BIOLOGY

ENVIRONMENTAL ECOLOGY OF NORTH QUEENSLAND CAVES: or WHY THERE ARE SO MANY TROGLOBITES IN AUSTRALIA.

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ABSTRACT

Forty-three species of troglobites (obligate cave-dwellers) are listed from the tropical caves of north Queensland, Australia. All display morphological adaptations to caves, i.e reduced eyes, wings, and bodily color, compared to their surface relatives. They live deep in caves and interconnected systems of medium-sized voids, where the air is stale, saturated with water vapor, and often with a high concentration of carbon dioxide and where the substrate is damp, although many species are found in, or make forays into, more exposed cave passages, where the air is fresher but still saturated with water vapor. Cave habitats are zonal, and five zones are described based on the physical parameters that correspond to ecological communities. These are the entrance, twilight, transition, deep cave, and stagnant air zones. A community composed almost entirely of terrestrial troglobites is found in the stagnant air zone. Twenty-four of these troglobites live in Bayliss Cave, making this 190,000 year old lava tube one of the world's most significant biological caves. The existence of these troglobites and the potential for many new troglobitic species as the numerous caves of northern Australia are surveyed should lay to rest long-held assumptions and confirm that terrestrial troglobites are well represented in Australian caves, as well as in tropical caves in general.

INTRODUCTION

Conventional wisdom has long assumed that obligate cave-dwelling animals, i.e. troglobites, were poorly represented in continental Australian caves, and Moore (1964), Hamilton-Smith (1967) and Barr (1973) have published salient arguments explaining the apparent paucity of troglobites here. Their reasoning stressed the aridity of the continent, which was thought to have caused the extinction of a supposed earlier fauna, and the absence of preadapted moist litter species, which could colonize the caves. For completely different reasons, obligate cave animals were thought to be virtually non-existent in tropical caves, which are numerous in Australia. Vandel (1965), Barr (1968, 1973), Mitchell (1969), and Sbordoni (1982) explained the absence of terrestrial troglobites in tropical caves as resulting from the absence of climatic vicissitudes during the Pleistocene, which they felt were necessary to extirpate the epigean populations of evolving troglobites. However, the discoveries in the Galapagos (Leleup, 1968), Hawaii, and elsewhere (reviewed in Howarth, 1983b), have revolutionized our thinking on the evolution of troglobites and the biology of tropical caves.

On the basis of work in Hawaii, several hypotheses were put forward to explain the apparent disjunct distribution of troglobites in the world's karst regions. The more important are the tropical winter effect (Howarth, 1980; 1983a), a bioclimatic model (Howarth, 1980), a redefinition of the subterranean biome (Howarth, 1983b), and physiological ecology of troglobites (Howarth, 1980; Ahearn and Howarth, 1982).

Briefly, troglobites are behaviorally and physiologically specialized and appear to have evolved to exploit resources within the medium-sized voids (mesocaverns) and to colonize cave-sized passages (macrocaverns) only where the environment to which they are adapted is found or approximated. Since tropical caves are warm, limestone solution and evaporation rates are high, and in the tropics night-time temperature often falls below mean average surface temperature, creating nocturnal drying winds almost daily (the tropical winter effect). Therefore, the bioclimatic model predicts that it is more difficult to find troglobites in cave-sized passages in the tropics than in the temperate regions. In 1980 I wrote, "In fact, the bioclimatic model predicts that many more troglobites will be discovered as more tropical caves are surveyed and also predicts that they will be found only in cave passages that have a stable saturated or nearly saturated atmosphere" (Howarth, 1980).

In 1984, Brother Nicholas Sullivan presented me with an opportunity to come to Australia to study the tower karst around Chillagoe. The Chillagoe karst with the neighboring lava tube area at Undara has proved to be an ideal location in which to test the theories developed in the insular caves of Hawaii. Cave adaptation in insular Pacific caves was considered a special case and not representative of the tropics, or temperate caves in general (Culver 1982; Holsinger, 1988; Holsinger and Culver, 1988).

These studies on environmental ecology and cave animal distribution are still in progress, particularly as the expeditions to Chillagoe have all been fielded in the cool winter season when the tropical winter effect would theoretically be most severe. Thus we may have a parochial view of the cave climatic regime and ecology, having seen only part of one season.

This report is also preliminary because of the huge wealth of specimens and data collected. It will take years of uninterrupted study to sort through this material, obtain reports from the systematics collaborators, and decipher the story. It cannot be stressed too strongly that a study of this type is only as good as the systematics research upon which it is based. However, the story that is unfolding expands our view of the environmental ecology of caves, the evolution of cave faunas, and the numbers of troglobites in Australia.

The Chillagoe caves provide an ideal locale for conducting evolutionary and ecological studies of importance. They lie in an extremely complex area geologically with old, relatively isolated limestone pinnacles (tower karst) separated by both igneous intrusions and alluvial deposits. The climate is tropical with a monsoonal rainfall regime. Each tower has several entrances leading to numerous caves. Each cave can be quite different morphologically, environmentally, and faunistically. Within each tower, a suite of different cave types often occurs, while suites of similar cave types can be found in neighboring towers. In other words, each tower or group of nearby towers can be viewed as an island, its fauna having developed in isolation but under similar gross (i.e., long term) geological, biological, and climatic regimes with those of neighboring towers. This happenstance presents a unique opportunity for significant comparative research on environmental ecology. For one can conduct detailed ecological studies in each of several analog caves with very similar features but which are isolated from each other. One can also study animal distribution and resource exploitation in the suite of caves in one tower and then find analog caves in other towers which differ in one or only the few biotic or abiotic factors being examined. This comes as close to having an experimental control as is possible in ecological studies.

Adding further to this potential for comparative evolutionary studies is the existence of the significant caves in the McBride Formation lavas only 100 km southwest of the limestone. These lava caves have had a very different geological history, being much younger but possibly more interconnected than the limestone caves. Many of the same taxonomic groups have invaded each of these insular cave regions. In some cases perhaps the same ancestral species may have colonized several different caves and evolved independently in adapting to the caves. Some of our results are reported here. See also Hoch (this issue) and Stone (this issue).

METHODS

Biosurveys

Field work was done in conjunction with the 1984, 1985, and 1986 Chillagoe Caves Expeditions. Over 50 separate caves were visited in 15 towers in the Chillagoe-Mungana area, another two caves in two towers in the Rookwood area, 8 caves in 4 towers in the Mt. Mulgrave sector of Mitchell-Palmer area, and 10 lava tubes in two separate lava flows south of Mt. Garnet. We attempted to visit as many separate caves as possible and as many different types of caves as possible, but concentrated on larger caves and those known to contain moisture, guano, roots, or other abundant food resources, as these were found to support the most diverse fauna.

The caves were searched for animals, paying special attention to arthropods. Methods used were visually searching, placing baits (especially tubers, meats, cheese, and grains), and, to a lesser extent, setting pitfall traps. Promising caves were visited repeatedly. Voucher specimens of the arthropod species and some other invertebrate groups were collected. Additional specimens, which had been collected on previous expeditions or by members of the Chillagoe Caving Club, have been incorporated in the results where possible. The voucher specimens are deposited at the Queensland Museum in Brisbane, the B.P. Bishop Museum in Honolulu, and when appropriate at the home institution of the collaborating systematists.

Environmental ecology

The distribution of each of the different species of invertebrates was noted within the caves and correlated with cave and passage shape, relative humidity, temperature, moisture, food resources, and in selected caves also with carbon dioxide concentration. Temperature and relative humidity were measured with a battery-powered portable Bendix aspirating psychrometer. In Tea Tree, Bayliss, Nasty, Barker's, and Long Shot Caves, the concentrations of CO_2, O_2, NH_3, and CO were measured with a Draeger Multi Gas Detector.

CAVE ECOLOGY

Geologic history

The geology of the study area is complex, and ages of surface rocks range from Precambrian granites to Recent basaltic lavas. The 416-434 million year old Silurian limestone in the Chillagoe Formation outcrops as a band of over 300 isolated, cavernous marble towers, extending 150 km from Chillagoe north to the Palmer River (Best, 1983). The current main dry caves formed by phreatic solution during the last 5-10 million years (Ford, 1978; Pearson, 1982; Jennings, 1982), but there are remnant older passages and solution breccias near the tops of many towers, indicating that there may have been caves continually available for colonization since the area was uplifted and the limestone exposed in the mid-Tertiary about 25 million years ago. Near Chillagoe, the limestone towers stand nearly 100 m higher than the surrounding plain, which is between 350-400 m above sea level. The tower karst of Mitchell-Palmer 100 km to the north has experienced different rates of uplift and erosion, which have produced larger and higher towers (up to 200 m) often with a wide apron of limestone talus at their bases. Since the caves generally open only above the talus slope, they are often more open and more vertical than those at Chillagoe.

The lava tubes south of Chillagoe are strikingly different. The 190,000 year old Undara lava flow is less than 5% of the age of the Chillagoe caves. The pahoehoe lava flow, however, covers portions of older flows within the McBride Formation (Atkinson, Griffin, and Stephenson, 1976) and therefore, the cave fauna could have migrated through the numerous cracks and voids in young basalt and colonized caves in each flow in succession. Some McBride Formation lava flows may date from the Pliocene, more than 2.5 million years ago (Best, 1983). The troglobitic species could be, and probably are, older than the age of their caves.

Physical environment

Caves are strongly zonal environments. There are 3 obvious zones: entrance, twilight, and dark, based on degree of light penetration and its associated environment. From a biological perspective, the dark zone can be subdivided, based on the degree of climatic disturbance, into three distinct subzones: 1) transition, 2) deep, and 3) stagnant air zones. The transition zone, as the name implies, is a passage that is in total darkness but where the climatic events on the surface are still operative. The deep zone is beyond the transition zone. The substrate remains moist, the atmosphere remains saturated with water vapor, and the cave climate remains stable for extended periods. Air exchange with the surface keeps the air fresh. The stagnant air zone is beyond the deep zone, where air exchange with the surface is too slow, allowing the build-up of gasses, especially carbon dioxide, from organic decomposition.

Whether these zones occur in a given cave, and the location of the dynamic boundaries between them are determined by -

(1) the size, shape, attitude, and location of the entrances in relation to the surface environment and the size and shape of the cave passages,

(2) the availability of water, and

(3) the climatic regime on the surface.

Since water vapor is considerably lighter than air it will tend to diffuse out of deep open caves. Carbon dioxide on the other hand is much denser than air and will accumulate only in deeper passages. Thus the two gasses rarely reach high levels together in cave-size passages. However, U-, n, or N-shaped passages into dead-end rooms can trap both gasses, and it is here that troglobites are often found in abundance.

The main caves within the study area are described in Ford (1978) and Robinson (1982a), Atkinson et al., (1976), and in issues of Tower Karst. Cave types range from open aerated caves; e.g. the transition zones between large entrances in the main passages of Royal Arch, Carpentaria, and Spring Caves, to stagnant foul-air cave passages like Bayliss, Nasty, and Long Shot Caves. Most caves are complex with both open, aerated passages near the entrances and deep, remote passages, which approach stagnant conditions at least temporarily, e.g., Donna, Royal Arch, Arena, and Rhino Caves. In Chillagoe area caves there are 3 passage configurations that act in consort to trap air masses and lead to stagnant air conditions (stagnant air zone) and an environment suitable for troglobites.

a.) Deep caves reaching water or moisture near the water table;

b.) Small crawl way entrance to dark room, i.e. large cave volume to entrance size ratio; and

c.) a U-, n-, or N-shaped passage separating an inner passage from all entrances.

a]. Caves that are deep enough to reach water or moist soil layers; Spooked Cave and the main chamber in Donna Cave are the simplest examples. Many of the larger caves in the tower karst near Chillagoe have similarly deep, moist passages but also have a mixture of the other configurations. Marachoo has a crawl way entrance, U- and n-shaped inner passages, and water in its lowest level. Surprise Packet has an offset n-shaped crawl to the pit leading to the lowest moist level. If the pit was not so offset, the mud at the bottom would dry out much more quickly.

b]. Small crawl way entrance into large dead-end passage. Nasty Cave at Undara is the simplest example. Bayliss Cave at Undara and well-known Marachoo, Carpentaria, and Rhino Caves at Chillagoe combine the crawl way entrance with the next configuration.

c]. A U-, n-, or N-shaped crawl way or constricted passage leading into a dead-end upper level. This configuration is an excellent one for defining passages where troglobites can be found. The Snake-pit area of Carpentaria Cave is so different in environment and fauna from the rest of the cave that visitors are surprised. Hercules Cave contains one of the most diverse troglobitic faunas in the Chillagoe Karst, and the rich passage is an upper level beyond a particularly complex N-shaped passage. Arena Cave has a U-shaped entrance crawl which leads into a moist room with a high dead-end upper level. It is a much smaller cave than Spring Cave in the same tower, but the constricted and convoluted entrance allows the cave to support greater populations of troglobites than Spring Cave.

The long downwardly sloping lava tubes in the Undara and Collins systems are particularly well suited to trap both carbon dioxide and water vapor. The lava is old enough for a surficial soil layer to have formed which seals the cave from leakage except through entrances and larger cracks, The mud floor holds both moisture and organic debris for gas build up. In both Long Shot

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and Bayliss Caves constrictions at the entrance and within the cave help trap both moisture and carbon dioxide. Nasty Cave has a nearly sealed entrance, which when disturbed can lead to air overturn and exchange.

Temperature

Cave temperatures are generally near MAST (mean annual surface temperature) ca. 26° C (Robinson, 1982b); however, passage shape can significantly dictate the equilibrium temperature within a cave. Passages below entrances often act as cold traps and are cooler than MAST. These passages are also subject to the winter effect and are often dry, e.g. Spring (T = 19° C), Haunted (T = 21° C), and Donna Caves (T = 20-21.5° C). Passages above entrances or dead-end upsloping passages within the cave act as heat traps and remain warmer than MAST, e.g., Tea Tree Cave (T = 30° C) or at least warmer than the lower parts of the caves e.g. the Snake Pit room (T = 26° C) compared to 20° C in the Grand Canyon room of Carpentaria Cave. Many Chillagoe caves have several entrances at different elevations and the passages between have variable temperatures because of the chimney effect between the entrances, e.g. the main room in Donna Cave varied between 21.5° C and 20° C between 3 and 12 June 1985, during a period of cool nights and a strong winter effect.

Several caves near Chillagoe contain permanent pools of water, which were surprisingly warm in May to July during our visits, ranging from 27° C in Marachoo Cave to 29.5° C in Tea Tree Cave. Although a geothermal source of the heat is possible, it seems more probable that the water temperature results from the stored heat of the summer rains entering the caves. Mean temperature during the wet summer months approaches 30° C (Robinson, 1982b). In Centenary Cave, two small pools probably isolated from groundwater connection had a temperature of 19° C and 20.5° C respectively on 1 July 1984.

Biodiversity

About 5000 specimens of cavernicolous arthropods have been collected from the caves in the study area. These represent hundreds of species, many of them new to science. Over 40 species of troglobites are so far recognized in the material (Appendix I). Only one of these troglobites was known and named before the current survey. Three quarters of the troglobites live in two lava tube systems within the McBride Formation, and over one half (24) species are found in Bayliss Cave, underscoring the significance of this cave.

Bayliss Cave, with a total known fauna of at least 52 resident species, also supports the most diverse assemblage of arthropods of any cave in the area, either limestone or lava. However, as discussed below the Bayliss Cave fauna is segregated into distinct communities based on the physical environment.

Food resources

The major food energy in North Queensland cave ecosystems is supplied by -

(1) guano from trogloxenes, especially bats and swiftlets,

(2) abundant leaf litter and organic debris falling or washing into the doline entrances and cracks,

(3) abundant tree roots, and

(4) accidentals i.e. those animals that blunder into caves but can not survive there.

Accidental animals, both vertebrate and invertebrate visitors, which die or become easy prey in the cave, supply abundant food for troglobites. Several trogloxenous ant and termite species penetrate deeply into cave habitats in search of water and may be a large resource for cave animals, but evidence of significant use is weak. The defensive and navigational abilities of these social insects may be sufficient to prevent significant exploitation.

The most abundant tree roots probably belong to Ficus and Brachychiton, but the roots have not been authoritatively identified. In the tropics on karst and young lava flows, water washes off the barren rocky surfaces into cracks and sinkholes and sinks rapidly to the water table. Vadose water held in a surficial soil layer, as typically occurs in temperate regions, rarely occurs on tropical karst or new lava flows. Vegetation growing on these porous rocky substrates must cope with this stressful rapid percolation of water. One of the common specializations shown by trees able to grow on these terrains is deeply penetrating roots. Their roots must extend to the water table often 30 m or more below ground. These deeply penetrating roots provide energy resources for troglobitic animals, which accounts for the better development of troglobitic root feeders in tropical caves than in temperate caves.

The food resources in these caves are relatively abundant compared to those recorded for temperate regions, but the availability of each is highly seasonal. The monsoonal rainfall climate washes most of the leaf litter and other organic matter into the caves during the three wetter summer months; bats and birds use the caves seasonally, dumping fresh guano in the caves over a short period of time, which then ages before additional guano is deposited; and flushes of the trees in response to rainfall and warm weather bring more food to the roots. All of these would pulse populations of cavernicoles and synchronize their life cycles. Possibly these caves are as seasonally variable as many temperate caves, but the seasonality is driven by a completely different climatic and biologic regime.

Communities

Species exploiting the same food resource often form communities which interact and support separate food webs within the cave. Generalists and predators may interact with several food webs. As in other zonal habitats, these communities can sometimes be better defined by the physical parameters dictating animal distribution than by the food resources present. Distinct Chillagoe cave communities include the entrance and twilight zone communities, the aquatic community, the terrestrial tree root community, the transition zone bat and swiftlet guano communities, and the stagnant air zone community. There is some overlap as some generalists may exploit more than one resource or zone. Troglobites occur mainly in the deep and stagnant air zones, and it is these zones and their fauna that are the focus of this paper.

The aquatic cave communities in Chillagoe and Undara are so far inhabited by only one macroscopic invertebrate group, the amphipods. These are scavengers in every permanent pool of water in the study area. Why there appear to be no predators or other species in this habitat remains an enigma.

The tree root community contains not only plant feeding species but also a number of predators and scavengers which prefer to forage on or near roots. Many species are host specific, that is occurring on only one type of root, e.g. the meenoplid and cixiid planthoppers, or are found on roots only in certain zones within the caves, e.g. the cixiid planthoppers and the moths. Among the latter, the noctuids (undetermined species of Schrankia) all prefer wetter roots in the deep and stagnant air zones, while the pyralid (Bocchoris acamesalis, det. G. B. Monteith, Queensland Mus.) prefers drier sites in the transition zone. Several ant species, including Paratrechina longicornis and Paratrechina sp. 1 (det. R. Taylor, CSIRO, Canberra) use roots for navigation to gain access into the cave both for water and for food when available.

Several guano communities overlap within the caves depending on zone and type of guano, and its age. Some of the guano food webs appear to develop differently on the same food resource in different caves. Is this succession as the resource ages or history of animal colonization within the cave? For example, in Taylor Cave at Undara, and Collins Cave No. 1, the bat guano seethes with mites, which are preyed upon by pseudoscorpions, Protochelifer cavernarum Beier (det. M.S. Harvey, Mus. of Victoria). Numerous small beetles and fly maggots also live in or on the guano. In contrast, in nearby Pinwill Cave, large cockroaches, Paratemnopteryx sp., and isopods dominate the guano surface. How did these two different distinct communities develop? Most of these guano species are considered guanobites or troglophiles, although many of them show some troglomorphies.

The cave environment and the distribution of troglobites

The distribution of most cavernicoles within caves and their degree of cave adaptation are more clearly correlated with the physical environment within the cave than with either food resources or cave geology. As already described, troglobites are found in passages with stagnant air, which is saturated with water vapor, although many species do make forays into the transition zone for food or by accident. For example, the meenoplid planthoppers in the Grand Canyon passage of Carpentaria Cave maintain water balance by sucking sap from their host roots.

The relationship between environment and distribution of cave troglobites is nowhere more dramatic than in Bayliss Cave at Undara. During our surveys in May and June of 1985 and 1986, a community made up almost entirely of troglobites occurred in the inner parts of the cave. Most of the 21 troglophilic species occurred only in the outer transition and deep zones within the cave, while 3/4 of the 24 troglomorphic species were found only in the stagnant air zone, where the carbon dioxide concentration ranged from 0.6% to 6% (200 times ambient) (Howarth and Stone, in prep.). With 24 troglobitic species, Bayliss Cave supports one of the most diverse specialized faunas known in the world. The long term stable inner atmosphere in Bayliss Cave approaches equilibrium with the gas concentrations within the surrounding mesocaverns. The discovery of a community of troglobites in a foul air cave supports the hypothesis that troglobites are specialized to exploit the resources within the medium-sized voids in cavernous rock, where gas mixtures, especially CO_2 and H_2O, are limiting for most surface species.

With the able assistance of Douglas Irvin, I was able to repeat the studies in Bayliss Cave in 1986, confirming the 1985 results and to study two additional foul air lava tubes, Nasty and Long Shot Caves. Although neither cave is as large or as diverse as Bayliss Cave, the results corroborate those from Bayliss. Long Shot Cave is in the Collins Lava Tube System on Spring Creek Station about 30 km southeast of Bayliss. It has a crawl way entrance down slope to a small room in twilight. The cave extends over 360 m as a 3-5 m wide tunnel dissected by short crawl ways over or through breakdown piles. The constrictions trap both water vapor and CO_2. On 27 May, 1986, the carbon dioxide ranged from 0.1% at the base of the entrance slope (Site 1) to about 2.75% near the end. Relative humidity ranged from about 90% at Site 1 to saturated beyond the first constriction, where the first troglobites were found. Temperatures ranged from 20.2° C at Site 1 to 25.2° C near the end. The arthropod community in the final room was composed mostly of troglobites. Eight of the 13 troglomorphic species appear to be the same as those that occur in Bayliss Cave (Appendix I), but the systematic research is preliminary.

Nearby Two-Ten-Cave trends upslope from the entrance and does not trap CO_2, but the inner rooms were saturated or nearly so (RH = 98-100%) On 26 May 1986, the temperature ranged from 20.1° C in twilight at the base of the entrance slope to 21.8° C in the final room, 200 m from the entrance. The inner fauna consisted mostly of troglophiles, but a few troglobites similar to those in Long Shot were found. However, the cixiid species in Two-Ten-Cave belongs to a different genus and shows fewer troglomorphies than the cixiid found in Long Shot Cave (Hoch and Asche, this volume).

Nasty Cave is a 100 m long segment of the Undara system down slope of Bayliss Cave. The entrance is nearly sealed and must be enlarged to enter. On 29 May, 1986, the first troglobites were found only 50 m from the entrance (where RH = 98%; T = 25.5° C, O_2 = 14.8%, and CO_2 = 3.5%). Less food was available than in Bayliss Cave, and the number of species and populations were less. The final room was in the stagnant air zone and contained a community of troglobites (RH = 100%, T = 26.7° C, 0_2 = 13.7%, and CO_2 = 5.1%).

In spite of the apparent or implied stability of the environments of these zones, the boundaries between them and indeed the environmental conditions themselves can be dynamic. For example, on 30 May, the day after the entrance had been reopened and following an exceptionally cool night of the 29th, the air in Nasty Cave had changed. The readings in the final room had changed to RH = 100%, T = 26.5° C, CO_2 = 3.25%, and most of the troglobites had disappeared. Two common species on the 29th, a Nocticola cockroach and a polydesmid millepede, could not be found, and the populations of the other 9 troglobites were greatly reduced. Most of the troglobites appeared to have retreated into cracks during the unfavorable conditions of the previous night and were beginning to recolonize the cave as the environment improved.

Many troglobites are capable of making short forays into less than ideal environments to gather food or to disperse. This explains the effectiveness of baits and the apparent rarity of cave species, which is often related to the serendipity of being at the right place at the right time to find an animal that is normally wandering deep within the mesocaverns.

CONCLUSIONS

Why are there so many troglobites in Australia? There are potentially as many or more troglobites in Australia than on other continents because (1) there are so many caves, especially in the tropics and subtropics; (2) the cave areas are more or less isolated from one another, allowing the faunas to evolve and diverge independently; (3) food energy entering the caves is diverse and abundant; (4) the arthropod fauna of Australia is large and diverse, providing many preadapted colonists for the invasion of caves; and (5) a sampling of a few caves on the northeastern corner of the continent found a troglobitic fauna more diverse than most of the world's better studied cave areas.

Future surveys will certainly turn up additional new troglobites, both in the areas that we studied and in other limestone and lava regions. Most biological surveys in north Queensland have been done in the dry season. Surveys during the wet season, when the major drama in the cave ecosystem probably occurs, should be more productive.

We sampled just 2 lava flows in the northern corner of the McBride Formation and found about 30 new highly troglomorphic species. Many other caves and additional cave-adapted species can be expected further south in the McBride Formation. There are four other areas of Cainzoic basaltic provinces in north Queensland (Atkinson, et al., 1976), and each can be expected to harbor additional unique troglobites.

Over 300 limestone towers are known in a band from Chillagoe north to the Mitchell-Palmer area. About 7% of these have been sampled to date. Many of the more than 280 unsurveyed towers contain caves suitable for troglobites, and a large percentage of these troglobites could be new species. Additional karst areas occur at Camooweal, the Kimberleys, and at scattered localities elsewhere in northern Australia.

It is ironic that lava tubes were once thought to be exceptional environments for the evolution of troglobites (Barr, 1968), for lava tubes are now found to support far greater numbers of troglobites than neighboring limestone caves. The observation is real. Young basalt typically has far greater systems of mesocaverns than does most limestone, and so is a better habitat for troglobites.

One has to actually enter a cave and look for troglobites before proclaiming on theoretical grounds that none could exist. The results of the environmental ecology studies reported herein can be used to predict what types of caves and cave passages will most likely yield troglobites. The developing theory portrays troglobites as specialized to exploit resources within medium-sized cracks and crevices in subterranean rock and to colonize or stumble into cave-sized passages only where the physical environment is close enough to their favorite one. Thus the passages where troglobites would be expected will be dark, damp, saturated with water vapor, draft-free, and stable in temperature. Troglobites appear to be tolerant of the relatively high concentrations of carbon dioxide that exclude many troglophiles from deeper passages. This fact makes sense for an animal inhabiting a complex maze, where CO_2 concentrations fluctuate rapidly. The longer the air mass and other parameters of the physical environment in cave-sized passages are stable, measured in days, the more likely troglobites will be present. The presence of appropriate food resources and hiding places, such as roots and rock piles will improve the habitat for troglobites. Their environment is an inhospitable one for most organisms.

Contrary to earlier views that mainland Australia was devoid of troglomorphic troglobites, the preliminary data reported herein indicate that Australia will be found to support one of the most diverse troglobitic faunas of any of the continents.

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REFERENCES

AHEARN, G.A. and F.G. HOWARTH, 1982. Physiology of cave arthropods in Hawaii. **J. Experim. Zool.** 222: 227-238.

ATKINSON, A., T.J. GRIFFIN, & P.J. STEPHENSON, 1976. 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. **Evol. Biol.** 2: 35-102.

BARR, T.C., 1973. Refugees of the Ice Age. **Nat. History** May 1973: 26-35,72.

BEST, J. G., 1983. 1:250,000 geological series, explanatory notes. Atherton, Qld., Geological Survey of Queensland. 36 p. 2nd printing, originally publ. 1962.

CULVER, D.C., 1982. Cave Life. **Evolution and Ecology.** Harvard Univ. Press, Cambridge, MA. pp x, 190.

FORD, T.D., 1978. Chillagoe - a tower karst in decay. **Trans. British Cave Research Assoc.** 5(2): 61-84.

GRAY, M.R., 1973. Survey of the spider fauna of Australian caves. **Helictite** 11(3): 47-75.

HAMILTON-SMITH, E., 1967. The Arthropoda of Australian caves. **J. Aust Ent. Soc.** 6: 103-118.

HOCH, H. and M. ASCHE, 1988. Cave-dwelling planthoppers of Australia (Insecta: Homoptera: Fulgoroidea). **(this issue).**

HOLSINGER, J.R., 1988. Troglobites: The evolution of cave-dwelling organisms. **American Scientist** 76: 146-153.

HOLSINGER, J.R. and D.C. CULVER, 1988. The invertebrate cave fauna of Virginia and a part of eastern Tennessee: Zoogeography and Ecology. **Brimleyana** 14: 1-162.

HOWARTH, F.G., 1980. The zoogeography of specialized cave animals: a bioclimatic model. **Evolution** 34: 394-406.

HOWARTH, F.G., 1983a. Bioclimatic and geologic factors governing the evolution and distribution of Hawaiian cave insects. **Entomol. Generalis** 8:17-26. (1982).

HOWARTH, F.G., 1983b. Ecology of cave arthropods. **Annual Rev. of Ent.** 28:365-389.

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

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

JENNINGS, J.N., 1982. Karst of northeastern Queensland reconsidered. **Tower Karst** 4: 13-52.

LELEUP, N., 1968. Introduction. Mission zoologique belge aux iles Galapagos et en Ecuador (N. et J. Leleup, 1964-1965) Resultats scientifiques. Koninklijk Museum voor Midden-Africa = Musee Royal de l'Afrique Centrale. **Premier Partie:** 9-34. Tervueren, Belgium.

MITCHELL, R.W., 1969. A comparison of temperate and tropical cave communities. **Southwestern Natur.** 14: 73-88.

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

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

ROBINSON, T.W.L. (editor), 1982a. **Chillagoe Karst - A Speleological Field Guide of the Chillagoe - Mungana - Rookwood Areas in Far North Queensland, Australia.** Chillagoe Caving Club, Cairns, Old. 187 pp.

ROBINSON, T.W.L., 1982b. Limestone solution experiment - Chillagoe Area. **Tower Karst** 4: 71-76.

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(1): 297-321.

SBORDONI, V., 1982. Advances in speciation of cave animals. Pp 219-240. **In Mechanisms of Speciation.** Alan R. Liss, NY, USA.

STONE, F.D., 1988. **(This issue).**

VANDEL, A., 1965. Biospeleology. **The Biology of Cavernicolous Animals.** Pergamon, London. pp xxiv, 524.

WAHRBERG, R., 1922. Terrestre Isopoden aus Australien. Results of Dr. E. Mjoberg's Swedish Scientific Expedition to Australia, 1910-1913. No.30. **Ark. Zool. Stockholm** 15: 1-298.

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APPENDIX I

Annotated list of troglobites (obligate cave-dwelling species) known from the Chillagoe and McBride Formation caves, north Queensland.

Onychophora: - peripatus: A new, possibly troglobitic species of these unusual living fossils, which share features with both the earthworms and arthropods, was found in the deep zone of 210 Cave and stagnant air zone of Long Shot Cave.

Crustacea: Amphipoda; (det. by A. Friend and B. Knott, Univ. W. Australia, Nedlands). Blind, white, aquatic amphipods occur almost wherever permanent water is found in caves (Bayliss, Road, Tea Tree, Marrachoo, Christmas Pot, and Centenary Caves). The distribution of the different species may provide clues to ground water flow.

ISOPODA: Family Armadillidae - the pill bugs (det. by Miss A. Green, Tasmanian Mus., Hobart). Two presumed troglobites occur in Chillagoe caves: Armadillo (Troglarmadillo) cavernae Wahrberg (1922), and an undescribed species.

Superfamily Oniscoidea - Two white, vestigial-eyed species, still undetermined, live in Bayliss Cave, and other Undara lava tubes.

ARACHNIDA: SCHIZOMIDA --schizomids: (Det. J. Reddell, Texas Mem. Mus.) Family Schizomidae: Cave populations are known from Barker's, Marrachoo, and Tea Tree Caves but are doubtfully troglobitic.

pseudoscorpionida -- pseudoscorpions: (det. by M.S. Harvey, Mus. of Victoria, Melbourne).

Family Chthoniidae: A large Tyrannochthonius species with small eyes, possibly troglobitic, lives in washed in leaf litter in Royal Arch Cave in the transition zone.

PHALANGIDA -- daddy long legs: (undetermined). Pale, small-eyed specimens, possibly troglobitic, have been collected deep in Hercules and Long Shot Caves.

ARANEAE --spiders: (det. by V. E. Davies, Queensland Mus., and M. Gray, Australian Mus., Sydney.)

Family Pholcidae: Spermophora sp. nov. B (Gray, 1973): This long-legged pale spider with 6 vestigial eyes builds sloppy webs on roots, walls and across drip holes in the stagnant air zone in lava tubes in Undara and Collin's lava systems.

Family Linyphiidae (?): An eyeless sheet web builder lives in the stagnant air zone of Bayliss Cave. Other possible troglobites, presumably in this family, have been collected in Chillagoe caves. Several troglophilic species also occur, including a conspicuous sheet-web building species on old guano in Clam and Ryan Creek Caves.

Family Zodariidae: A remarkable large, dark colored species with vestigial eyes is found in Bayliss and Nasty Caves.

Family Nesticidae (?): Two species of small cob-web spiders live in Bayliss Cave, a troglophile in the transition zone and a blind troglobite in the stagnant air zone.

Family Oonopidae (?): Tiny eyeless hunting spiders, representing an unknown number of species, have been collected in several caves, including Bayliss, Ryan Creek, Arena, Gordale Scar Pot, Pioneer, Tea Tree, and Donna Caves.

Unknown Family: A large, pale, completely eyeless hunting spider with uncertain affinities lives in the stagnant air zone of Bayliss and Long Shot Caves.

DIPLOPODA -- millipedes (undetermined):

CAMBALIDA: A large white, eyeless cambaliform milleped lives in the stagnant air zone of Undara and Collin's Lava Tubes.

POLYDESMIDA: Two species, probably troglobitic, live in the stagnant air zone of Bayliss Cave.

POLYXENIDA: A blind, white species living in the stagnant air zones in Bayliss and Nasty Caves at Undara is a doubtful troglobite. However, it was among the most sensitive to the changing conditions in Nasty Cave.

CHILOPODA: SCUTIGEROMORPHA: -- long-legged cellar centipedes ("100 mph bugs"): A large (> 4 cm body length), pale, small-eyed, slow-moving species lives in the stagnant air zone of Bayliss, Nasty, and sometimes Barker's Caves at Undara. It is one of the largest terrestrial troglobites in the world.

COLLEMBOLA - springtails (det. by P. Greenslade, CSIRO, Canberra). Blind, white springtails are common in Bayliss Cave and other caves. Most are soil forms or troglophiles; however, it seems likely that some are troglobitic.

INSECTA: DIPLURA: bristle tails: (undetermined). A possible troglobite is common in the stagnant air zone of Bayliss Cave.

THYSANURA: silverfish: (undetermined). Two blind, white species live in the stagnant air zone of Bayliss Cave. One appears to be associated with ants (Paratrechina); the other may be troglobitic.

DICTYOPTERA - cockroaches, {det. by L.M. Roth (1988), MCZ, Harvard, and F.D. Stone, (This issue)}.

Family Blattellidae: Paratemnopteryx sp. This large, eyeless cockroach is still known only from females and nymphs from the stagnant air zone of Bayliss and Nasty Caves.

Family Nocticolidae: Nocticola australiensis Roth: This small, pale, tiny-eyed cockroach is known from the moist areas (deep zone) of Donna Cave and other Chillagoe caves, with each tower having a distinctive race. Two other Nocticola are known: one from Long Shot Cave, and one from Bayliss and Nasty Caves (See Stone, this issue).

HEMIPTERA: -- true bugs: (det. by G.B. Monteith, Queensland Mus., Brisbane, M. Malipatil, Northern Territory Mus., Darwin, and the late W.C. Gagne, Bishop Mus., Honolulu.)

Family Enicocephalidae: A single blind white nymph is known from Arena Cave and is possibly troglobitic.

Family Reduviidae: assassin bugs,Two troglobitic species live in the high CO_2 areas of Bayliss Cave. The larger (> 1 cm long), a Pirates sp., has small pink eyes and tiny wings and stalks prey on the wet, muddy floor. Each leg has a thickened tip covered with water repellent hairs ("mud shoes"!). The smaller species (0.5 cm long) belongs to Micropolytoxus and is pale straw white in color with vestigal eyes and wings.

Subfamily Emesinae: -- The thread-legged bugs: A blind flightless species lives in the high CO_2 stagnant air zone of Long Shot Cave. An apparently closely related troglophile lives in the deep zone of nearby 210 Cave.

HOMOPTERA: Superfamily Fulgoroidea -- planthoppers, (det. H. Hoch, Marburg, Germany).

Family Meenoplidae: One troglobite from Carpentaria and Marrachoo Caves (See Hoch & Asche, this issue).

Family Cixiidae: Four troglobites are known from the Chillagoe area: one each from Hercules Cave, Queenslander Cave, and Two-Ten-Cave and one from Bayliss, Nasty, and Long Shot Caves. (See Hoch & Asche, this issue).

COLEOPTERA: Family Pselaphidae: A blind species is known only from the stagnant air zone of Bayliss Cave and is presumed troglobitic. Another blind species lives in Trezkinn Cave.

Family Staphylinidae: A small blind species lives in the stagnant air zone of Bayliss Cave, it may be a deep soil species or a troglobite.

Family Curculionidae: Subfamily Rhytirhininae: -- weevils (det. by E.C. Zimmerman, CSIRO, Canberra). Two remarkable blind cave weevils are known from the Undara Lava tubes, one from the deep zone of Taylor Cave and one from the stagnant air zone of Bayliss Cave.