

Elevated Carbon Dioxide Levels in Bayliss Cave, Australia: Implications for the Evolution of Obligate Cave Species¹

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ABSTRACT: In May and June 1985, the deeper passages of Bayliss Cave, North Queensland, Australia, contained up to 200 times the ambient atmospheric level of carbon dioxide and a water-saturated atmosphere, yet supported the most diverse community of highly modified, obligate, terrestrial cave species yet known. The obligate and facultative cave species were mostly segregated by the environment, with the 24 obligate cave-adapted species being largely restricted to the “bad-air” zone. The discovery of this previously unknown “bad-air,” obligate cave community corroborates other behavioral and distributional studies that suggest that cave-adapted animals are specialized to exploit resources within the smaller underground voids, where fluctuating carbon dioxide concentrations are theoretically intolerable to most surface and facultative cave species.

EYELESS, PALE, GHOSTLIKE OBLIGATE cave species (trogllobites) have long intrigued evolutionary biologists and laymen, and many theories on their evolution have been proposed (Barr 1968, Culver 1982, 1986, Howarth 1988a). Howarth (1983a) and Huppopp (1986) postulated that some of the physiological adaptations displayed by cave animals (e.g., their low metabolic rate) might be in response to selection to cope with high levels of carbon dioxide theoretically possible in their environment. “Bad-air” caves are common in many karst and volcanic areas of the world (James 1977, Lewis 1981, Renault 1982, Deharveng and Bedos 1986), but until now they have been assumed to be devoid of life.

During our continuing survey of the biology of North Queensland caves, we had the opportunity to survey Bayliss Cave (about 200 km southwest of Cairns, 18°10' S, 144°30' E, 700 m elevation). Bayliss Cave

(Figure 1, *bottom*) is 900 m long with a maximum height of 11.5 m (average 5 m) and a maximum width of 18.9 m (average 8 m). It is the largest of many remnant lava tube sections within the massive Undara Lava Flow, which is ca. 190,000 yr old and covers roughly 1550 km² of land surface (Atkinson et al. 1976). We first visited Bayliss Cave from 21 to 23 May 1985 and noted a strong zonation in which the distribution of many new species of trogllobites correlated with increasing concentrations of carbon dioxide. We were especially impressed with the existence of a community of trogllobites at and near The Wall (a large rock dam 630 m from the entrance) and returned on 14–15 June 1985 to conduct a more thorough survey correlating the distribution of species with the concentration of carbon dioxide. This first biological survey of a “bad-air” cave yielded the discovery of a unique cave-adapted community and more than doubled the number of trogllobites known from continental Australia.

Until recently, morphologically specialized terrestrial cave species were thought to be rare or absent from tropical caves and to occur almost exclusively in unglaciated temperate limestone caves. That distribution corroborated the theory that most were relicts and evolved from facultative cave species that had

¹This project was supported by The Explorer's Club, Dupont (Australia) Co., and NSF Grant BSR 85-15183. Manuscript accepted October 1989.

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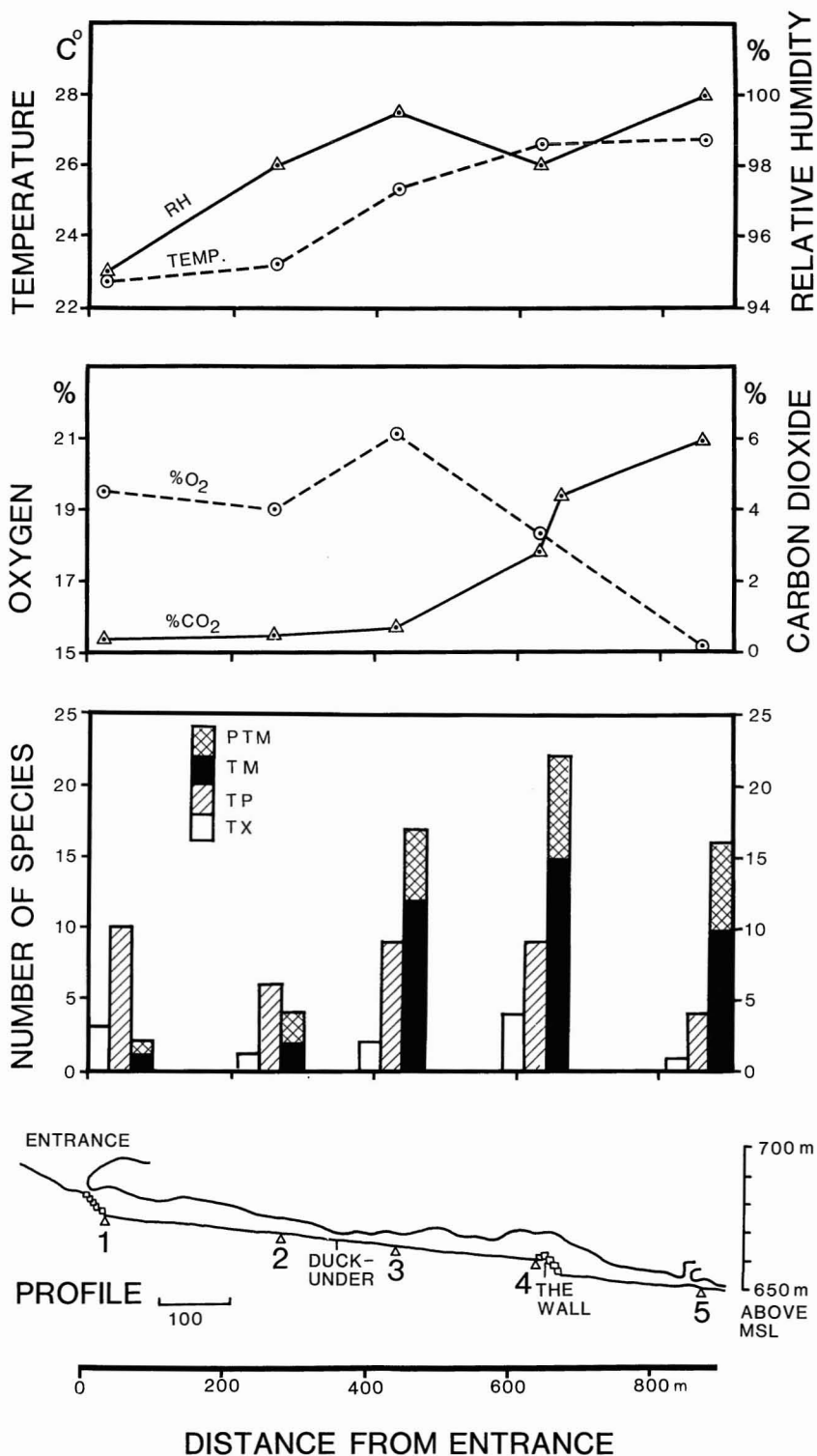


FIGURE 1. The environment and animal distribution in Bayliss Cave on 14–15 June 1985. Horizontal scale shows distance from the entrance and is the same for the map and graphs. *Bottom*: profile view of Bayliss Cave, vertical scale 4 × horizontal. Numbers 1–5 indicate locations of study sites. Bar Graph: number of species of macroinvertebrates collected or observed at each study site. The mites (Acari) were excluded because of their small size. Cross-hatched bar, partly troglomorphic (PTM); solid bar, troglomorphic (TM); single-hatched bar, trogliphilic (TP); clear bar, troglaxenic (TX). Middle Graph: dashed line (left-hand scale) volume % O₂ and solid line (right-hand scale) volume % CO₂ measured 15 cm off floor. Top Graph: dashed line (left-hand scale), temperature and solid line (right-hand scale), percent relative humidity measured 15 cm off floor.

become isolated in caves by changing climates (Barr 1968, 1973, Culver 1982). Furthermore, very few troglobites were previously known from the Australian continent, and Moore (1964), Hamilton-Smith (1967), Richards (1971), Barr (1973), Gray (1973), and Peck (1980) argued that their rarity in Australia was real and related to the climatic history of the continent, especially secondary extinctions of a presumed specialized cave fauna by episodes of extreme aridity. Peck (1980) further speculated that the absence of cool forest biotopes near Australian karst areas limited the number of preadapted species that could serve as potential colonists in the caves. However, Richards (1971) listed six highly troglomorphic (cave-adapted) species from the Nullarbor Plain, and Gray (1973), pointing out the potential for additional discoveries, listed 11 troglomorphic spiders from Australian caves.

The recent discoveries of highly troglomorphic species in tropical caves, in lava tubes, and in smaller voids in rocky substrates elsewhere (Howarth 1983a, Juberthie 1983) have provided new arenas for critically testing the paradigms concerning the origins of cave species developed from work in temperate caves. These discoveries also demonstrate the need to conduct biological surveys of such caves in other regions (Howarth 1983a, 1988a).

MATERIALS AND METHODS

On 14–15 June 1985, we established study sites, all in total darkness, at 30 m, 270 m, 430 m, 630 m, and 860 m from the entrance (Figure 1 *bottom*). Environmental data were collected, and an arthropod survey was conducted at each site. In addition to the site surveys, notes and collections were made of species seen between sites. The distributions of the larger, more conspicuous species could be accurately assessed and recorded in the cave. Because the different mite species could not be distinguished in the field, their distributions within the cave were not determined. Voucher specimens of the taxa listed are deposited in the Queensland Museum, Brisbane, Australia, with duplicates in the Bishop

Museum, Honolulu. Oxygen and carbon dioxide concentrations (as volume percentage) were measured 15 cm above the cave floor using a Draeger Multi Gas Detector with oxygen (5%/B) and carbon dioxide (0.1%/a) tubes, respectively. An extra set of CO₂ readings was taken at the base of The Wall. Two readings were taken at each site and corrected for barometric pressure (96.4–96.5 kPa) measured with a Thommen no. 2000 (5000 m) altimeter. Temperature and relative humidity were measured 15 cm above the cave floor at each site using a battery-powered Bendix aspirating psychrometer.

RESULTS

Bayliss Cave Environment

When we returned on 14–15 June 1985 the cave was drier and contained less carbon dioxide than on 21–23 May 1985, but it was still conspicuously zoned. The remarkable environmental zonation is hypothesized to result from the location and size of the entrance, shape and size of the passage, and availability of moisture and organic matter. The single crawlway entrance opens into the upslope end of the cave at the top of a talus slope 10 m high. The small size and tortuous shape of the entrance restricts air exchange between the surface and the interior to a small percentage of the volume within the cave. Two constrictions in the sinuous passage trap air into three compartments (Figure 1): an outer transition zone from the entrance to The Duckunder (a 1.5-m-high passage, 345 m into the cave) (Figure 2A); a middle zone, from 345 to 630 m, between The Duckunder and The Wall; and an inner zone beyond The Wall. The temperature and relative humidity profiles (Figure 1) are maintained by The Duckunder. Rising warm cave air and water vapor are blocked by The Duckunder. During our visit in June, a zone of thick mist 100 m wide was present downslope of The Duckunder. The high level of moisture in Bayliss Cave comes from rainfall, which occurs mostly between January and April, and a ground-water aquifer, which flows just beneath the

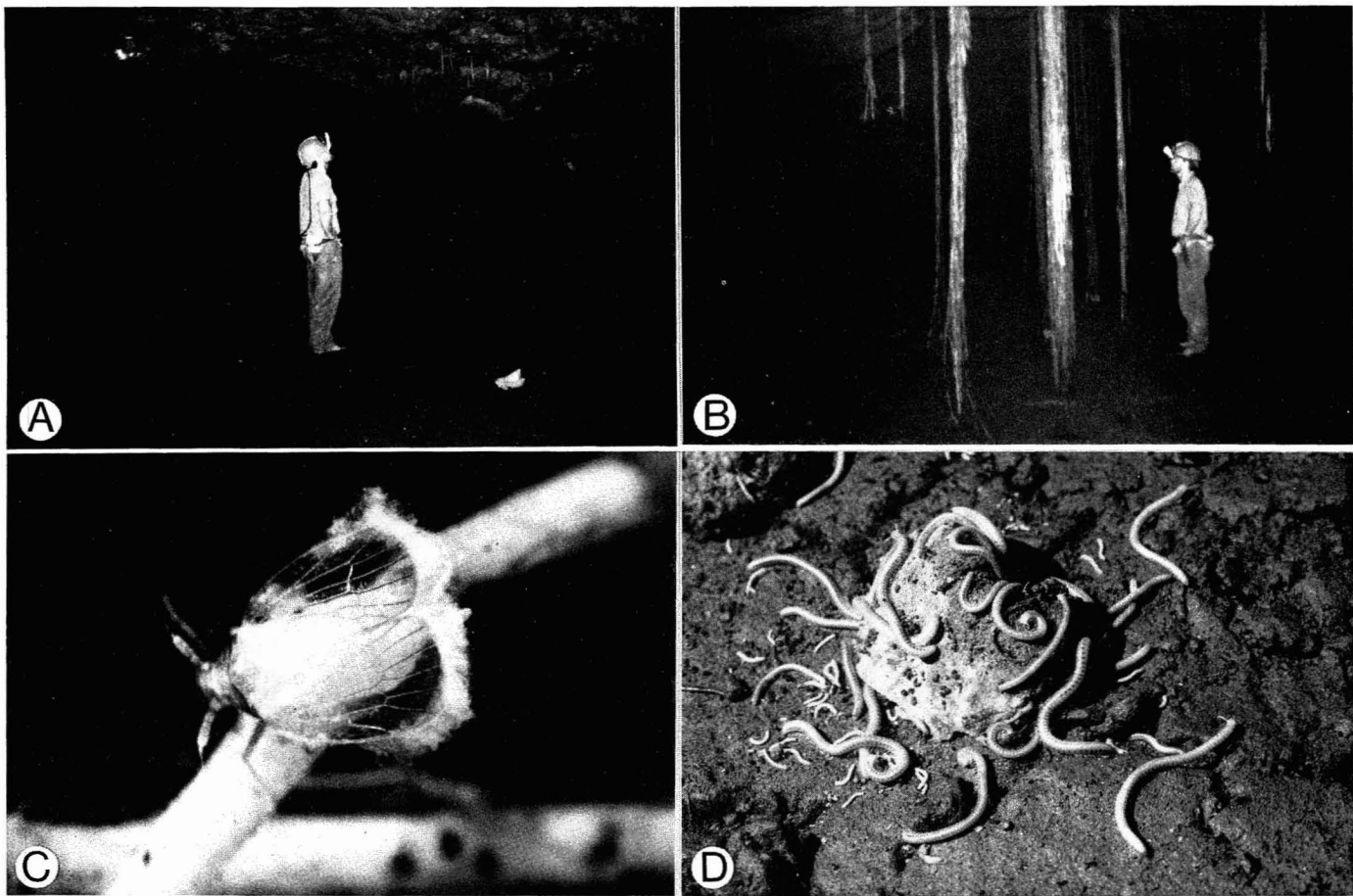


FIGURE 2. *A*, Cross-sectional view of upslope part of The Duckunder in Bayliss Cave (photograph by F. G. Howarth). *B*, Portion of the luxuriant root patch in the fog zone downslope of The Duckunder (photograph by F. G. Howarth). *C*, The blind cave cixiid planthopper, *Solonaima baylissa*, on a tree root. The distal wax fringe on the tegmina resembles a light blue halo in life (photograph by Hubert Reimer, Philipps University, Marburg, Federal Republic of Germany). *D*, Millipedes at sweet potato bait at the base of The Wall. Larger species is the camballid, and smaller species is the polydesmid species no. 2 (photograph by F. G. Howarth).

cave fill (erosional material accumulating in the cave). There are intermittent springs and stream channels near the entrance and below The Wall.

The downward-sloping cave acts as a trap for CO₂, because CO₂ is 1.5 times heavier than air. Between The Wall and The Duckunder is a zone of mixing in which the CO₂ concentration increased nearly five times (from 0.6 to 2.8 volume %). Beyond The Wall the CO₂ increased dramatically to a maximum of 5.9% at site 5 (Figure 1). The O₂ concentration (15.1%) was correspondingly lower at site 5, indicating the in situ production of CO₂ from the oxidation of organic matter (James 1977). Soil formation and erosion of the lava surface have filled many of the smaller voids in the lava and sealed the cave from additional air exchange through cracks, as evidenced by the stagnant conditions and the degree of silt and clay fill. The original cave floor is nowhere visible, the fill being up to several meters deep.

The relatively abundant food resources include living and dead roots, bat guano, dead animals and organic matter washing in through cracks and the entrance. Small patches of bat guano (<2 m diameter) occur in scattered locations throughout the cave, and individual Eastern Horseshoe Bats (*Rhinolophus megaphyllus*) were seen flying throughout the cave, even in the areas with highest CO₂ levels.

Bayliss Cave Fauna

Of the 51 species of cavernicoles collected in Bayliss Cave (Table 1), 17 are obligate cave species (e.g., Figure 2C and D) showing extreme troglomorphy (e.g., loss or reduction of eyes, pigments, and wings; changes in body form; elongated appendages; and increased setation). Seven species display troglomorphic characters to a lesser degree and are provisionally also considered troglotic. Twenty-one species are classified as facultative permanent residents (troglaphiles), although some of the rarer species (e.g., the scolopendrid and geophilid centipedes and the scarabaeid beetle) may in fact be accidental in the cave. Six species are temporary visitors or foragers (troglonexes).

The distributions of five species of pre-

sumed troglaphiles are not included in Table 1 and Figure 3. Four of these are mites that were too small to identify and map the distribution of individual species in the field. Four morphospecies were collected, usually associated with bat guano. The fifth species is the primitive vascular plant *Psilotum* sp., a small patch of which was found growing saprophytically on the moist clay near The Duckunder.

The three ant species and the subterranean termite are soil-nesting social insects able to enter caves and forage for food or water along chemical trails. Some termites are known to burrow 30 m below ground to obtain water. Many soil-nesting ants and termites are known to tolerate, at least temporarily, high concentrations (up to 20%) of CO₂ (Peakin and Josens 1978). The atelurine thysanuran appeared to be associated with the common ant *Paratrechina* sp. (Australian National Insect Collection species no. 1). The other troglonex was granny's cloak moth, *Sericea spectans*, which commonly uses caves as day-time retreats.

With 24 species of troglobites, Bayliss Cave is the most biologically diverse lava tube known. The diversity and degree of adaptation of the troglobites seem at first surprising, given the youth of the cave. However, the age of the cave is not necessarily the maximum age of cave colonization by the ancestors of the troglobites, since part of the Undara Lava Flow covers portions of older basalts within the McBride Formation (Atkinson et al. 1976), and since, as has been shown in Hawaii (Howarth 1983a), troglobites can colonize younger lava tubes from neighboring older ones. Among the more remarkable cave-adapted insects discovered in the cave are a blind brachypterous cixiid planthopper (*Solonaima baylissa* Hoch & Howarth [1989b]) (Figure 2C); a tiny-eyed, white assassin bug (*Micropolytoxus cavicolus* Malipatil & Howarth [in press]); a new genus and species of eyeless weevil in the subfamily Rhytirhininae; and two eyeless cockroaches (a large *Paratemnopteryx* and a long-legged *Nocticola*-like species) (Stone 1988). The troglotic spiders include a large (1 cm body), eyeless, pale spider, which represents a new genus and

TABLE 1

LIST OF MACROINVERTEBRATE TAXA FOUND IN BAYLISS CAVE DURING 14-15 JUNE 1985
(NUMBERS REFER TO TAXA LISTED ON FIGURE 3)

Trogloxenic

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

Troglophilic

7. Aranae: Sparrasidae: *Heteropoda* sp. 1
8. Aranae: Pholcidae: *Spermophora* sp. 1
9. Aranae: Nesticidae: *Nesticella* sp. 2
10. Scolopendrida: *Scolopendra* sp. undet. sp. 1
11. Geophilida: undet. sp. 1
12. Symphyla: undet. sp. 1
13. Blattodea: Blattellidae: *Paratemnopteryx* sp. 1
14. Homoptera: Cixiidae: *Undarana rosella* Hoch & Howarth (1989a)
15. Homoptera: Cixiidae: *Oliarus* sp. 1
16. Homoptera: Coccoidea: undet. sp. 1
17. Coleoptera: Scarabaeidae: 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. 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 and 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. Scutigera: undet. blind sp. 1
 39. Collembola: Entomobryidae: *Pseudosinella* sp. 1
 40. Blattodea: Blattellidae: *Paratemnopteryx* sp. 2
 41. Blattodea: Nocticolidae: *Nocticola* sp. 1
 42. Heteroptera: Reduviidae: *Micropolytoxus cavicolus* Malipatil & Howarth (in press)
 43. Homoptera: 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.
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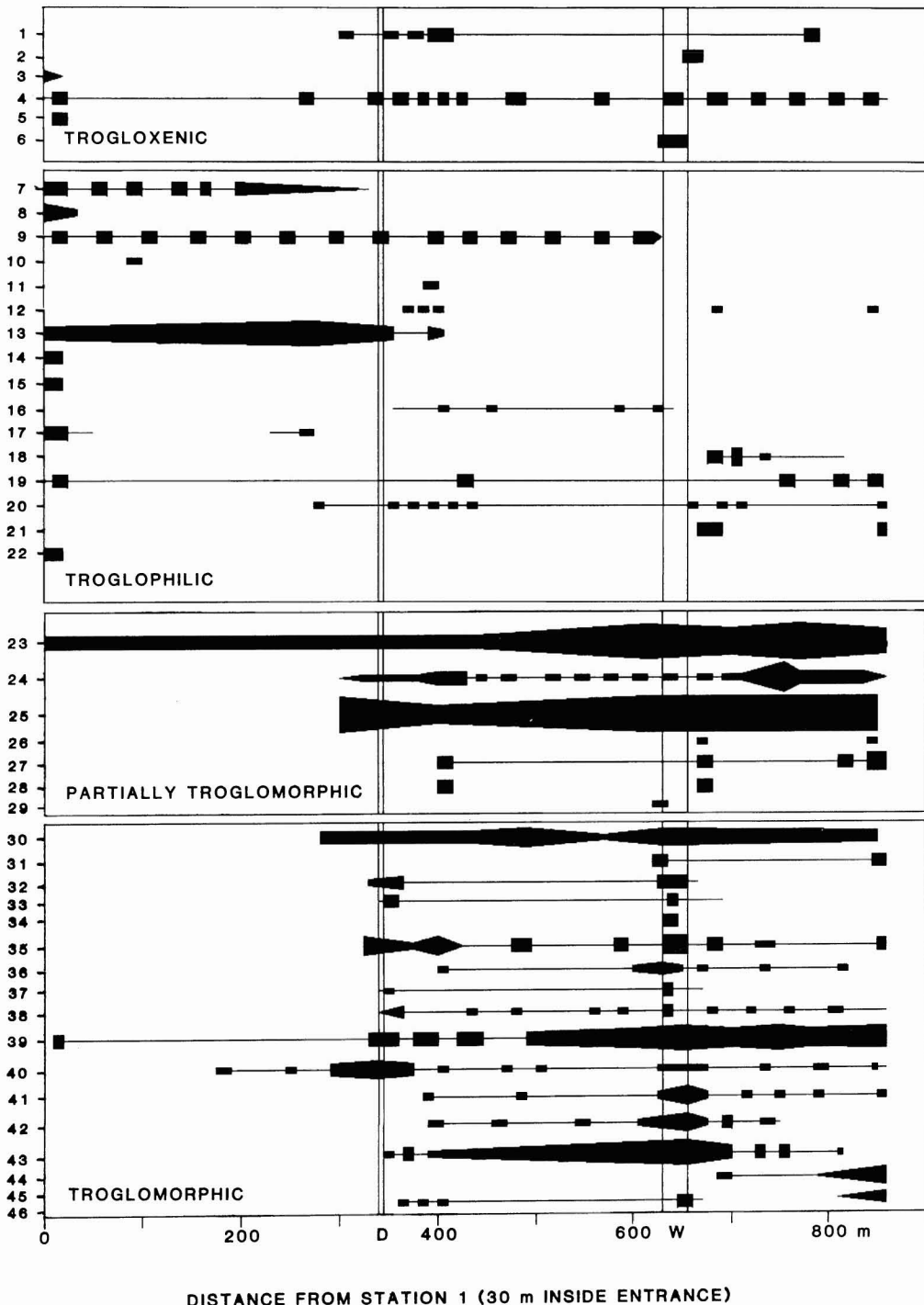


FIGURE 3. Relative abundance of the macroinvertebrates in Bayliss Cave in relation to distance from the entrance during 14–15 June 1985. See Table 1 for key to taxon names. Thickness of distribution bar is proportional to relative numbers present at that locality in the cave. Thin line indicates species probably present. Smallest square indicates 1 specimen confirmed; next larger square indicates ca. 4 specimens; thickest bar indicates abundant or over 50 animals, except for the *Paratrechina* spp. for which the code refers to number of foraging groups, each with 25 or more individuals. Vertical lines at D and W indicate the location of The Duckunder and The Wall, respectively.

species of machadoniine Muturgidae, and a large blind zodariid in the genus *Storena*. At the top of the food chain is a 4-cm-long vestigial-eyed, creamy yellow, slow-moving scutigerial centipede.

Animal Distribution within Bayliss Cave

The most abrupt change in species composition occurred at The Duckunder (Figures 1 and 3). At the time of our June survey, 7 of the 16 troglophilic species (excluding the mites) did not extend further into the cave than there (Figure 3). Two of these are noteworthy. A large, brachypterous, small-eyed cockroach, *Paratemnopteryx* sp. 1, was abundant near guano patches, and the numerous individuals were especially conspicuous as they scurried along the silt floor right up to The Duckunder, after which only a few were seen up to site 3. The other was a large sparrasid spider, *Heteropoda* sp. 1, whose conspicuous eyeshine made censusing especially accurate. The last individual was seen on the cave wall just outside The Duckunder.

Nine troglophilic species were found beyond The Duckunder, but none was abundant there. Only five troglophiles were widespread beyond The Duckunder. The web-building ambush predator, *Nesticella* sp. 2, was common in drip holes on the floor from the entrance to The Wall. At The Wall and beyond it was replaced by an eyeless relative, *Nesticella* sp. 1. Three of the widespread species (the symphylan, coccid, and noctuid moth) were associated with plant roots. The gelechiid moth was associated with guano.

Only four species of troglobites were present upslope of site 2, and an additional four species first appeared between site 2 and The Duckunder. All of these species were much more abundant beyond The Duckunder. Sixteen troglobitic species (67% of the total) were found only downslope of The Duckunder (Figure 3). Furthermore, most of the troglobitic species occurring upslope of The Duckunder were represented there by either single dispersing individuals or were found in protected microhabitats, whereas those beyond The Duckunder were often found in more

exposed situations (Figure 2D). The Duckunder and The Wall harbored greater numbers of species than neighboring passages because the rocky substrate contained more cracks, surface area, food, and hiding places. The exceptionally luxuriant roots (Figure 2B) hanging from the ceiling within the fog zone just beyond The Duckunder also supported a high diversity of species.

DISCUSSION

Zonation

Caves are conspicuously zonal environments, and four distinct zones (entrance, twilight, transition, and deep or true cave) have been described, based on the degree of light and the physical and biotic environments (Barr 1968, Howarth 1983a,b). We now recognize a fifth zone, the stagnant air zone. At the time of our visit, Bayliss Cave supported all five zones. The entrance zone included the entrance pit and was contiguous with the surface environment. The twilight zone was very small, comprising only the entrance crawlway. The transition zone extended from the maximum extent of light penetration at the top of the breakdown pile nearly to The Duckunder. During the night of 14 June a cold draft, caused by the winter effect (Howarth 1980), was perceptible in the twilight and transition zones. The deep cave zone included the area near The Duckunder, and, because of the large passage size and its linear extent, the deep zone had broad, dynamic boundaries with both the transition zone and the stagnant air zone. The stagnant air zone extended from below The Duckunder to the end of the cave.

Cave-adapted species are thought to be restricted generally to the deep or true cave zone of caves and other voids where there is a stable atmosphere saturated with water vapor (Barr 1968, Howarth 1980, 1983a,b, Culver 1982, Juberthie 1983). Cave passages with stable, saturated air are less common in the tropics than in temperate regions because the higher temperature allows greater evaporation and because the daily range of surface temperatures usually fluctuates above and

below the local cave temperature, thereby generating drying ventilation throughout much of the year—the tropical winter effect (Howarth 1980, 1983*b*). This does not mean that troglobites are less numerous in the tropics, only that cave passages with a suitable stable environment are less accessible to exploration.

Many tropical and temperate cave passages that we have studied resemble the transition zone upslope of The Duckunder, both in their abiotic environments and in behaviors and low percentages of troglobitic species (Howarth 1983*b*). Most lowland tropical caves have environments either drier than or similar to conditions at site 1, or rarely site 2 (Howarth 1980, 1983*b*), because of the tropical winter effect and large or multiple entrances (Howarth 1980). In a few temperate and tropical caves one can approach the environment found at site 3, and these areas are often lower-level dead end passages that also contain a high diversity of troglobitic species (Howarth 1980, Chapman 1986, Martin and Oromi 1986) and where CO₂ would be expected to accumulate occasionally (James 1977, Lewis 1981).

Most of the CO₂ in caves is produced locally from respiration by microorganisms in decaying organic matter, plants, and animals. Additional CO₂ can be brought into caves by flowing water, especially rainwater flushing CO₂ from overlying soils, and some CO₂ may diffuse from crevices in the surrounding rock and soil (James 1977).

Carbon dioxide accumulates in poorly ventilated cave passages, and its concentration is often dynamic (James 1977, Howarth 1988*b*). The level of CO₂ present fluctuates in response to the amount of gas available and to the degree of ventilation. Rain and floods can initially wash CO₂ out of cave passages, but the resulting input of moisture and organic debris increases the production of CO₂ from respiration. In Drum Cave, Bungonia, New South Wales, Australia, the CO₂ concentration rises to over 6% in summer when a nursery colony, which contains more than 1000 unidentified bats, is present, but returns to near the surface ambient level in winter, when the bats are absent and the cave is better

ventilated because of the winter effect (James 1977).

High Carbon Dioxide Environments

Some aquatic cave species are known to be able to survive in high carbon dioxide and low oxygen concentrations (Istenic 1986, Palmer et al. 1986, Yager 1986, 1987), and Yager (1987) indicated that a low level of O₂ is a characteristic feature of the anchialine habitat of remipedes and associated cave-adapted species.

Finding a community composed largely of cave-adapted species in the bad-air zone of Bayliss Cave provides additional evidence that troglobites are physiologically, behaviorally, and morphologically specialized to exploit resources in the harsh, seemingly inhospitable environment within the medium-sized interconnected voids in cavernous rock (i.e., the mesocaverns) and that they enter cave-sized passages only if their environment, especially the stable saturated atmosphere, is approximated (Howarth 1983*a,b*, 1988*a*). The atmosphere within the deeper mesocaverns is expected to experience periodic stressful gas mixtures, since these smaller voids would have even less air exchange with the surface than does Bayliss Cave.

Adaptations to exploit environments with other than normal gas mixtures have evolved independently many times (Peakin and Josens 1978, Ghilarov 1983, Magnuson et al. 1983, Vannier 1983, Nicolas and Sillans 1989). The abnormally high concentrations of CO₂ and other decomposition gases in underground environments have been an important selection factor in the evolution of soil animals, including burrowing mammals (Nevo 1979, Vannier 1983). Nicolas and Sillans (1989) recently reviewed the effects of carbon dioxide on insects. Insects living under bark, in tree stumps, in animal dung, and in soil spend part of their life in 2–5% CO₂ or above without ill effect. Social insects with large colonies (bees, ants, termites) tolerate CO₂ concentrations up to 6% and many species alter their nest at concentrations above 2% (Peakin and Josens 1978, Nicolas and Sillans 1989). Soil insects, especially those in warm, moist soils, are

well adapted to CO₂ concentrations up to 3–5% and O₂ concentrations down to 10% (Ghilarov 1983), and some can tolerate CO₂ concentrations above 35% (Vannier 1983).

Magnuson et al. (1983) reported that the fish *Umbra limi* evolved facultative air-breathing to survive in winter-kill lakes. When dissolved oxygen is depleted beneath the ice of its lake habitat, the fish swallows floating trapped bubbles containing unusual gas concentrations. The fish were not harmed by bubbles containing 100% methane or 100% nitrogen and seemed to obtain sufficient oxygen if they had access to bubbles containing 2.5% O₂.

Recent surveys in other McBride Formation lava tubes, as well as in limestone caves in Thailand, indicate that the presence of humid foul air is often correlated with a community of troglobites (Howarth 1988*b*; Stone and Howarth, unpublished data). We predict that humid, bad-air caves elsewhere also will be found to harbor unique communities of obligate cave species, and, therefore, that biological surveys of bad-air caves will add significantly to our knowledge of the distribution, ecology, and evolution of troglobites, as well as provide a more complete view of the ecology of subterranean habitats. Research on the mechanisms of troglobitic adaptations to these stressful gas concentrations may also greatly improve our understanding of the physiology of respiration.

ACKNOWLEDGMENTS

We thank Brother N. Sullivan for coordinating the expedition; members of the Chillagoe Caving Club, especially D. Irvin, for outstanding logistic and field assistance; D. and L. Pinwill and J. Collins for permission to work on their stations and for logistic support; J. Bresnan, for field assistance; G. B. Monteith, V. Davies, S. Robson, E. C. Zimmerman, H. Hoch, L. M. Roth, R. Taylor, and M. Gray for identifications; and E. Ligus (Draeger, USA) for assistance in interpreting the gas data. N. C. Howarth, Bro. N. Sullivan, G. B. Monteith, D. Irvin, S. Robson, E. O.

Wilson, H. Hoch, M. Asche, C. Simon, and S. E. Miller reviewed and made helpful suggestions on the manuscript.

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