# CAVE-DWELLING PLANTHOPPERS OF AUSTRALIA (INSECTA: HOMOPTERA: FULGOROIDEA)

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## *ABSTRACT*

*Recent investigations in caves in Cape York Peninsula, Queensland, have revealed the existence of at least 11 previously unknown cavernicolous Fulgoroid species of the families Cixiidae and Meenoplidae. These species represent at least 7 separate evolutionary lines within the Fulgoroidea that have invaded caves. The species belong to the genera Solonaima Kirkaldy, Undarana Hoch & Howarth, and Oliarus Stal within the Cixiidae, and to Phaconeura Kirkaldy within the Meenoplidae. In the present paper a preliminary account of the known Australian cave Fulgoroids is given, the morphological alterations they have undergone during the process of cave-adaptation are briefly described, and notes on the geographic distribution and ecology of each species are given.*

## INTRODUCTION

Until recently terrestrial troglobites (obligate cavernicoles) seemed to be poorly represented in Australia compared to similarly large areas in temperate regions, e.g. the United States (Matthews and Kitching, 1976). Various authors (e.g. Moore, 1964; Hamilton-Smith, 1967) have tried to rationalize this apparent impoverishment by the ecological stability of tropical surface environments. Recent investigations in Karst and lava caves in tropical northern Queensland, however, have revealed a remarkably diverse cave-adapted fauna (Howarth, this issue).

In the collections from the caves were several Homoptera species of the Fulgoroid families Cixiidae (Hoch and Howarth, in press) and Meenoplidae. Epigean Fulgoroidea are distributed worldwide and comprise about 15,000 species. Some groups of Fulgoroidea are pre-adapted for a life underground - their nymphs live close to or within the soil where they suck sap from roots. Prior to the investigations in Queensland caves only one troglobitic Fulgoroid species was known from Australia: the meenoplid Phaconeura pluto Fennah (Fennah, 1973) from Quandong Cave, Nambung National Park, Western Australia. Outside Australia, cavernicolous Fulgoroidea are known to exist in New Zealand, New Caledonia, Hawaii, Mexico, Jamaica, Zimbabwe, Madagascar and the Canary Islands (see table 1 in Remane and Hoch, 1988: 405). As a result of the recent findings of cavernicolous planthoppers, which belong to at least 11 species, Queensland now has the highest concentration of cave-adapted Fulgoroidea in the world.

## GEOLOGY AND CAVE LOCATIONS OF THE STUDY AREA IN QUEENSLAND

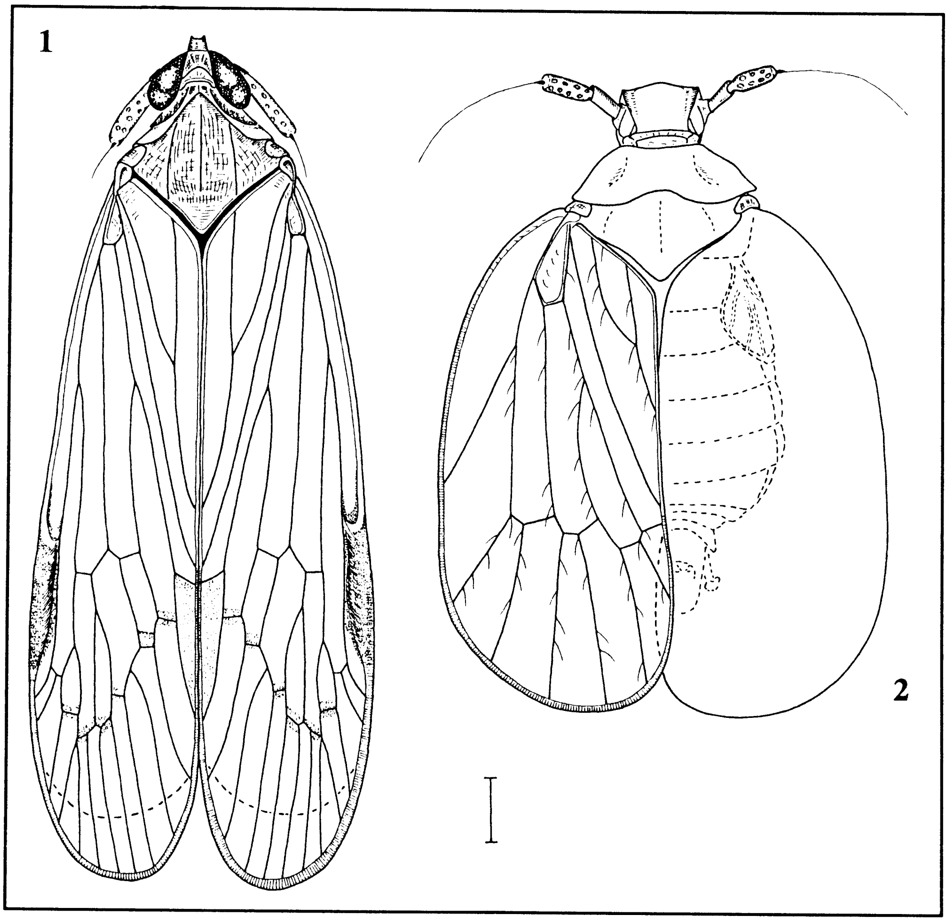
The caves studied are located in Cape York Peninsula, North Queensland, and have different geologic histories with surface rocks ranging in age from Precambrian granites to Recent basaltic lavas. The karst caves of Mt. Mulgrave and Chillagoe areas are within the same limestone formation deposited during late Silurian (416-434 m.y. ago) as coral reefs in shallow seas similar to the Great Barrier Reef. Since then the limestone has been subject to uplift and inundation, and erosion has left highly dissected cavernous limestone towers (Ford, 1978). In the area around Chillagoe these towers stand up to 100 m above the surrounding plain, in the Mt. Mulgrave area, about 100 km to the north, they may reach heights up to 200 m. The current cycle of uplift and cave formation started during Tertiary (Ford, 1978), about 30 - 35 million years ago, and fossil bearing sediments indicate that the caves have been colonizable at least that long. The current cave passages have existed for perhaps 5-10 million years (Pearson, 1982). The main caves are described in Ford (1978) and Robinson (1982). The lava tubes south of Chillagoe are of a much younger age than the limestone caves of Chillagoe and Mt. Mulgrave. Bayliss, Nasty and Pinwill's Caves are in the Undara lava flow which is 190,000 years old. The Undara lava flow covers portions of older lava flows of the McBride Formation (Atkinson, Griffin and Stephenson, 1975). Collins and Long Shot Caves are in an undated lava flow 30 km SE of Bayliss. The two flows, however, are connected by other basaltic flows. The caves studied provide a variety of ecological conditions: due to the more vertical development within limestone and also to the more advanced state of erosion the caves at Chillagoe and Mt. Mulgrave areas are often characterized by numerous entrances which allow airflow and desiccation within vast passages of the caves. In contrast, the lava tubes at Undara form more closed passages with stagnant air, high relative humidity and increased carbon dioxide concentration (Howarth and Stone, in prep.).

So far, Fulgoroid species have been found in 2 karst towers in the Mt. Mulgrave area, in 11 towers in the Chillagoe area and in 6 lava tubes near Mt. Surprise south of Chillagoe (see table 1).

## RESULTS

### CIXIIDAE

The Cixiidae found in Queensland caves belong to 3 genera: Solonaima Kirkaldy (6 species), Undarana Hoch and Howarth (in press) (2 species) and Oliarus Stal (1 species). Solonaima and Undarana are endemic in Australia, while Oliarus species have a worldwide distribution. The species of each genus are clearly distinct in characters of the male genitalia. The 3 genera are also represented in the epigean fauna of Australia: Solonaima with 7 species in Queensland (Kirkaldy, 1906; Distant, 1907; Hoch, in press), Undarana with 4 species in Queensland (Hoch and Howarth, in press), and Oliarus with 16 species in Queensland, New South Wales, Western Australia (Kirkaldy, 1906, 1907; Distant, 1907; Jacobi, 1928; Muir, 1931).



*Figs. 1-2. Habitus of Solonaima Kirkaldy (Cixiidae) species. 1. S. solonaima Kirkaldy (epigean species); S. baylissa Hoch and Howarth (troglobitic species). Scale: 0.5mm*

The 6 known cavernicolous Solonaima species (Hoch & Howarth, in press) display varying degrees of cave adaptation (Hoch and Howarth, in press). Examination of the male genitalia revealed that they form 4 morphological groups which were interpreted to represent 4 separate evolutionary lines that have invaded caves (Hoch and Howarth, in press).

1. **S. sullivani**, the least cave adapted species, shows virtually no modifications from surface-dwelling Solanaima species: it has nearly fully developed compound eyes and is flighted.

2. **S. pholetor** and **S. stonei** still have well developed eyes, but are weakly flighted.

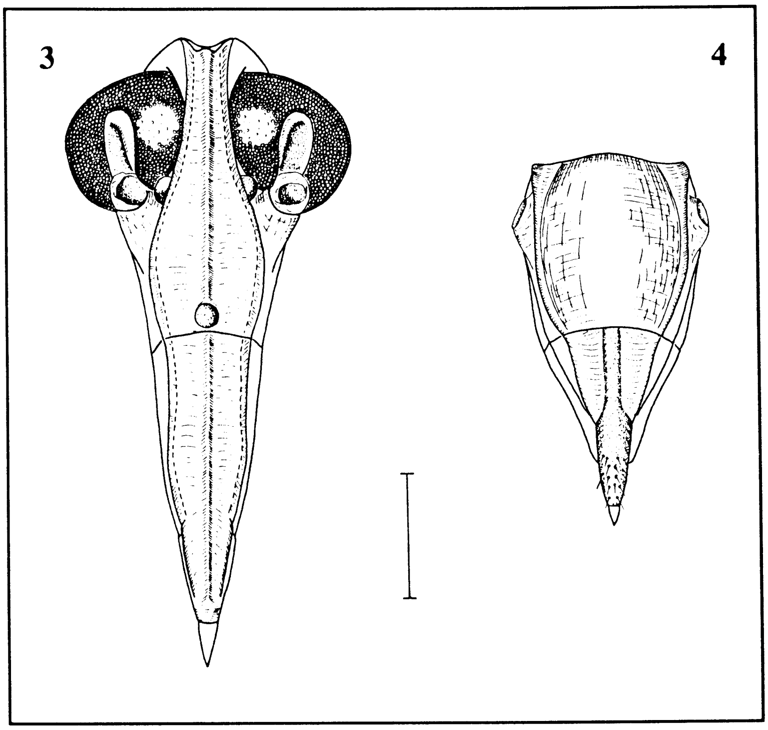
3. **S. irvini** and **S. halos** are pigmentless and display only remnants of compound eyes and strongly reduced wings.

4. **S. baylissa** is completely blind as well as flight- and pigmentless.

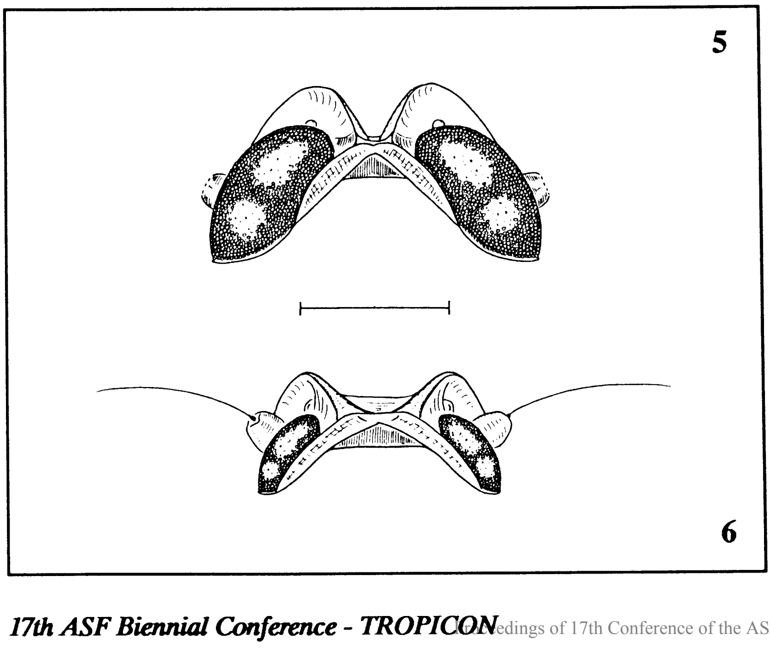
Besides these reductive characters (troglomorphies) that are usually found in correlation with cavae adaptation, additional specialized structures were found in obligate cavernicolous Solonaima species, e.g. the pilose antennae and clypeus, the apical spinulation of the tarsal segments of the hind legs, a blue wax fringe of the wings as well as a more planate general body form (Hoch and Howarth, in press). Except for S. sullivani which appears to be closely related to the epigean S. solonaima Kirkaldy, none of the other invasions showed evidence of closer relationship either to each other, or to any of the epigean species.

**Ecology and Distribution:**

Solonaima nymphs and adults suck sap from tree roots of possibly Ficus spp. (Hoch and Howarth, in press) which are common on the towers as well as on the surface above the tubes. Unfortunately, the host trees have not been identified. The six cave-dwelling Solonaima species are found to occur allopatrically in different caves (Hoch and Howarth, in press). Amazingly, the degree of troglomorphy was observed to be correlated with the particular cave environment rather than with the age of the caves (Hoch and Howarth, in press): S. sullivani, the least cave adapted species occurs in two vertical caves which are subject to desiccation by cool air flow from outside within a single tower at Mt. Mulgrave. The two weakly cave-adapted and presumably facultative (troglophile) cave species, S. pholetor and S. stonei, are - although poor flyers - presumably still capable of some epigean dispersal: each species is found in two separate towers near Chillagoe. The two nearly blind and flightless Solonaima species, S. halos and S. irvini, each occurring in a single tower near Chillagoe, seem to be restricted to deeper passages with stagnant air, and are thus regarded intermediate obligate cave species. S. baylissa which is morphologically highly modified (completely blind, strongly reduced wings) is found only in the deep cave zone passages with stagnant air, saturated atmosphere and high carbon dioxide concentrations in 3 lava tubes at Undara. Since no morphological differences between S. baylissa populations from Bayliss and Nasty Caves in the Undara lava flow and Long Shot Cave, which is at least 30 km away, could be found, it is assumed that gene-flow between these populations is maintained by subterranean dispersal (Hoch and Howarth, in press). This indicates that the geographic range (and also its population size) of this troglobitic species is much larger than that of the less cave-adapted Solonaima species (Hoch and Howarth, in press). Within this genus the morphological differences between surface- and cave-dwelling species are less strongly pronounced than in Solonaima (Hoch & Howarth, in press). Within the two known cave-dwelling species of this genus the degree of troglomorphy is less advanced in U. rosella which in several characters is intermediate between epigean species and U. collina, e.g. in comparison to epigean species, the compound eyes are reduced but the ommatidia-bearing area is still comparatively larger than in U. collina. Accordingly, U. rosella is sometimes attracted by bright head lamps, while U. collina does not show any reaction to light. Other characters undergoing gradual changes between epigean Undarana species and U. collina are the ability to maintain sustained flight, pigmentation, proportions and carination of the vertex as well as reduction in number of the lateral hind tibial spines. Although proportions of tegmina and wings do not differ significantly from those of epigean Undarana species, U. rosella is a weak flyer and capable of only short sustained flights, while U. collina is nearly flightless, being able to hop and flutter only a few metres.



*Figs. 3-4. Solonaima species: head, ventral aspect. 3. S. pallescens (Distant) (epigean species); 4. S. baylissa (troglobitic species). Scale: 0.5mm.*



*Figs. 5-6. Undarana species: head, dorsal aspect. 5. U. towomba Hoch & Howarth (epigean species); 6. U. collina Hoch & Howarth (troglobitic species). Scale: 0.5mm.*

According to the morphological similarity in structures of the male genitalia of U. rosella and U. collina it seems likely that these two species are the result of a single invasion into the caves and that speciation has occurred subsequently rather than two separate cave invasions (Hoch and Howarth, in press). The cavernicolous Undarana species do not appear to be closely related to any of the four known epigean species.

**Ecology and Distribution:**

Cavernicolous Undarana species have so far been found only in 2 lava tubes in the Undara region. Also in Undarana species, the degree of trogolomorphy is correlated with their physical environment: U. rosella, the less cave-adapted species, inhabits the transition zone of Bayliss Cave, while U. collina seems to be restricted to deeper passages within Collins Caves. Although permanently dark, the transition zone is subject to influences from the surface environment (desiccation, changes in temperature and relative humidity), whereas deep cave zone passages are characterized by stable conditions (saturated atmosphere, constant temperature, stagnant air) (Howarth, 1982). From their degree of cave-adaptation, different flight ability and different reaction to light we regard U. rosella as troglophilic, and U. collina as troglobitic (Hoch and Howarth, in press).

In contrast to Solonaima baylissa which obviously manages to maintain gene-flow between populations from Bayliss and Long Shot Cave (which is in the same flow as Collins Caves) the Undarana populations from Bayliss and Collins Caves differ significantly in external and genital morphology which was interpreted by Hoch and Howarth (in press) to be an indication for interrupted gene-flow and the existence of two separate biological entities. This may be due to the less advanced degree of cave-adaptation which may not allow subterranean dispersal along voids and cracks over long distances (Hoch and Howarth, in press).

Both cave-dwelling Undarana species have been observed feeding on roots; possible hosts are Myrtaceae (Melaleuca spp. and Eucalyptus spp.) which are common in the surface vegetation (Hoch and Howarth, in press).

### Oliarus Stal

In lava tubes at Undara, several adult specimens of an (apparently undescribed) Oliarus species with normally developed compound eyes, wings and pigment were found.

**Ecology and distribution:**

In Bayliss Cave, adult specimens were found in the entrance zone, in Pinwill's Cave adults and one nymph also in transition zone and deep cave zone passages.

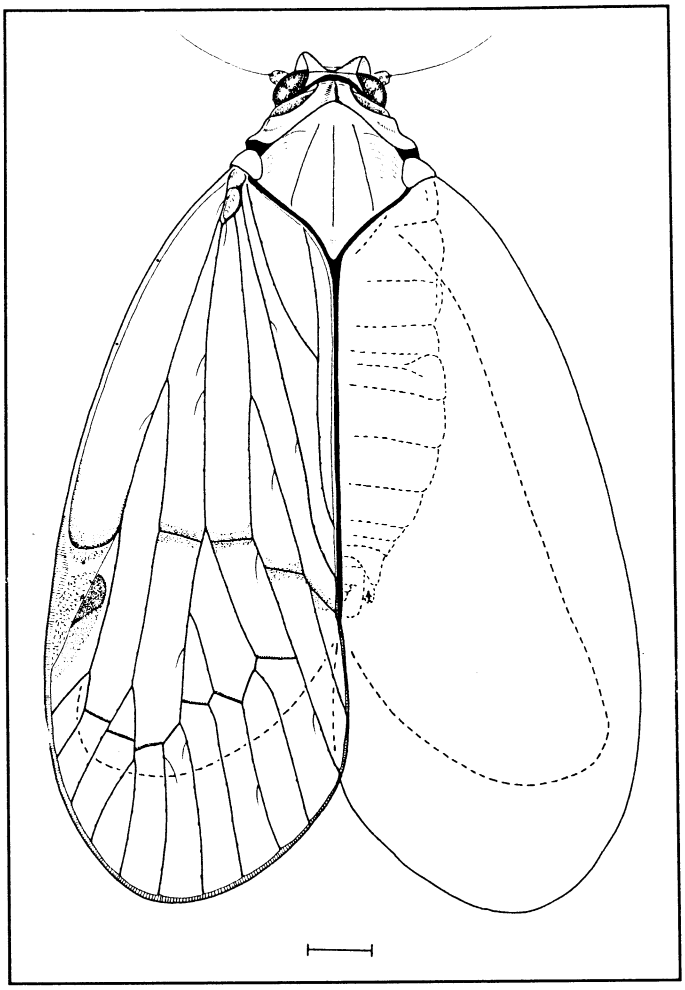


*Fig. 7. Habitus of Undarana rosella Hoch and Howarth (Cixiidae) (troglophilic species). Scale: 0.5mm.*

These specimens represent accidentals, trogloxenes, or belong to troglophilic but not yet morphologically modified populations of a surface-dwelling species.

### Meenoplidae

The cavernicolous Meenoplidae so far known from Australia belong to the genus Phaconeura Kirkaldy which is represented in the epigean fauna of Australia with 6 species (Fennah, 1963; Kirkaldy, 1906; Woodward, 1957).

Cave-dwelling Phaconeura species are so far known from Western Australia (Phaconeura pluto) and Queensland. In Queensland, cavernicolous Meenoplidae have been found in 6 caves, and belong to at least two species. Taxonomic descriptions of these previously undescribed species are in preparation and will be published in a taxonomic journal.

1. **Phaconeura spec. 1** shows troglomorphies such as the reduction of eyes, wings and pigment.
2. **Phaconeura spec. 2** morphologically is intermediate between surface-dwelling Phaconeura species and P.

spec.1: the compound eyes are present, although smaller than in epigean species, the adults are able to maintain a sustained flight, and the bodily pigment is not as significantly reduced as in P. spec. 1.

Amazingly, the male genital structures of the two cavernicolous Phaconeura species which in one cave near Chillagoe were even found to occur syntopically are very similar. We do not yet know whether these two species represent a single cave invasion, or two separate invasions by the same or closely related epigean ancestors. Within Phaconeura, the two cavernicolous species from Queensland belong to the P. smithi Woodward group, although no closer relationship to a particular epigean species could so far be assessed.

Phaconeura pluto of Western Australia although belonging to the same genus clearly represents a separate evolutionary line that has invaded caves.

**Ecology and distribution:**

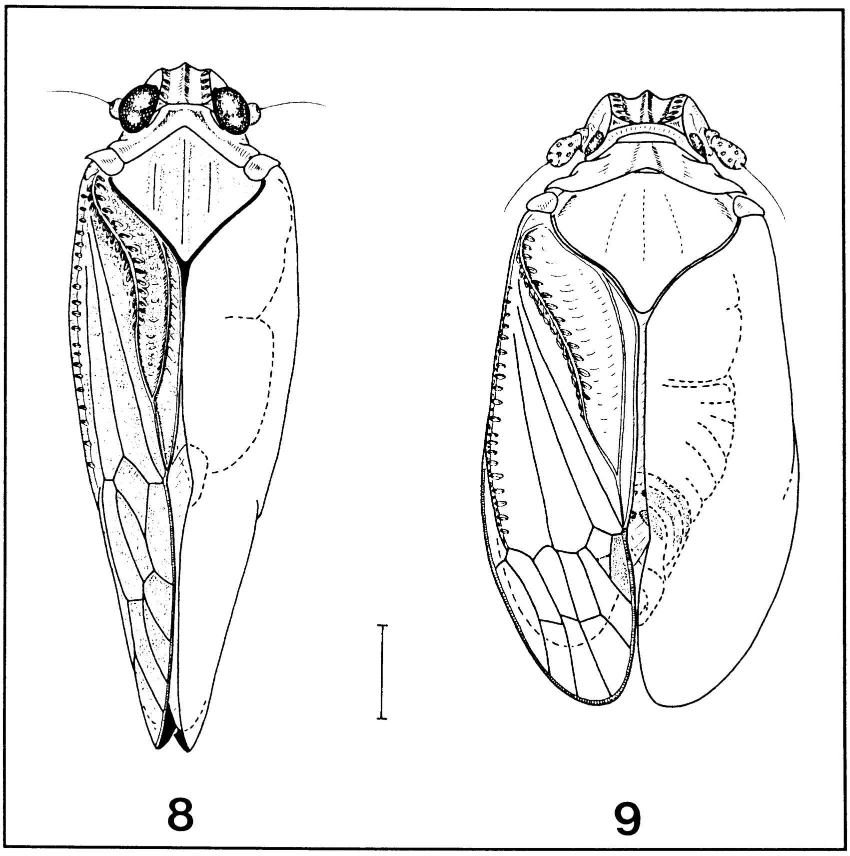
Phaconeura sp. 1 has so far been found in the transition and deep cave zones of caves within 3 different towers in the Chillagoe area. According to its degree of troglomorphy Phaconeura sp. 1 is not likely to be able to survive and disperse outside the cave environment and is thus regarded troglobitic. Since no morphological differences were observed between populations of different but neighbouring towers, we assume that gene-flow is maintained by subterranean dispersal through voids in the cavernous rock. It cannot yet be decided, however, whether the specimens from one tower in the Mt. Mulgrave area, which is about 100 km away, belong to the same biological entity. The population from Mt. Mulgrave is so far represented in the collections only by females and nymphs, which do not allow a doubtless assessment to any particular species.

Phaconeura spec. 2 has been collected in the twilight and transition zones of caves within 3 different towers. Two of these populations (from Ryan's Creek and Queenslander Towers) are represented by males. Since no morphological differences either in external or genital structures could be found we assume that gene-flow is maintained between these populations and thus regard them conspecific. From Carpentaria Tower only a single female is known, occurring syntopically with P. spec. 1, virtually feeding side by side on the same root. According to its external morphology, size and coloration we assume it to be conspecific with the populations from Ryan's Creek and Queenslander Towers. Its degree of troglomorphy indicates that this species is able to survive outside caves and we thus regard it as a troglophile.

The two cavernicolous Phaconeura species most likely feed on roots of the same or similar host plants as the cave-dwelling Cixiidae. Nymphs are possibly attended by ants, which would help explain their dispersal ability. The adults are much more closely associated with their host roots than are the cixiids.

P. pluto, the cavernicolous Meenoplid described from Quandong Cave, Nambung National Park, Western Australia, displays a degree of troglomorphy (complete reduction of compound eyes and pigment, strongly reduced wings) that suggests it to be an obligate cave species, although no ecological information concerning its habitat is available to the authors. It is still unclear whether the nymphs of Cadda Cave (already mentioned in Fennah 1973) are conspecific with the population from Quandong Cave.

We examined an adult Phaconeura male from Tick Cave, also Nambung National Park (ex coll. CSIRO, Canberra), which in its degree of troglomorphy and genital characters resembles P. pluto; however, its conspecifity with P. pluto can only be confirmed after re-examination of the holotype.



*Figs. 8-9. Habitus of Phaconeura species (Meenoplidae). 8. P. spec. (epigean species); 9. P. spec. 1 (troglobitic species).*
*Scale: 0.5mm*

## DISCUSSION

The recent findings of cave-dwelling planthoppers in Queensland caves pose several research questions:

Are there more evolutionary lines of Fulgoroidea which have invaded caves in Australia?

As already mentioned previously, Queensland now has the highest concentration of cave-adapted Fulgoroidea in the world. So far, comparatively few karst towers and lava tubes have been investigated biologically, and research has concentrated in the areas around Chillagoe, Mt. Mulgrave, and Undara. The karst band, in which the towers at Chillagoe and Mt. Mulgrave are found, continues to the north for over 150 km, providing over 300 isolated exposed towers. Recent studies (Hoch and Howarth, in press) indicate that most of them might house additional species of cave-adapted Fulgoroidea, many of which are likely to be highly modified obligate cave species.

But not only in Queensland caves are more species of cave-adapted Fulgoroidea to be expected: the Australian Karst Index (1985) lists an immense number of caves, especially in the Northern Territory that by containing tree-roots as the essential food resource within deep cave zone passages are theoretically suited to support cave-adapted Fulgoroidea.

What factors have led to the convergent evolution of cave-adapted species of Fulgoroidea in tropical North Queensland?

There are two major hypotheses to explain the evolution and distribution of cave-dwelling animals. The isolation-hypothesis, as formulated by Barr (1968) and Poulson and White (1969), assumes that climatic changes, such as during glaciation, cause extinction or extirpation of surface populations. By this, troglophilic populations are trapped within caves and subsequently acquire cave-adaptations. The alternative model as suggested by Howarth (1988) explains the evolution of troglobites by parapatric speciation from surface species. According to this hypothesis, cave invasions are the result of adaptive shifts which enable the organisms that are accidentals in caves to exploit new food resources. In this model extinction or extirpation of surface populations are not prerequisites for cave-adaptation, and close surface relatives may still be extant (Howarth, 1988).

We cannot at present decide which of these models applies to each case of cave-dwelling Fulgoroidea of Australia. Although there is evidence of climatic change in Australia during Miocene - according to palaeoclimatic data rain forest vegetation retreated due to an onset of increased aridity in association with the ice expansion in the Antarctic (Kemp, 1981) - the cave-adapted Fulgoroid species might as well be the result of adaptive shifts since in some cases close epigean relatives exist in the same area. Evidence supporting either hypothesis might be gained by relating genetic distance estimates within the different taxa to evolutionary time (e.g. Nei, 1972, 1975).

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## REFERENCES

ATKINSON, A., GRIFFIN, T.J. and STEPHENSON, P.J., 1975. A Major Lava Tube System from Undara Volcano, North Queensland. **Bull. Volcanol.** 39(2): 1-28.

BARR, T.C., 1968. Cave ecology and the evolution of troglobites. **Evolut. Biol.** 2: 35-102.

DISTANT, W.L., 1907. Rhynchotal notes XLIL. **Ann. Mag. Nat. Hist.** (7) 19: 277-295.

FENNAH, R.G., 1963. A new species of Phaconeura (Fulgoroidea Meenoplidae). **Ann. Mag. Nat. Hist.** (13) 5: 299-301.

FENNAH, R.G., 1973. Three new cavernicolous species of Fulgoroidea (Homoptera) from Mexico and Western Australia. **Proc. Biol. Soc. Wash.** 86 (38): 439-446.

FORD, T.C., 1978. Chillagoe - A Tower Karst in Decay. **Trans. Brit. Cave Res. Assoc. (BCRA)** 5(2): 61-84.

HAMILTON-SMITH, E., 1967. Fauna of the Nullarbor Caves. In J.R. Dunkley and T.M. Wigley (eds.), **Caves of the Nullarbor.** Sydney: University of Sydney Press: 35-42.

HOCH, H., (in press) Five new epigean species of the Australian plant hopper genus Solonaima Kirkaldy (Homoptera Fulgoroidea Cixiidae). **The Beagle.**

HOCH, H. and HOWARTH, F.G., (in press) Six new cavernicolous Cixiid planthoppers in the genus Solonaima from Australia (Homoptera Fulgoroidea). **Invert. Taxon.**

HOCH, H. and HOWARTH, F.G., (in press) Reductive evolutionary trends in two new cavernicolous species of a new Australian cixiid genus (Homoptera Fulgoroidea). **Syst. Ent.**

HOCH, H. and HOWARTH, F.G., (in press) The evolution of cave-adapted cixiid planthoppers in volcanic and limestone caves in North Queensland, Australia (Homoptera Fulgoroidea). **Mem. Biospeol.**

HOWARTH, F.G., 1982. Bioclimatic and geologic factors governing the evolution and distribution of Hawaiian cave insects. **Entom. Gen.** 8(1): 17-26.

HOWARTH, F.G., 1988. The evolution of non-relictual tropical troglobites. **Int. J. Speleol.** 16: 1-16.

HOWARTH, F.G., **this issue**

HOWARTH, F.G. and STONE, F.D, (in prep) Elevated carbon dioxide levels in Bayliss Cave, Australia: implications for the evolution of cave faunas.

JACOBI, A., 1928. Rhynchota Homoptera. 1. Fulgoridae and Cercopidae. In: Results of Dr. E. Mjoberg's Swedish Scientific Expedition to Australia (1910-1913). **Arkiv Zool.** 19(28): 1-50.

KEMP, E.M., 1981. Tertiary palaeogeography and the evolution of Australian climate. In: **Ecological Biogeography of Australia** (A. Keast, ed.), Dr. W. Junk Publishers, The Hague-Boston-London, 31-49-

KIRKALDY, G.W., 1906. Leafhoppers and their natural enemies (Pt. IX. Leafhoppers. Hemiptera). **Bull. Hawaiian Sugar Pl. Assoc. Div. Ent.** 1(9): 271-479, pls. 21-32.

KIRKALDY, G.W., 1907. Leafhoppers supplement. (Hemiptera). **Bull. Hawaiian Sugar Pl. Assoc. Div. Ent.** 3: 1-186, pls. 1-20.

MATTHEWS, P.G. (Ed.), 1985. **Australian Karst Index**, Park Orchards, Victoria, Australia.

MATTHEWS, E.G. and KITCHING, R.L., 1976. **Insect Ecology.** University Queensland Press, Brisbane, 211 pp.

MOORE, B.P., 1964. Present day cave beetle fauna in Australia. A pointer to past climatic change. **Helictite** (October 1964): 3-9

MUIR, F.A.G., 1931. Descriptions and records of Fulgoroidea from Australia and the South Pacific Islands. **No. I. Rec. Australian Mus.** 18: 63-83.

NEI, M., 1972. Genetic distance between populations. **Am. Nat.** 106 (949): 283-292.

NEI, M., 1975. **Molecular population genetics and evolution.** American Elsevier, New York.

PEARSON, L.M., 1982. Chillagoe Karst Solution and Weathering. **Tower Karst** 4: 58-70.

POULSON, T.L. and WHITE, W., 1969. The cave environment. **Science**, N.Y. 165: 971-981.

REMANE, R. and HOCH, H., 1988. Cave-dwelling Fulgoroidea (Homoptera Auchenorrhyncha) from the Canary Islands. **J. Nat. Hist.** 22: 403-412.

ROBINSON, T. (Editor), 1982. **Chillagoe Karst - A speleological field guide to the Chillagoe - Mungana - Rookwood Areas in Far North Queensland, Australia.** Chillagoe Caving Club, Cairns, 187 pp.

WOODWARD, T.E., 1957. Studies on Queensland Hemiptera. Part II. Meenoplidae (Fulgoroidea). **University of Queensland Papers. Dept. of Entomology**, 1 (4): 57-70.

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**TABLE 1. DISTRIBUTION OF AUSTRALIAN CAVE FULGOROIDEA.**

| Cave locations | Cixiidae<br>Solonaima | Undarana | Oliarus | Meenoplidae<br>Phaconeura |
|---|---|---|---|---|
| **QUEENSLAND:** | | | | |
| **Mitchell-Palmer Karst** | | | | |
| West Mordor Tower: | | | | |
| Crystal Cascades C. | + (a) | - | - | - |
| Here-it-is C. | + | - | - | - |
| Capricorn Tower: | | | | |
| Swiss Cheese C. | n | - | - | * (?l) |
| **Chillagoe Karst** | | | | |
| Markham Tower: | | | | |
| Swiftlet Scallops C. | * (e) | - | - | - |
| Hercules C. | * (e) | - | - | * (l) |
| Ryan Imperial Tower: | | | | |
| Marachoo C. | n | - | - | * (l) |
| Carpenteria Tower: | | | | |
| Carpentaria C. | n | - | - | *(l), + (?m) |
| Queenslander Tower: | | | | |
| Queenslander C. | * (d) | - | - | + (m) |
| Haunted Tower: | | | | |
| Spooked C. | + (c) | - | - | - |
| Spring Tower: | | | | |
| Spring C. | + (c) | - | - | - |
| Arena C. | + (c) | - | - | - |
| The Throne Room C. | + (c) | - | - | - |
| Gordale Scar Pot | n | - | - | - |
| Suicide Tower: | | | | |
| Christmas Pot | n | - | - | - |
| Ryan's Creek Tower: | | | | |
| Ryan's Creek C. | n | - | - | + (m) |
| Donna Tower: | | | | |
| Donna C. | + (b) | - | - | - |
| Trezkinn C. | + (b) | - | - | - |
| Royal Arch Tower: | | | | |
| Royal Arch C. | + (b) | - | - | - |
| Walkunder Tower: | | | | |
| Clam C. | n | - | - | - |
| Rhino C. | n | - | - | - |
| Octopus Hollow | n | - | - | - |

*: troglobite;
+: troglophile;
o: trogloxene;
n: nymphs (not identifiable to species level);
a: Solonaima sullivani;
b: S. pholetor;
c: S. stonei;
d: S. halos;
e: S. irvini;
f: S. baylissa;
g: Undarna rosella;
h: U. collina;
i: Oliarus spec.;
k: Phaconeura pluto;
l: P. spec. 1;
m: P. spec. 2.

**TABLE 1. DISTRIBUTION OF AUSTRALIAN CAVE FULGOROIDEA (CONTINUED).**

| | Cixiidae | | | Meenoplidae |
|---|---|---|---|---|
| **Cave locations** | **Solonaima** | **Undarana** | **Oliarus** | **Phaconeura** |
| **QUEENSLAND (Continued):** | | | | |
| **McBride Lava Tubes** | | | | |
| Bayliss C. | * (f) | + (g) | ? o,+ (i) | - |
| Nasty C. | * (f) | - | - | - |
| Pinwill's C. | - | - | ? o,+ (i) | - |
| Long Shot C. | * (f) | - | - | - |
| Two-Ten-Tunnel | - | * (h) | - | - |
| Collins No. 2 C. | - | * (h) | - | - |
| **WESTERN AUSTRALIA:** | | | | |
| **Nambung Nat. Park:** | | | | |
| Quondong C. | - | - | - | * (k) |
| Cadda C. | - | - | - | n |
| Tick C. | - | - | - | * (?k) |

*: troglobite;
+: troglophile;
o: trogloxene;
n: nymphs (not identifiable to species level);
a: Solonaima sullivani;
b: S. pholetor;
c: S. stonei;
d: S. halos;
e: S. irvini;
f: S. baylissa;
g: Undarna rosella;
h: U. collina;
i: Oliarus spec.;
k: Phaconeura pluto;
l: P. spec. 1;
m: P. spec. 2.