Bayliss Lava Tube and the Discovery of a Rich Cave Fauna in Tropical Australia Fred D. Stone, Ph.D.

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Abstract

Australia, including the tropical north, is currently recognized as having one of the world's richest underground faunas. Until fairly recently, it was widely believed that cave adapted species (troglobites) did not exist in the tropics. Lava tubes were also considered to be devoid of troglobites, and the Australian continent was thought to have relatively few cave adapted species due to its aridity. Leleup in the Galapagos in 1968, Howarth in Hawai'i in 1971, and subsequent researchers discovered numerous troglobites in lava tubes on volcanic islands in the tropical Pacific. Based on his work in Hawai'i, Howarth developed a bioclimatic model including the "tropical winter" effect to explain the restriction of troglobites to deep cave zones and small subsurface voids (mesocaverns) with constant high humidity. Brother Nicholas Sullivan, with the Sydney Speleological Society and the Chillagoe Caving Club, began to survey the biology of the Chillagoe limestone caves and in 1984 invited Francis Howarth and Fred Stone to join the 1984 to 1986 expeditions with support from The Explorers Club. During the 1984 expedition, they learned of Anne Atkinson's detailed studies of a number of lava tubes in the McBride Volcanic Province at Undara and in 1985, guided by Douglas Irvin of the Chillagoe Caving Club, they went to investigate. With enthusiastic support of the Pinwill family, who held the grazing lease, they were able to enter many of the lava tubes at Undara and on the neighbouring cattle stations managed by the Collins brothers. Bayliss lava tube had an ideal conformation to foster a stable, humid deep cave climate, with a restricted entrance, a sealed back end, and barriers to air circulation plus abundant food supplies from bat guano and tree roots. Two dozen previously unknown cave adapted species were discovered. An additional feature was a high level of carbon dioxide in the deep cave where troglobites were the most abundant. This combination of high humidity and carbon dioxide makes Bayliss lava tube a "window" into the much broader mesocavernous zone. Other lava tubes in the McBride Province with similar conditions were found to have several additional troglobitic species. These discoveries complemented the work on tropical volcanic islands by showing that tropical continental lava tubes were also rich in troglobitic species. Comparisons between the old Chillagoe limestone caves and relatively young (190,000 year old) lava tubes confirmed the bioclimatic model. Subsequent work across Australia by Humphreys, Clarke, Eberhard and numerous others has resulted in discovery of subterranean "hot spots" in other geologic formations in which caves and/or mesocaverns occur. Where these formations lack caves, well bores and mining test bores are being sampled with bait traps. Other Australian volcanic areas, such as Black Braes, show high potential for cave species, and where lava tubes are lacking well bore sampling could reveal their mesocavernous fauna.

No tropical troglobites

Until fairly recently, it was widely believed that cave adapted species (troglobites) did not exist in the tropics. For one hundred years or more, according to conventional wisdom, no truly cave adapted species had been found in the tropics, except for some aquatic species (Vandel 1965). The dominant evolutionary theory was based on allopatric speciation, the necessity for a complete physical barrier to gene flow between populations in order for separate species to evolve (Mayr 1963). Biospeleologists developed the Glacial Relict Theory of troglobite evolution, hypothesizing that continental glaciation could have caused widespread populations of epigean troglophiles to become extinct, allowing the isolated cave dwelling populations (in areas marginal to the glaciers) to undergo reorganization of the genome and evolve specialized adaptations to deep cave existence (Barr 1968, 1973).

The glacial relict theory has two important components; first, the lack of troglobites in tropical areas (and their presence in temperate zone areas) and second, the necessity that there be a lack of epigean (troglophilic) sibling species that could explain the isolation of cave populations and their subsequent evolution of obligate cave species.

Since the apparent lack of tropical troglobites was based on lack of evidence, the possibility existed that tropical caves had not been sufficiently searched for obligate cavernicoles. However, the discovery of tropical troglobites does not falsify the relictual speciation hypothesis, since other major climate changes or geological processes might cause the epigean populations to become extinct. Therefore, it is necessary to find both tropical troglobites and their epigean relatives, and to determine their close evolutionary relationship as sympatric or parapatric species. In the 1960s, my colleague Francis (Frank) Howarth and I worked in Southeast Asia with International Voluntary Service, and in our free time we began searching for troglobitic species in caves of Thailand and Laos. We were successful in finding several candidate troglobite species, but without the evidence of epigean sister species. It was also difficult to find systematists with experience in Southeast Asia for many of the taxa.

In 1971, Howarth, then a Ph.D. student in Entomology at the University of Hawai'i, was working as site manager for the International Biological Program at the Hawaii Volcanoes National Park. On his time off, he was exploring a lava tube in Bird Park and he discovered a blind planthopper on a tree root (Howarth 1972).

This led to his employment as an Entomologist at Bishop Museum (where he currently has an endowed chair), grants, and intensive searches in lava tubes throughout the Hawaiian Islands. In the next few years, he discovered many more cave adapted species, and new species are still being discovered at the present time. These include cave water striders, noeyed "big-eyed" hunting spiders, cave moths and cave crickets (Howarth 1973, 1981)

In 1986 planthopper specialists Dr. Manfred Asche and Dr. Hannelore Hoch visited Bishop Museum to study the planthopper collection, and Hannelore became entranced by the blind cave planthoppers. They joined the research, and have discovered numerous species in caves and lava tubes around the world (Hoch 1999; Hoch & Asche 1993).

Frank Howarth's discovery of the troglobitic planthoppers, followed by over 75 other troglobitic species from Hawaiian lava tubes, falsified the "No Tropical Troglobite" hypothesis. However, it has taken much longer to do the detailed research that will determine whether epigean sibling species exist, and how closely they are related to the cave species, work that is still ongoing, currently assisted by the development of new genomic approaches to DNA analysis (Wessel 2008; Taiti & Howarth 1997; Rivera *et al.* 2002).

Soon, troglobites were reported from other tropical and subtropical areas, including Jamaica, Galapagos (Leleup in 1968), Canary Islands, Congo, Thailand and Central America (Peck & Finston 1993).

Howarth developed the bioclimatic model to explain the distribution (and difficulty of finding) tropical troglobites. This model showed that troglomorphic species are restricted to habitats at or near saturated humidity. In humid temperate climates, cave adapted species move into deep cracks in the winter to escape the drying effect of cold air entering the caves (Barr, 1973). The "Tropical Winter Effect" occurs on a diurnal basis, with cool, desiccating surface air flowing into caves every night, limiting the suitable troglobite habitat to cave areas where the entrance effect is minimal or absent. Certain cave morphology, including goose-neck passages, upward sloping passages, dead-end passages, rooms accessed from low crawl passages, and areas far from entrances reduces the winter effect and allows water vapour to accumulate (Howarth 1980, 1983a, b, 1988a).

According to Howarth's model, caves have five zones: the Entrance Zone and Twilight Zone are strongly influenced by surface air and temperature. The Transition Zone is influenced by surface air, and experiences the "Tropical Winter Effect". The Deep Cave Zone is not affected by surface air, and has constant high humidity, close to saturation. The fifth zone is the Stagnant Air Zone. This zone does not have air circulation, and carbon dioxide can increase. Troglobitic species cannot survive in the Entrance, Twilight and Transition zones, so to find them it is necessary to find the high humidity and low air flow zones of the Deep Cave and Stagnant Air zones (Fig. 1).

Lava flows are porous and contain numerous small lava tubes and mesocaverns. These small spaces tend to have restricted air flow and high humidity. Cave species live in the mesocaverns and move into the larger lava tubes when conditions permit (deep cave zones) (Fig. 2).

Many biolospeleologists did not agree that the "Glacial Relict Theory" had been falsified: Oceanic Pacific islands were thought to have "special conditions" that permitted cave species to evolve (Culver 1982; Holsinger 1988; Holsinger & Culver 1988). However, Peck & Finston (1993) supported Howarth's model by citing many cases of sibling cave and surface species in tropical Pacific Islands.

Tropical Australia was considered to have very few cave adapted arthropods due to its aridity following a series of continental drying events (Hamilton-Smith 1967). Brother Nicholas Sullivan, based on earlier cave surveys by the Sydney Speleological Society and the Chillagoe Caving Club, in 1982 began to survey the biology of the Chillagoe limestone caves and in 1984 invited Frank Howarth and Fred Stone to join the 1984 to 1988/9 expeditions with support from The Explorers Club (Sullivan 1976, 1983a, 1983b, 1984, 1989) (Fig. 3).

Chillagoe tower karst in northern Queensland is an ideal tropical continental area to compare with the Hawaiian Islands. It has numerous isolated karst



Fig. 1. Cave Zones [after F. Howarth]. E: Entrance Zone; TW: Twilight Zone; TR: Transition Zone; D: Deep Cave Zone; S: Stagnant Air Zone.



Fig. 2. Mesocaverns in lava flow (photo: F. Howarth) towers spread over 200 kilometres, similar to an island archipelago. There are abundant caves with tree roots, including *Ficus* and *Brachychiton*, that send their roots deep into caves to reach water. Chillagoe and

has both large and small caves, in which humid areas are present and where troglobites could occur. Planthoppers and cockroaches are two groups in which cave adapted forms have been discovered in Chillagoe caves (Hoch & Asche 1988; Howarth 1988b; Stone 1988; Stone *et al.* 2005, Sullivan 1988; Slaney 1996).

During the 1984 expedition, we learned of Anne Atkinson's detailed studies of a number of lava tubes in the McBride Volcanic Province at Undara, and in 1985, guided by Douglas Irvin of the Chillagoe Caving Club, and with the support of Brother Nick and the Explorers Club, went to investigate (Atkinson, Griffin & Stephenson 1976) (Fig. 4).

With enthusiastic support from the Pinwill family, who held the grazing lease for Yaramulla Station, we were able to enter many of the lava tubes at Undara and on the neighbouring cattle stations of Spring Creek and Rosella Plains, managed by the Collins brothers (Fig. 5).

We investigated Barkers Cave because it has a lake at its far end. It has a large entrance and a large passage throughout, but because of the large, open entrance, the deep cave environment does not occur. Many of the Undara caves are fairly

short and are open at both ends, such as the Wind Tunnel. These tubes have mostly Entrance, Twilight and Transition zones, but no Deep Cave zone.



Fig. 3. Explorers Club Expedition 1989: Frank Howarth, Stefan Eberhard, Hannelore Hoch, Manfred Asche, Bro. Nicholas Sullivan, Don Matts, Fred Stone, Grace Matts, Terry Matts & friend. (Photo Eileen Carol)



Fig. 4. Undara lava flow [from aerial photo].



Fig. 5. Manfred Asche, Frank Howarth, Hannelore Hoch, Lauren, Sonia, Michael, Troy & Don Pinwill & friends, 1989

We finally entered Bayliss Cave. A low entrance crawl opened into the top of a breakdown slope into a large passage. The cave felt humid, and water was condensing on the ceiling just inside the entrance. Bayliss has a restricted entrance and it is sealed at its lower end, so there is minimal air circulation. At about 350 metres, there is a low ceiling that traps water vapour, which is less dense than air. The downward sloping cave and a rock barrier at about 650 metres ('The Wall') trap carbon dioxide, which is denser than air. The cave has bat roosting areas, and the carbon dioxide is most likely generated by decomposition of the bat guano, which also consumes oxygen (Figs 6, 7, 8, 9).

The cave was appreciably more humid beyond the Duckunder, and roots become more abundant (probably Ficus or Brachychiton, although they haven't been positively identified). The cave floor has accumulated a thick layer of soil, and the roots grow through it. Besides providing moisture to the roots, the bat guano is a rich source of nutrients. The roots, in turn, provide a food source for the cave troglobite community. Passing the Duckunder is like Alice going down the rabbit hole-the far side has creatures that are very strange indeed. We found about 24 troglobites, all previously unknown, making it one of the most diverse cave communities in the world (Howarth & Stone 1990) (Fig. 10).

A list of the species found in Bayliss Cave is appended. Included are three species of troglobitic millipedes, a troglobitic Scutigeromorph



Fig. 6. Bayliss Cave profile (after Howarth & Stone 1990)



Fig. 7. Base of entrance breakdown, Bayliss Cave.

Fig. 8. S. Robson at Duckunder, Bayliss Cave (photo: F. Howarth).



Fig. 9. F. Howarth and S. Robson on The Wall, Bayliss Cave (photo: S. Robson).

centipede that walks slowly, doesn't react to light but is sensitive to touch, and *Pirates*, a troglobitic predatory bug common in the deep cave zone. The highly troglomorphic Bayliss planthopper, *Solonaima baylissa*, completely eyeless, and a surface species, *Solonaima pholetor*, are good candidates as sibling species (Hoch & Asche 1988; Hoch & Howarth 1989a, b) (Figs 11, 12, 13, 14, 15).

Paratemnopteryx stonei is a partially troglomorphic cockroach that occurs in entrance, twilight and transition zones, as well in deep zones, of caves at Chillagoe and Undara. It occurs in the outer section of Bayliss Cave. An eyeless troglobitic species, *Neotemnopteryx baylissensis* Slaney 2000, occurs from the Duckunder into the deep cave and stagnant air zones. A small-eyed cave species, *N. undarensis* Slaney 2000, occurs in other lava tubes in the Undara area. Slaney believed that the cave species were relicts from continental drying, based on their distribution and DNA evidence (Roth 1990; Slaney 1996, 2000, 2001; Stone 1988) (Figs 16, 17).

A highly troglomorphic cockroach in the family Nocticolidae, genus *Nocticola*, occurs on The Wall and in the deep and stagnant air zones. I am currently preparing a description of this species. *Nocticola*

Fig. 10. S. Robson beyond the Duckunder, Bayliss Cave (photo: F. Howarth).

australiensis from Royal Arch Cave and Donna Cave in Chillagoe is less cave adapted than the Bayliss species, and occurs in twilight and transition zones as well as in the deep cave zone. These two species are potentially sibling species, but further work on their DNA is necessary to determine how closely they are related (Stone 1988) (Figs 18, 19).

On 14 and 15 June 1985, we did a complete inventory of populations and species in Bayliss at five locations (base of the entrance slope, just before the Duckunder, the top of the Wall, the bottom of the Wall, and just before the tight crawl that was considered the end of the cave), and measured the temperature, relative humidity, carbon dioxide and oxygen (Fig. 20).

The temperature increased from about 23°C at the base of the entrance breakdown to just over 26° at the inner end. Humidity was over 94% below the entrance and increased to 98-100% from the Duckunder (although humidity measurements above 90% are not very accurate). Oxygen was between 19 and 21% (ambient) from the entrance to the Duckunder, and then dropped rapidly to 15% at the inner end. Carbon dioxide was less than 0.5% below the entrance, increased to 0.5% at the Duckunder, then increased to 2.5% at the top of The Wall, 4.5% at the bottom of The Wall, and 6% at the inner end (Howarth & Stone 1990) (Fig. 21).



Fig. 11. Bayliss Cave millipedes (photo: F. Howarth)

Fig. 12. Bayliss Scutigeromorph centipede (photo: F. Howarth)



Fig. 13. Bayliss Pirates troglobitic assassin bug (photo: F. Howarth)



Fig. 14. Bayliss planthopper, Solonaima baylissa (photo: Hubert Reimer)





Fig. 16. Troglophilic cockroach, Paratemnopteryx stonei

Fig. 15. Surface planthopper, Solonaima pholetor (photo: Hubert Reimer)



Fig. 17. Bayliss troglobitic cockroach, Neotemnopteryx baylissensis (*photo: G. Thompson, Queensland Museum*)



Fig. 18. Bayliss troglobitic Nocticolidae cockroach (photo: F. Stone)



Fig. 19. Nocticola australiensis from Chillagoe (photo: D. Ward)



Fig. 20. Frank Howarth recording data. (photo: Eileen Carol)

The six trogloxenic species (which spend part of their lives in caves and part outside, generally going out to feed) were found throughout the cave. The 16 troglophilic species (which can live both in caves and out of caves) tended to be more abundant before the Duckunder, although some of them were also in the deep cave and stagnant air zones. The 24 troglobitic species (obligate cave dwellers, partially troglomorphic and troglomorphic) had their highest



Fig. 21. Plots of Bayliss Cave temperature, relative humidity, oxygen and carbon dioxide (after Howarth & Stone 1990)



Fig. 22. Distribution of species through Bayliss Cave (after Howarth & Stone 1990)

populations in the deep cave and stagnant air zones (Figs 22, 23).

Undara Lava Tubes, Bayliss and other lava tubes studied in 1985 and 1986, were important in establishing that Australia could support rich subterranean communities where the deep cave and mesocavernous conditions occurred. This confirmed that Hawai'i and other tropical oceanic islands are not "special cases", but that the same bioclimatic controls



Fig. 23. Species distribution through Bayliss Cave (after Howarth & Stone 1990)

are present in both continental and island caves, and that troglobitic communities exist wherever the conditions support them.

In 1986, while Frank and the Explorers Club expedition went back to Undara to continue with the study there (Fig. 24), I joined Louis Deharveng and Anne Bedos for a trip to Thailand. Deharveng had recorded several high CO_2 caves in his previous Thai expeditions, but hadn't spent a lot of time looking for cave species in them. We visited limestone caves in northwest Thailand, and in most of the high CO_2 (and high humidity) caves, I discovered new species of highly cave adapted Nocticolidae cockroaches. This gave further confirmation to the presence of troglobites in tropical caves with the right deep cave conditions (Deharveng & Bedos 1986).



Fig. 24. 1989 expedition members Manfred Asche, Frank Howarth, Terry Matts, Douglas Irvin and Hannelore Hoch.

However, climatic shift and relictual speciation due to continental drying is an alternative hypothesis. It is possible that both processes (relictual or allopatric speciation and para- or sympatric speciation) may be represented (Humphreys 1991, 1999; Slaney, 2001).

Further work depends on getting the species identified, described and compared using both traditional morphology and current DNA analysis. This involves seeking the expertise of specialists and provision of grant money to pay for their work.

The work of Bill Humphreys at Western Australian Museum and biospeleologists including Arthur Clarke, Stefan Eberhard, and members of many caving clubs have established that a rich diversity of subterranean life occurs wherever there is a porous substrate and a food source (Humphreys 1993a, b, c, 1994, 1995, 1999).

Credits

Dr. Frank Howarth of B.P. Bishop Museum, biospeleologist and cave colleague for fifty years and photographer for most of the Bayliss species, The

Explorers Club of New York and Brother Nicholas Sullivan who sponsored several trips to Australia, Eileen Carol for photographs of the Explorers Club expeditions, The Chillagoe Caving Club, especially Doug Irvin, Tom Robinson and many others who provided hospitality and logistic help, The Sydney Speleological Society, particularly the Matts family, the Pinwill family of Yaramulla Station who permitted us to study the Undara Lava Tubes and stay in their donga, Lana Little and the rangers of Chillagoe and Undara National Parks, Mick Godwin who helped with location of many lava tubes, Anne and Verne Atkinson at Undara, the Collins brothers who allowed access to lava tubes on Spring Creek and Rosella Plains stations, Dr. Geoff Montieth and colleagues at The Queensland Museum, Dr. Manfred Asche and Dr. Hannelore Hoch of Humboldt University, Berlin, who helped with many field expeditions, Deborah Ward for untiring assistance and photographs on numerous collecting trips, biospeleologists Stefan Eberhard who assisted with the 1989 expedition to Undara and Arthur Clarke who conducted biological surveys at Undara.

Appendix: Species from Bayliss Cave

(Howarth & Stone, 1990)

Trogloxenic

- 1. Thysanura: Atelurinae: undet. sp. 1
- 2. Isoptera: undet. Sp. 1
- 3. Lepidoptera: Noctuidae: *Sericea spectans* Guerin
- 4. Hymenoptera: Formicidae: Paratrechina sp.1
- 5. Hymenoptera: Formicidae: *Paratrechina longicornis*
- 6. Hymenoptera: Formicidae: *Platythyrea* sp. 1

Troglophilic

- 7. Aranae: Sparrasidae: Heteropoda sp. 1
- 8. Aranae: Pholcidae: Spermophora sp. 1
- 9. Aranae: Nesticidae: Nesticella sp. 2
- 10. Scolopendrida: Scolopendra undet. Sp. 1
- 11. Geophilida: undet. Sp. 1
- 12. Symphyla: undet. Sp. 1
- 13. Blattodea: Blattellidae: *Paratemnopteryx stonei* Roth (1990)
- 14. Hemiptera Auchenorrhyncha: Cixiidae: Undarana rosella Hoch & Howarth (1989a)
- 15. Hemiptera Auchenorrhyncha: Cixiidae: *Oliarus* sp. 1
- 16. Hemiptera Auchenorrhyncha: Coccoidea: undet. Sp. 1
- 17. Coleoptera: Scarabacidae: undet. Sp. 1
- 18. Coleoptera: Ptiliidae: undet. Sp. 1
- 19. Lepidoptera: Gelechiidae: undet. Sp. 1
- 20. Lepidoptera: Noctuidae: Schrankia sp. 1
- 21. Diptera: Psychodidae: Phlebotominae: undet. Sp. 1
- 22. Diptera: Phoridae: undet. Sp. 1

Troglobitic (partially troglomorphic)

- 23. Isopoda: Oniscomorpha: undet. Sp. 1
- 24. Isopoda: Oniscomorpha: undet. Sp. 2
- 25. Diplopoda: Polydesmida: undet. Sp. 1
- 26. Collembola: undet. Sp. 1
- 27. Diplura: undet. Sp. 1
- 28. Thysanura: Nicoletidae: Nicoletia? Sp. 1
- 29. Hemiptera: Heteroptera: Reduviidae: *Pirates* sp. 1

Troglobitic (strongly troglomorphic)

- 30. Aranae: Pholcidae: Spermophora sp. 2
- 31. Aranae: Nesticidae: Nesticella sp. 1
- 32. Aranae: Miturgidae: new genus & species
- 33. Aranae: Zodariidae: Storena sp. 1
- 34. Aranae: Linyphiidae? Undet. Blind sp. 1
- 35. Diplopoda: Polyxenida: undet. Blind sp. 1
- 36. Diplopoda: Polydesmida: undet. Blind sp. 2
- 37. Diplopoda: Cambalida: undet. Blind sp. 1
- 38. Scutigerida: undet. Blind sp. 1
- 39. Collembola: Entomobryidae: *Pseudosinella* sp. 1
- 40. Blattodea: Blattellidae: *Neotemnopteryx baylissensis* Slaney (2000)
- 41. Blattodea: Nocticolidae: Nocticola sp. 1
- 42. Hemiptera: Heteroptera: Reduviidae: *Micropolytoxus cavicolus* Malipatil & Howarth (1990)
- 43. Hemiptera Auchenorrhyncha: Cixiidae: Solonaima baylissa Hoch & Howarth (1989b)
- 44. Coleoptera: Pselaphidae: undet. Blind sp. 1
- 45. Coleoptera: Staphylinidae: undet. Blind sp. 1
- 46. Coleoptera: Curculionidae: Rhytirhininae: n. gen. and sp. 1

Additional species from lava tubes in the McBride Province (Howarth 1988b):

- Onychophora: peripatus: 210 and Long Shot Caves (Troglobitic?)
- Arachnida: Schizomida: Barkers Cave (cave adapted?)
- Phalangidae: Long Shot Cave (troglobitic?)
- Blattodea: *Nocticola* sp. 2: Long Shot Cave (troglobitic)
- Blattodea: Blattellidae: *Neotemnopteryx undarensis* Slaney (2000). Undara lava tubes (troglobitic?)
- Hemiptera: Heteroptera; Reduviidae (Emesinae): *Ploiaria* species 1 Long Shot Cave (troglobitic)
- Hemiptera: Heteroptera; Reduviidae (Emesinae): *Ploiaria* species 2 Long Shot and 210 Caves (troglobitic)
- Hemiptera Auchenorrhyncha: Cixiidae: *Undarana collina* 210 Cave, Collins Cave
- Coleoptera: Curculionidae, Rhytirhininae: sp. 2 Taylor Cave

References:

- Atkinson, A., Griffin, T.J. & Stephenson, P.J. 1976 A major lava tube system from Undara Volcano, North Queensland. *Bull. Volcanol.*, 39(2): 1-28.
- Barr. T.C. Jr. 1968 Cave ecology and the evolution of troglobites. *Evolutionary Biology*, 2: 35-102.
- Barr. T.C. Jr. 1973. Refugees of the Ice Age. *Natural History*, 82:26-35, 72, 73.
- Culver, D. 1982 Cave life, evolution and ecology. Harvard Univ. Press. Cambridge, MA.
- Deharveng, L & Bedos, A. 1986 Gaz carbonique. [In] *Expedition Thai-Maros 85, rapport speleologique et scientifique.* pp. 144-152 A. Pyrénées de Spel. Toulouse, France
- Hamilton-Smith, E. 1967 The arthropoda of Australian caves. J. Aust. Entomol. Soc., 6: 103-118.
- Holsinger J.R. 1988 Troglobites, the evolution of cave-dwelling organisms. *Am. Sci.*, 76: 147-153.
- Holsinger J.R. & Culver, D.C. 1988 The invertebrate cave fauna of Virginia and a part of eastern Tennessee: Zoogeography and ecology. *Brimleyana*, 14: 1-162.
- Hoch, H. 1990 Cavernicolous Meenoplidae of the genus *Phaconeura* (Homoptera: Fulgoroidea) from Australia. *Bishop Museum Occasional Papers*, 30: 188-203.
- Hoch, H. 1999 The Hawaiian cave planthoppers (Homoptera: Fulgoroidea: Cixiidae) – a model for rapid subterranean speciation? *Int. J. Speleol.*, 26(1–2): 21–31.
- Hoch, H. & Asche, M. 1988 Cave-dwelling planthoppers of Australia. (Insecta: Homoptera: Fulgoroidea). [In] Pearson, L. (ed.) *Preprints of Papers, Tropicon (Biennial Conf. of ASF)*, pp. 67-75.
- Hoch, H. & Asche, M. 1993. Evolution and speciation of cave-dwelling Fulgoroidea in the Canary Islands (Homoptera: Cixiidae and Meenoplidae). Zool. J. of the Linnean Soc., London, 109: 53-101.
- Hoch, H. & Howarth, F.G. 1989a Six new cavernicolous planthoppers in the genus *Solonaima* from Australia (Homoptera: Fulgoroidea). *Systematic Entomology*, 14: 377-402
- Hoch, H. & Howarth, F.G. 1989b Reductive evolutionary trends in two new caverniculous species of a new Australian cixiid genus (Homoptera: Fulgoroidea). Systematic Entomology, 14: 179-196.

- Howarth, F.G. 1972 Cavernicoles in lava tubes on the island of Hawaii. *Science*, 175: 325-326.
- Howarth, F.G. 1973. The cavernicolous fauna of Hawaiian lava tubes. I. Introduction. *Pacific Insects*, 15: 139-151.
- Howarth, F.G. 1980. The zoogeography of specialized cave animals: A bioclimatic model. *Evolution*, 34: 394-406.
- Howarth, F.G. 1981. Community structure and niche differentiation in Hawaiian lava tubes.
 [In] Mueller-Dombois, D., Bridges, K.W. & Carson, H.L. (Eds). *Island Ecosystems* pp. 318-336. Hutchinson Ross Pub. Co.: Stroudsburg, PA.
- Howarth, F.G. 1983a Ecology of cave arthropods. Annual Review of Entomology, 28: 365-389.
- Howarth, F.G. 1983b Bioclimatic and geologic factors governing the evolution and distribution of Hawaiian cave insects. *Entomol. Gen.*, 8: 17-26.
- Howarth, F.G. 1988a The evolution of non-relictual tropical troglobites. *Int. J. Speleol.*, 16: 1-16.
- Howarth, F.G. 1988b Environmental ecology of North Queensland caves: or why there are so many troglobites in Australia. [In] Pearson, L. (ed.) *Preprints of Papers, Tropicon (Biennial Conf. of ASF)*, pp. 76-84.
- Howarth F.G. & F.D. Stone, 1990 Elevated carbon dioxide levels in Bayliss Cave, Australia: Implications for the evolution of obligate cave species. *Pacific Science*, 44: 207-218.
- Humphreys, W.F. 1991 Experimental re-establishment of pulse-driven populations in a terrestrial troglobite community. *J. Animal Ecology*, 60: 609-623.
- Humphreys, W.F. (Ed) 1993a *The Biogeography of Cape Range, Western Australia.* Western Australian Museum: Perth.
- Humphreys, W.F. 1993b Stygofauna in semiarid tropical Western Australia: a Tethyan connection? *Memoires de Biospeologie*, 20: 111-116.
- Humphreys, W.F. 1993c Cave fauna in semi-arid tropical Western Australia: a diverse relict wetforest litter fauna. *Memoires de Biospeologie*, 20: 105-110.
- Humphreys, W.F. 1994 *The subterranean fauna of the Cape Range Coastal Plain, Northwestern Australia.* Report to Aust. Heritage Comm. and W.A. Heritage Committee, 202.
- Humphreys, W.F. 1995 'Limestone of the east Kimberley, Western Australia—karst and cave fauna.' Report to the Aust. Heritage Commission and W.A. Heritage Committee.

190 pp. (unpublished)

- Humphreys, W.F. 1999 Relict stygofaunas living in sea salt, karst and calcrete habitats in arid northwestern Australia contain many ancient lineages. [In] Ponder, W. & Lunney, D. (Eds) *The Other 99%. The Conservation and Biodiversity of Invertebrates. Trans. Royal Zool. Soc. NSW.* Mosman: NSW. pp. 219-227
- Leleup, N. 1968 Introduction. Mission zoologique belge aux iles Galapagos et en Ecuador (N. et J. Leleup, 1964-1965) Resutats scientifiques. Koninklijk Museum voor Midden-Africa – Musee Royal de l'Afrique Centrale. Premier Partie: 9-34. Tervueren, Belgium.
- Malipatil, M.B. & Howarth, F.G. 1990 Two new species of *Micropolytoxus* Elkins from Northern Australia (Hemiptera: Reduviidae: Saicinae). *J. Aust. Ent. Soc.*, 29: 37-40.
- Mayr, E. 1963 Animal species and evolution. Belknap Press of Harvard Univ. Press: Cambridge, Mass.
- Peck, S.B. & Finston, T.L. 1993 Galapagos Islands troglobites: The questions of tropical troglobites, parapatric distributions with eyedsister-species, and their origin by parapatric speciation. *Memoires de Biospeologie*, XX: 19-37.
- Rivera, M.A.J., Howarth, F.G., Taiti, S. & Roderick, G.K. 2002. Evolution in Hawaiian caveadapted isopods (Oniscidea: Philosciidae): Vicariant speciation or adaptive shift. *Molecular Phylogenetics and Evolution*. 25:1-9
- Roth, L.M. 1988 Some cavernicolous and epigean cockroaches with six new species, and a discussion of the Nocticolidae (Dictyoptera: Blattaria). *Revue Suisse Zool.*, 95: 297-321.
- Roth, L.M. 1990 A revision of the Australian Parcoblattini (Blattaria: Blattellidae: Blattellinae). *Memoires of the Queensland Museum*, 28: 531-596.
- Slaney, D.P. 2000. New species of cave dwelling cockroaches in the genus *Neotemnopteryx* Princis (Blattaria, Blattellidae, Blattellinae). *Memoirs of the Queensland Museum*, 46(1): 331-336.
- Slaney, D.P. 2001. New species of Australian cockroaches in the genus *Paratemnopteryx* Saussure (Blattaria, Blattellidae, Blattellinae), and a discussion of some behavioural observations with respect to the evolution and ecology of cave life. *Journal of Natural History, London,* 35(7): 1001-1012.

- Slaney, D.P. & Weinstein, P. 1996 Geographical variation in the tropical cave cockroach *Paratemnopteryx stonei* Roth (Blattellidae) in North Queensland, Australia. *Int. J. Speleol.*, 25: 1-14.
- Stone, F.D. 1988 The cockroaches of North Queensland caves and the evolution of tropical troglobites. [In] Pearson, L. (ed.) *Preprints of Papers, Tropicon (Biennial Conf.* of ASF), pp. 88-93.
- Stone, F.D., Howarth, F.G., Hoch, H. & Asche, M. 2005. Root Communities in Lava Tubes. [In] Culver, D.C. & White, W.B. (Eds) *Encyclopedia of Caves*. Elsevier Academic Press, pp. 477-484.
- Sullivan, N. Bro. 1979 Chillagoe visited. J. Sydney Speleol. Soc., 23(6): 147-150.
- Sullivan, N. Bro. 1983a. Chillagoe caves biology–A summary 1982. J.Syd.Speleol.Soc., 27(1):3-6.

- Sullivan, N. Bro. 1983b. Chillagoe caves expedition, 1983. J. Syd. Speleol. Soc., 27(10): 169-171
- Sullivan, N. Bro. 1984. Chillagoe caves expedition, 1984. J. Sydney Speleol. Soc., 28: 161-169.
- Sullivan, N. Bro. 1988. Chillagoe caves faunal challenge. [In] Pearson, L. (ed.) Preprints of Papers, Tropicon (Biennial Conf. of ASF), pp. 94-97.
- Taiti, S. & Howarth, F. G. 1997 Terrestrial isopods (Crustacea, Oniscidea) from Hawaiian caves. *Mem. Biospeol.*, XXIV: 97–118.
- Vandel, A. 1965. *Biospeleology, the biology of cavernicolous animals*. Pergamon: London.
- Wessel, A. 2008. Incipient non-adaptive radiation by founder effect? *Oliarus polyphemus* Fennah, 1973 – a subterranean model case. (Hemiptera: Fulgoromorpha: Cixiidae). Ph.D. Dissertation, Humboldt Univ., Berlin.