cavernicolous Fulgoromorpha lineages in different parts of the world, thus making them ideal model organisms to study convergent evolution.

Progressive trends (specializations)

Many cavernicolous Fulgoromorpha species display specialized structures which are apparently not due to regressive evolution (HOCH & HOWARTH 1989b). In the highly troglomorphic cixiid species *Solonaima baylissa* from Australia the clypeus as well as the 2nd antennal segment bear tiny hairs which may have additional sensory function or serve as a protection against moistening in the saturated atmosphere of thier habitat. The tegmina of all troglobitic *Solonaima* species possess as well developed wax-fringe in life which is lost when the animals are disturbed, perhaps serving as an additional protection against moisture or to repel prospective predators. *Solonaima baylissa* also possesses a specialized hind tibial spinulation: although reduced in number, the apical hind tibial spines are distinctly stronger developed than in less cave-adapted *Solonaima* species. This specialization may enhance the skill to walk on wet or rocky surfaces. This skill has apparently also been acquired by Hawaiian cave *Oliarus*: compared to epigean species the pretarsal claws are modified for walking on rock (HOWARTH 1981).

Cryptic existences: biology and ecology of cave-dwelling planthoppers

Endogean and truly cave-dwelling Fulgomorpha are found to occur in a variety of subterranean habitats: the interstitial of soil, the mesocavernous rock system, lava tubes, and limestone caves. Interstitial soil-inhabiting Fulgormorpha seem to be the exception (*Hypochthonella caeca*). The mesocavernous rock system includes spaces varying greatly in size, ranging from few mm to several cm and beyond, eventually corresponding to the human concept of a „cave". However, size and substrate (volcanic or sedimentary rock) of the underground space play a far lesser role than e.g., food availability (occurence of roots) and humidity. The fact that most obligately cavernicolous Fulgoromorpha species have been found in open lava tubes and limestone caves, may be a collectors´ bias, and it is well conceivable that small voids and cracks in the mesocavernous rock system, largely unaccessible to human exploration, are the main habitat, and cave planthoppers only venture into „caves" when the other conditions are replicated (HOWARTH 1983).

Fig. 5:
Lava tube interior
(Photo: H. Hoch)

Fig. 6:
Biospeleologist F.G. Howarth in narrow cave entrance (Photo: H. Hoch)

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Fig. 7:
Solonaima baylissa,
Australia, habitus
(Photo: H. Reimer)

Fig. 8:
Tachycixius lavatubus, Canary Islands, habitus (Photo: E. Wachmann)

Most of the existing information on the biology and ecology of cavernicolous Fulgoromorpha stems from research on a single taxon: the cixiid genus *Oliarus* on Hawaii (HOWARTH 1973, 1981; HOCH & HOWARTH 1993, 1999; HOCH & HOWARTH, unpublished data).

Within the cave ecosystem, rhizophagous Fulgomorpha are primary consumers (HOWARTH 1972, 1981). HOWARTH (1973) presented a model showing the role of troglobitic *Oliarus* species in the food web of a Hawaiian lava tube. Nymphal instars of Hawaiian cave *Oliarus* suck sap from roots of native trees (predominantly *Metrosideros polymorpha*, Myrtaceae) and produce an irregular wax filament cocoon in which they remain while feeding unless disturbed. The final (V.) instar nymph moves to a protected area, makes another cocoon and transforms into an adult in about one week. While nymphs are usually closely associated with roots, the adult (which is the dispersal stage) can be found throughout the dark zone of the cave (HOWARTH 1981). Reproduction is apparently asynchronous, all stages can be found throughout the year (HOWARTH 1981, HOCH & HOWARTH 1993). Eggs are deposited 4-14 days after copulation in clusters of up to ten in nests of wax filaments on roots. Postembryonic development (hatching to adult) lasts at least 10-12 months (HOCH & HOWARTH 1993). The longevity of the adults, the long duration of a generation cycle and the small number of eggs deposited leads to the assumption of a comparatively low reproduction rate. It can be assumed that Hawaiian cave *Oliarus*, like many other obligate cavernicoles (see CULVER 1982) underlie selective forces typical for ecologically stable environments (K-selection).

An interesting aspect of the biology of obligate cave Fulgoromorpha is their mating behavior. To locate and to recognize a suitable conspecific partner for mating in total darkness poses a challenge which requires a specialized communication system. Chemical communication, e.g., by pheromones, has not been reported in the Auchenorrhyncha and may not exist, and optical information is unavailable (darkness, reduction of eyes). Like their epigean relatives, cave Fulgoromorpha not only use low-frequency substrate–borne vibrational signals which are transmitted via the substrate (subterranean parts of the host

plant), but may depend exclusively on this intraspecific communication channel. With usually low population density posing another challenge to mate location, living roots have proven to be very effective in the transmission of vibrational signals: in a field experiment carried out in a Hawaiian lava tube signals produced by an *Oliarus* individual of ca. 4 mm body length travelled at least 2.50 m in each direction of the source of vibration (HOCH & HOWARTH 1993, HOCH 2000).

Looking back over the past 5 decades, one may say that a tremendous knowledge on cavernicolous Auchenorrhyncha has been gained since their first discovery. Taking into account, however, how comparatively few researchers have dedicated their efforts to the exploration of underground faunas, it becomes clear that many more cave-dwelling Auchenorrhyncha await their discovery and investigation.

Zusammenfassung

Die Mehrzahl der bekannten Auchenorrhyncha Arten ist mit grünen Pflanzen assoziiert, insbesondere in Grasland und Wäldern. Einige Arten haben jedoch die oberirdischen Lebensräume trotz deren Reichtums an Nahrungsquellen und Licht verlassen und besiedelten im Laufe der Evolution unterirdische Gefilde (Höhlen) mit scheinbar so unwirtlichen Bedingungen wie z.B. Dauerdunkel. Der vorliegende Beitrag gibt eine Übersicht über diese Arten, ihre Lebensweise, ihr Verhalten, ihre Evolution und ihre Überlebensstrategien in diesen ungewöhnlichen Lebensräumen.

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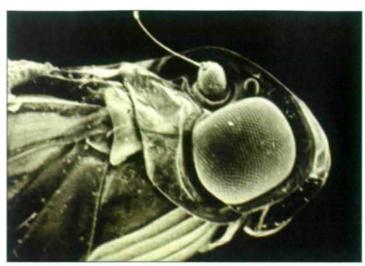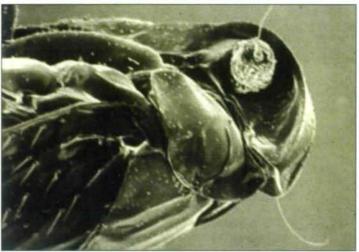
Fig. 9: Head of epigean (top) and troglobitic (bottom) *Oliarus*, Hawaii (SEM), (Photo: F.G. Howarth)

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