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BRITISH CAVE RESEARCH ASSOCIATION

TRANSACTIONS

Volume 7

Number 4

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Fish trap in Camburales Cave, Venezuela

Cave fauna in Venezuela

Scaling Poles

Anglesey Palaeokarst discussion

Solution erosion formula discussion

Cheddar conduit pulse wave experiment

BRITISH CAVE RESEARCH ASSOCIATION

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THE INVERTEBRATE FAUNA OF CAVES
OF THE SERRANIA DE SAN LUIS, EDO. FALCON, VENEZUELA

by Philip Chapman

ABSTRACT

95 cave-frequenting species are listed. The majority (82 species) are troglaphiles, but 9 terrestrial, and 2 aquatic species are considered to be troglobites. The fauna consists largely of guano scavengers (25 species) and detritivores (16 species) preyed on by a diverse collection of predators (43 species). The thirteen caves biologically studied are mainly high level "fossil" horizontal tunnels in limestones of Oligocene age, with evidence of intermittent flooding. The fauna is discussed in relation to other tropical cave faunas.

INTRODUCTION

The state of Falcon lies in the north-west of Venezuela, bounded to the north by the Caribbean and to the west by the oilfields of Lake Maracaibo. The state capital, Coro, lies in a 20 km wide desert strip fringing the sea. Looking south from Coro, the Serrania de San Luis appear as a long, green, cloud-strewn range of hills standing out in sharp contrast to the greys and browns of the surrounding desert scrub.

The Serrania consist largely of an upstanding block of limestone of Oligocene age, forming part of the San Luis formation (Liddle, 1928). To the north of the Serrania, in the plains between it and Coro, there is a series of younger Miocene sediments, mainly clastics. To the south of the Serrania older pelagic sediments of the Pauji formation are exposed. The San Luis limestone facies is a coralline limestone succession some 300 to 500 m thick, with small amounts of interbedded gritty limestone, shales, sandstones and ferruginous sandstones.

The structural relationships of the Serrania are fairly simple. There are west or southwest-trending fold axes, north or north-northeast-trending fault planes and a pattern of north-south and east-west joints well developed in regions of low dip. The Uria syncline is the major structural feature (Fig.1).

The principal feature in the Serrania is the totally enclosed basin containing the villages of San Joaquin de Uria and Curimagua, 31 sq Km in area below the 1080 m contour. This, the Curimagua valley, is bounded on all sides by high ridges and fault scarps, and its presence is largely due to the Uria syncline whose axis runs through it. The ridges are characterised by a "subdued" karst topography of solution-weathered limestone bedrock and boulders. On the undulating plateaux which lie between the high ridges bordering the basin, many large and deep dolines are formed and their development is at such a stage that a number of extensive uvalas can be observed.

A number of different types of caves are found in the Serrania, but those of the greatest biological interest are almost all of one type - large, fossil horizontal tunnels. These caves are generally between 5 and 15 m high with a single stratum roof. The passages vary from 5 to 50 m wide and are up to 1 km long. Their true floor is invariably hidden by boulders and thick mud, and often a small stream runs amongst these deposits. The cave tunnel always ends in an immense boulder ruckle, both upstream and downstream, these causing the backing up of water in wet periods. Caves such as el Burro, Camburales, Cuatro Vientos,

Zarraga, Coy-Coy de Uria and the resurgence caves of Hueque (especially Cuevas de Trinidad 1 and 2) typify this category. Often formed along the strike of the beds, the caves contain no pitches and slope only gently. The tunnel caves give the appearance of great age, being large and heavily calcited. Their passage shape and flow markings point to a phreatic development and most of them lie at a similar altitude (1000 m above sea level) on the flanks of the Curimagua valley at least 200 m above any known resurgence level. This suggests that they are remnants of what was once a huge interconnected phreas, since drained and divided by collapse and erosion.

The purpose of this paper is to present some of the biological results of fieldwork carried out in the caves of the Serrania by members of the 1973 "British Karst Research Expedition to Venezuela". In general, accidental cavernicoles are not mentioned unless judged to be of particular interest.

PREVIOUS STUDIES

The invertebrate cave fauna of Venezuela is poorly known. Pioneering work by de Bellard Pietri (1954, 1956, 1960) paved the way for a survey of the arthropod fauna of the Cueva del Guacharo (Monagas) by Bordon (1959) and by members of the Sociedad Cenezolana de Espeleologia (notably O. Linares). Strinati (1971) listed 14 species of cavernicoles known from Venezuela, 3 of these from the Serrania de San Luis. Over the last ten years, members of the S.V.E. have collected in a number of caves in the Serrania, but the only publications known to the author which deal with this material are recent descriptions of a troglaxene scorpion (Gonzalez, 1974), two troglophilic catopid beetles (Szymczakowski, 1975) and a troglobitic amblypygid (Ravelo, 1975).

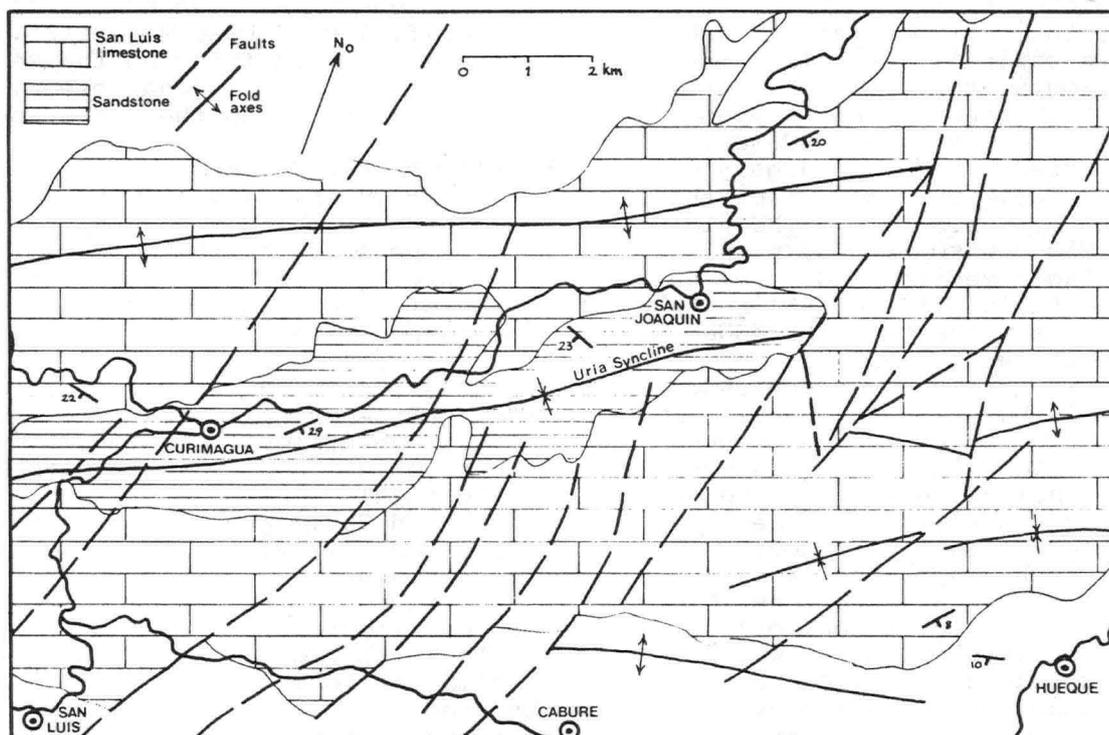


Fig. 1. The central part of the Serrania de San Luis showing the geology.

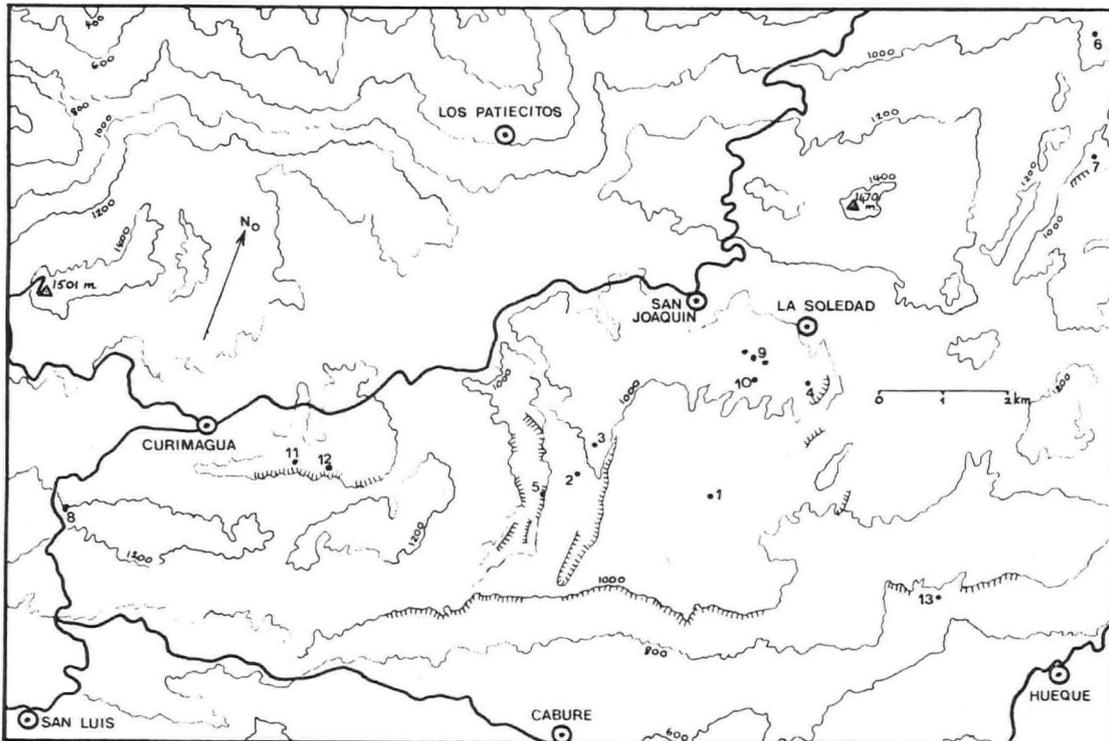


Fig. 2. The central part of the Serrania de San Luis showing locations of the caves (numbered as in text). Fine lines are 200m interval contours, heavy lines are metalled roads. Major cliffs are indicated by hatched lines.

DESCRIPTIONS OF CAVES AND THEIR FAUNAS

1. Cueva el Coy-Coy de Uria

Location: lat. $11^{\circ} 11' 12''$, long. $69^{\circ} 35' 58''$. Plan length 1,100 m. Depth 90 m.

Description. An impressive entrance slope leads via an awkward climb to the first guacharo-inhabited chamber, (Plate 1) which is a huge collapsed tunnel cave. A decorated section and short climb lead to the second, and largest, guacharo roost chamber. The cave continues via a large, block-strewn passage to a series of awkward climbs down through boulders. Eventually a vertical wall of calcite is reached and bypassed via a bedding to the left and tight vertical tube. The passage now becomes unstable and very collapsed and ends in a choke. There is an archaeological site (pre-columbian pottery) in the entrance doline.

Fauna. Coy-Coy is the only cave visited by the expedition which contained a breeding population of the guacharo or oilbird (*Steatornis caripensis* Humboldt). These birds forage for palm fruits which are carried back to the cave where the oily pericarp is digested and the large spheroidal seed is regurgitated. The oilbird colony in Coy-Coy is long established, as shown by the huge mounds of rotting seeds and seed remains, in places over 10 m deep. The main roosts are arranged along a series of inaccessible ledges high in the roof of the entrance chamber and in a second chamber 120 m into the cave. At the time of our visit the oilbird population was visually estimated at around 100 adults. However, it appears to vary greatly from year to year, for de Bellard, writing in 1957, estimated a population of 30 birds, while on a more recent visit members of the S.V.E. saw only two.

The liminal cavernicoles (i.e. animals which habitually frequent, and are

characteristic of the "twilight zone") include two notable predators - one a harvestman, the other a mygalomorph spider. *Santinezia albilineata* is a large, handsome gonyleptid harvestman (Plate 2) which is encountered in practically every cave entrance and limestone shaft visited by the expedition. It is most frequently seen on the damp walls and ceilings of passages. Feeding behaviour was not observed and it is hard to imagine what such a slow-moving predator is capable of catching. The entrance talus slopes of the cave are dotted with the dense, hammock-shaped webs of the mygalomorph, *Diplura soricina*. This spider is a talus slope specialist which waits for its prey to tumble off the adjacent boulders into its web.

The "active" seed beds (those beneath occupied oilbird roosts) are characterised by a rich community whose food base consists of regurgitated palm seeds and pericarp material together with oilbird faeces. Fresh seeds do not appear to be utilised by cavernicoles, but only by accidentals such as weevils and scolytid beetles. The scolytid, *Pagiocerus frontalis* (Fabricius), (S.L.Wood det.) is a pest which is carried into the cave inside palm seeds by the oilbirds. Living *P. frontalis* are uncommon in the cave, but their remains (usually legless carapaces) are often found in very large numbers inside decaying seeds, and probably form an important link in the food chain of the cavernicolous community. Nitidulid beetles (*Stelidota* sp.) continually roam about the seed bed until they encounter a patch of newly-dropped pericarp material where they congregate to feed. A number of detritivores are found in fairly well decomposed seeds. The most conspicuous of these are terrestrial isopods and campodeid *Diplura* (*Lepidocampa* (s.str.) *juradoi*), or small pink oligochaetes in the wetter areas. Collembola and small Acari are numerous but inconspicuous. The coprophiles include: a slender-spined, leaf-green-bodied gasteropod, the larvae of two tineid moths (*Tinea* sp. and *Amydria* sp.), terrestrial isopods, mites, and Diptera of the families Phoridae (*Conicera* (*Hypocerina*) sp. and *Megaselia* (s.str.) *scalaris*) and Empididae. All of these are preyed on by a formidable array of arthropod predators, including: several small symphytognathid spiders, an oonopid (*Dysderina* sp.), a caponiid (*Nops* sp.), a pholcid (*Priscula venezuelana*), and a ctenid (*Ctenus* ? *obscurus*), two phalangodid harvestmen (*Pellobunus camburalesi* and *Vima checkleyi*), three undescribed species of chernetid pseudoscorpions, a pselaphid beetle, two histerids (*Phelister* sp. and *Bacanius humicola*), a staphylinid (*Belonuchus* sp.) and a carabid (*Colpodes combayensis*). A parasitic tick (*Ixodes* ? *downsi*) is common on the seed bed in all stages from minute nymphs to adults. The smaller nymphs are probably an important prey of the pseudoscorpions. An undescribed species of omnivorous cave cricket (Rhophidophoridae) occurs throughout the cave and probably figures significantly as a predator or prey of most seed bed inhabitants at some stage of its life cycle.

Beyond the active seed beds, the cave continues to almost a kilometer as a large fossil phreatic tube. "Fossil" beds of powdery, well decomposed palm seeds indicate that the cave's oilbird population was once very much larger. There is little evidence of life in this remote region, except for the occasional cave cricket and campodeid dipluran in the damper, muddier areas. An unknown surface connexion probably exists at the far end of the cave, for here is found a large "fossil" seed bed on which an epigeal millipede (Oniscodesmidae) was taken. A small muddy passage leading from the terminal chamber is the home of a troglobitic phalangodid harvestman, *Vima chapmani* (Plate 3).

2. Cueva de Camburales

Location: lat. 11° 10' 00". long. 69° 37' 17". Plan length 780 m.

Description. At the bottom of the steep entrance slope a climb down through the calcited boulders leads to a large entrance passage. Left down a steep mud slope leads to a stream and a climb up in the roof to a collapsed rift and massive rubble pile. Right leads down to a stream passage, an easily bypassed duck and a series of large guano-filled chambers. The cave ends with a low canal passage and impenetrable choke.

Fauna. Camburales contains a large population of the bat *Pteronotus parnellii*.

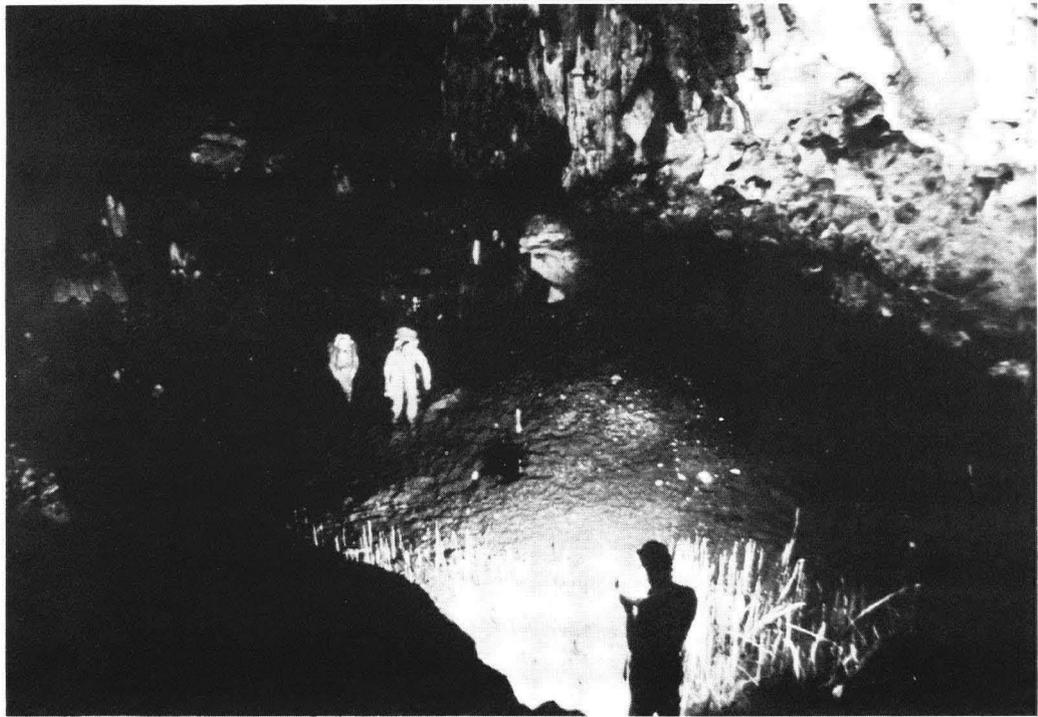


Plate 1. The entrance chamber of Cueva el Coy-Coy de Uria. The figures are climbing a mound of decomposing palm seeds introduced by roosting oilbirds. Such "seed beds" are the focus of a rich troglophile fauna.

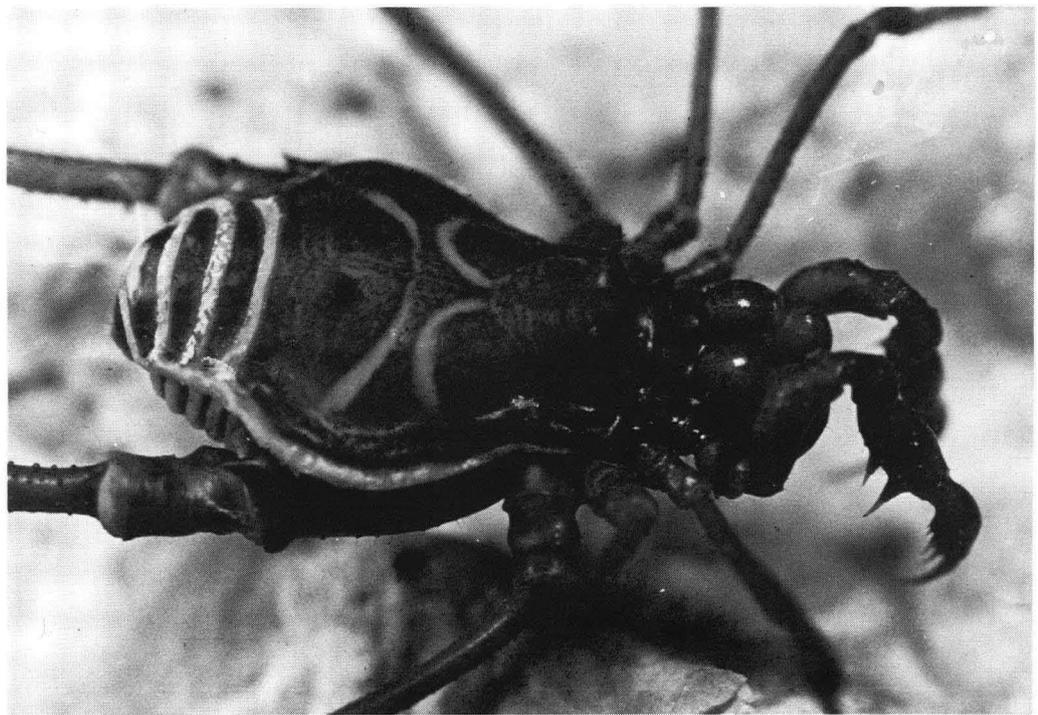


Plate 2. The large gonyleptid harvestman *Santinezia albilineata* is a conspicuous inhabitant of cave entrances throughout the Serrania.

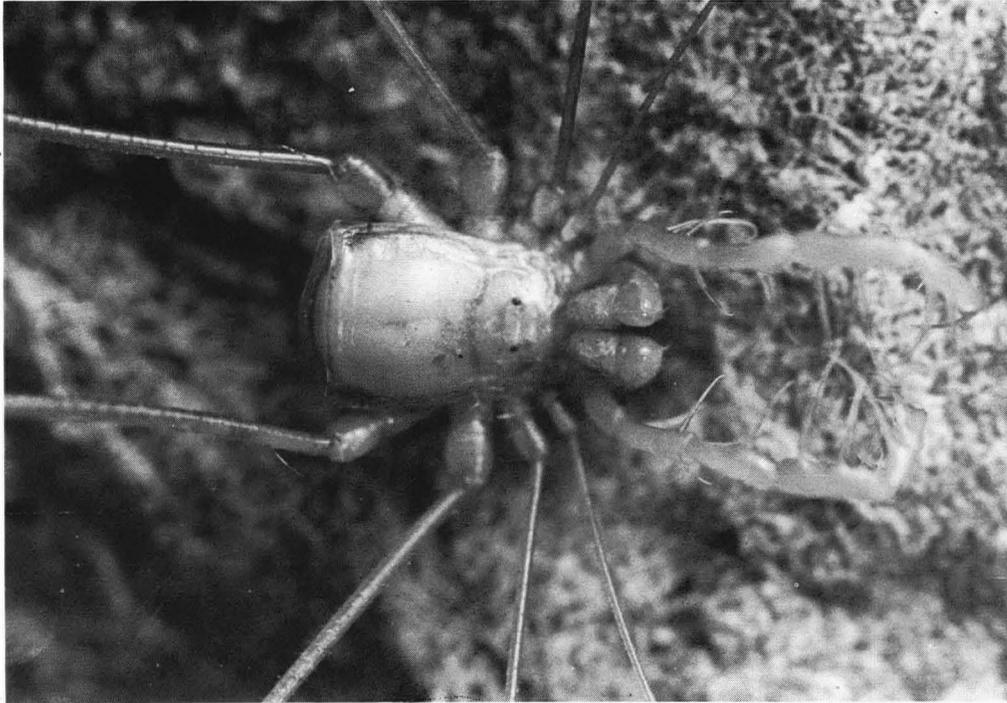


Plate 3. The phalangodid harvestman *Vima chapmani* is known from remote passages in three caves. It is largely depigmented, with reduced eyes and elongate appendages and is almost certainly a troglobite.



Plate 4. The large-eyed cricket (left) has pigmented eyes with c.200 corneal lenses per eye. The microphthalmic form (right) has largely depigmented eyes with c.60 corneal lenses per eye and extraordinarily long antennae (ratio antennal length: body length of 5.5). Both are from Cueva de Camburales which also contains a whole spectrum of intermediate forms.

The greatest density of roosting bats, and the greatest concentration of guano occur in a narrow passage containing a sluggish canal and christened the "bat sewer" due to its evil smell and almost unbearably high level of atmospheric CO₂ and NH₃. The guanobia in this passage are dominated by larvae of a tineid moth (*Tinea* sp.) present in concentrations as high as 200 per dm² on fresh guano. Adults are similarly plentiful. A catopid beetle (*Adelopsis brunneus orcinus*), several mites (including a dermanyssid, *?Hypoaspis* sp.), a phorid fly (*Conicera* (*Hypocerina*) sp.), a drosophilid, a psychodid, and a milichiid, complete the list of coprophages. These are preyed on by two chernetid pseudoscorpions (a *Lustrochernes* sp. and one undescribed genus). A cynipid wasp parasitises the tineid larvae. This association is common to all the guano patches in the final chamber. Other guano associated species have a more patchy distribution within the cave. These include at least three coprophages - a long-spined gasteropod, a terrestrial isopod, and a second catopid species, *Eucatops* nr. *glabricollis* ; one predator - a schizomid, *Schizomus* sp. and several guano scavengers or omnivores, including: three cydnid bugs (*Pangaeus piceatus*, *P. docilis* and *Amnestus* sp.), mites, Collombola, and an ant. The guano communities throughout the cave are subject to predation by two formidable, highly mobile predators - a scutigermorph centipede (*?Pselliodes* sp.) and an errant diplurid mygalomorph (Subfam. Ischnocolinae). As in Coy-Coy, a large cricket population is dispersed throughout the dark zone of the cave.

The stream in Camburales is shallow, sluggish and clear in low flow conditions, meandering through steep banks of sandy mud. Heavy rain causes spectacular flooding in the main chambers, resulting in removal of accumulated guano, and deposition of a rich organic mud. More frequent and less dramatic rises in the stream level result in deposition of vegetable detritus along the banks of the stream. This detritus supports a rich fauna, mostly of species judged to be accidental. However several troglophiles are found here, including: three polydesmoid millipeds - *Alcodesmus* sp. , *Lepturodesmus* sp. and a species of an unknown genus close to *Tunochilus*, and a phalangodid harvestman *Pellobunus camburalesi*.

The stream fauna is poor in species but abundant. There are two fish species - a synbranchid, *Synbranchus marmoratus*, and a catfish, *Trichomycterus knerii* Steindachner. The catfish is widespread in the local caves with different populations showing varying degrees of eye regression. The commonest stream inhabitants are white cyclopoid copepods (*Macrocyclops albidus*) which occur in particularly large numbers in the "bat sewer". There is also an omnivorous freshwater crab which is encountered on dry land almost as often as in the water. The only other common troglophile stream dweller is a gerrid water skater (*Brachymetra furva*), which scavenges on the water surface, probably feeding on the numerous tineid moths and other insect flotsam.

One of the more striking features of the cave ecosystem is the zoning of the dominant predator species. The entrance boulder slope is dominated by the web-spinning *Diplura soricina* which is gradually supplanted first by the large gonyleptid, *Santinezia albilineata*, then by the phalangodid, *Vima checkleyi*. The wetter parts of the cave and the guano beds are dominated by the errant mygalomorph spiders (subfamily Ischnocolinae), with some competition from the centipede, *?Pselliodes* sp. The more remote parts of the cave, where the only other inhabitants appear to be cave crickets, are inhabited by a troglobitic amblypygid *?Speleophrynus tronchonii*.

3. Cueva de los Cuatro Vientos.

Location: lat. 11° 11' 14". long. 69° 37' 10". Plan length 880 m.

Description. A draughting, low crawl entrance, followed by a clamber down boulders, leads to a large chamber which has mud banks on three sides. On the right is a tight inlet passage, and to the left, a low chamber containing attractive formations. Straight on is the main passage, an old phreatic tunnel 20 m high containing a stream flanked by large mud banks. 100 m upstream is a boulder pile covered with mud, marking the junction of two passages. To the left is a canal passage 200 m long; whilst on the right, the main stream flows over a series of gours. Upstream involves climbs up and down mud slopes until the cave ends in a mud choke.

Fauna. The fauna is similar to that of Cueva de Camburales, though far fewer

stream-borne accidentals are present. The cave community revolves around the bat guano ecosystem of the entrance chamber, where catopid beetles and larvae dominate rather than tineid moths as in Camburales. The dominant predators are zoned as in Camburales, and crickets are found throughout the cave. The catfish *Trichomycteris knerii* is very common in this cave. The ceilings of the lower, wetter passages are festooned with webs spun by the larvae of a mycetophilid fly.

4. Cueva del Burro.

Location: lat. 11° 12' 25". long. 69° 35' 48". Plan length 580 m.

Description. From the entrance below a small cliff a steep slope leads down to a boulder chamber where running water can be heard. A series of squeezes down through boulders leads to a large stream passage. Upstream is a large breakdown chamber, from which a high level passage takes off. After a low section on gravel, the cave ends in two sumps, one being a large flooded bedding plane.

Fauna. The fauna of the entrance chamber is similar to that of Camburales cave. Far fewer species are present in the stream passages due to the frequency of flooding. The dominant predators are zoned as in Camburales, and crickets, as always, are found throughout the cave. Mycetophilid larvae are abundant on the ceiling above the wide upstream sump. A large eyed fish (Cyprinidae) is common in the downstream sump.

5. Cueva de Zarraga.

Location: lat. 12° 10' 45". long. 69° 37' 30". Plan length 1,150 m.

Description. From the large entrance the cave drops steeply down a boulder slope into a chamber. To the left a well-decorated passage leads through to daylight again. To the right a complex series of low crawls lead to another entrance. Straight on, a climb over large boulders leads to a low level passage on the right hand side. An awkward route through boulders leads to a large muddy passage. A sharp left bend reveals a small vadose passage containing a stream. This runs at a low level and parallel to the main passage, linking with it occasionally. The main passage ends in a steep climb up an immense choke. The low level passage goes via a sump into a long and difficult draughting crawl through boulders, finally becoming too tight.

Fauna. There is no bat colony in this cave and the cavernicolous community therefore revolves around a few detritivores and the cavecricket. The dominant predators are zoned as in Camburales, but the errant mygalomorph (Ischnocolinae) is uncommon. The rare troglobitic phalangodid harvestman *Vima chapmani* occupies a similar niche to the troglobitic amblypygid *?Speleophrynus tronchonii* and is probably a predator on the younger, smaller crickets. This is the only cave in which cricket eggs were observed. They are relatively large and are laid singly in moist sand about 1 cm below the surface.

6. Cueva de Macuquita.

Location: lat. 11° 15' 52". long. 69° 34' 19". Plan length 320 m. Depth 115 m.

Description. This is a collapsed dip tube sink cave formed mainly in limestone and shale. The entrance is large and dips steeply north into a massive and dangerous boulder choke. Two obscure eight metre pitches through loose boulders lead down to a large passage. Here a side passage leads off, narrow at first, but soon opens into a large steeply descending passage which terminates in another boulder choke. This is the deepest point in the cave. The main passage continues down the bedding and leads to a large terminal chamber.

Fauna. The fauna is similar to that of Cueva de Zarraga and includes the troglobitic amblypygid *?Speleophrynus tronchonii*.

7. Cueva del Trueno.

Location: lat. $11^{\circ} 14' 47''$. long. $69^{\circ} 34' .04''$. Surveyed length 347 m. Depth 42 m.

Description. The cave is an active sink. The initial stream passage opens out after 80 m when it strikes a shale bed and a collapse chamber is developed. Beyond this boulder choke the passage continues low and wet at first, but soon develops into a rift. There follows a series of pools which are in sandstone beds, until again the cave opens out into a large passage 8 m high. After only another 40 m the way on is blocked by a collapse where the passage meets the shales.

Fauna. Not visited by the author, but D. Checkley reported a similar fauna to that of Cueva de Zarraga. The catfish *Trichomycterus knerii* is again present in the stream, and two troglobitic predators were taken - the amblypygid *?Speleophrynus tronchonii* and the harvestman *Vima chapmani*.

8. Cueva del Guarataro.

Location: lat. $11^{\circ} 09' 09''$. long. $69^{\circ} 41' 17''$. Plan length 640 m. Depth 305 m.

Description. The entrance is very impressive. The first pitch of 52 m lands on a small bridge spanning the shaft. The second drops a further 112 m to a boulder strewn floor. At the eastern end of this floor, and after a short climb up, the top of the 55 m third pitch is reached. A further 19 m pitch leads into a vadose passage containing a small stream which continues down to a 6 m drop into a larger streamway. This can be followed upstream to a large aven, or downstream via two more pitches and several short climbs to a terminal choke.

Fauna. The fauna consists largely of accidentals which enter the cave by two routes. The majority (gammarid amphipods, dytiscid beetles, trichopteran larvae) are washed in by the cave stream. Others such as millipedes, woodlice, frogs, snakes and a cosmetid harvestman have simply fallen in. Non-accidental cavernicoles are few in number. Apart from the inevitable cave crickets and phalangodid harvestmen, only two species of interest were collected. The first is a depigmented troglophile gammarid shrimp (*Hyaletta ?meinerti*) which inhabits a large pool in the main passage of the cave. The second is a small, eyeless, white and possibly troglobitic trichopolydesmid millipede which was taken on the ceiling of the terminal chamber of the cave.

9. Cuevas Casas de Piedras.

Location: lat. $11^{\circ} 12' 25''$. long. $69^{\circ} 36' 17''$. Plan length 350 m.

Description. There are three casas. The first has a low entrance followed by a large passage which breaks out into an enclosed deroofed chamber. The stream continues through the second casa for 60 m then comes out into daylight again before sinking beneath a cliff and entering the third casa. In the collapse area between the first and second casas three passages lead off to the right. Several entrances in the cliff face lead into the smaller passage of the third casa, which ends in a sump. Just above the sump the exit leads out to a small resurgence pool. This system follows the strike of the beds through a small ridge for the first and second casas, while the third runs up-dip.

Fauna. There are few species of interest. The large gonyleptid harvestman *Santinezia albilineata* is very common, together with the scutigermorph centipede, *?Pselliodes* sp.. There are numerous crabs and cyprinid fishes in the stream and especially in the sump of the third casa. The cyprinid fishes are also found in Cueva del Burro, which receives the water from this stream.

10. Cueva de la Madame.

Location: lat. $11^{\circ} 12' 13''$. long. $69^{\circ} 36' 06''$. Plan length 320 m. Depth 50 m.

Description. The entrance pitch of 24 m leads into a large, superbly decorated chamber 85 m long by 20 m wide. At the southern end of the chamber a 55° mud slope leads to a vertical drop of 11 m into a lower passage which is well decorated and picturesque upstream. Downstream a narrow muddy trench leads

to a mud choke. At the eastern end of the large chamber another pitch of 20 m can be descended into a further series of passages. This is an old collapsed system largely of phreatic origin, which has now become well calcited and stabilized.

Fauna. An interesting cave in that the only inhabitants appear to be largely depigmented and microphthalmic cave crickets. (Plate 4).

11. Cueva de Trapichito (Sumidero de Trapichito).

Location: lat. 11° 09' 13". long. 69° 39' 22".

Description. A 5 m drop between sharp boulders leads to about 30 m of mostly tight joint-controlled passage with two small chambers. This cave is the sink for a small but highly flood prone stream.

Fauna. Consists largely of guanobia and accidentals. The guanobia inhabiting the apex of the guano mound below the main roost of the bat, *Carollia perspicillata*, were quantitatively sampled, and hence rather more attention was paid to the mites and Collembola than in the other caves discussed herein. At least two collembolan species, six species of mites, a tick, six species of Diptera, a ctenid spider and a staphylinid beetle were sorted from a sample equivalent to an area of 0.001 m² of guano surface and 4 cm depth. Quantitatively this represented a density of 460,000 macroscopic arthropods per m². The cave is most notable for the apparent absence of the cave cricket.

12. Cueva de Chasea.

Location: lat. 11° 10' 18". long. 69° 38' 55". Plan length 24 m.

Description. A four metre crawl leads to a chamber containing bat guano.

Fauna. The fauna is similar to that of Cueva de Trapichito; but with two additions - a green-bodied, slender-spined guanobious gasteropod, and a white guanobious terrestrial isopod. In contrast to these two species, all of the guanobious species inhabiting Cueva de Trapichito are highly mobile during some stage of the life cycle. This would suggest that the absence of the above two species and of the cave cricket in the sink cave is a result of regular flooding.

13. Cueva de Trinidad No. 4 (Hueque cave).

Location: lat. 11° 11' 00". long. 69° 33' 58". Plan length 450 m.

Description. From the entrance chamber, two parallel vadose stream passages lead to a sump chamber. Just before this chamber, a phreatic maze leads off to the right. Also from the entrance chamber, a passage leads off left to a well decorated chamber. There are four other caves to the west at the base of the same cliff.

Fauna. Not visited by the author, but three troglobitic species were collected here in 1956 by Nino Sanfilippo. They are a dytiscid beetle *Trogloguignotus concii*), a talitrid amphipod (*Hyalella anophthalma*), and an eubellid terrestrial isopod (*Neosanfilippia venezuelana*).

FAUNAL LIST

This list of non-accidental macroscopic invertebrates includes the collections we made in 1973 and all previous and subsequent collections known to the author through literature references. The terms liminal cavernicole, troglaxene, troglophile and troglobite are tentatively used to indicate probable levels of ecological restriction to caves, and are defined below:

1. Liminal cavernicoles habitually frequent and can maintain permanent populations in the 'twilight zone' of cave entrances. The term 'liminal' is introduced here as a replacement for the inapt 'parietal' which is unfortunately in current use.

2. Troglonexes habitually frequent caves but must leave the cave for part of their life cycle (e.g. to feed or to mate).
3. Troglaphiles can maintain permanent populations in caves as well as in non-cave habitats.
4. Troglobites are limited to caves. In practice 'cave limitation' is almost impossible to verify, especially in regions where the epigean fauna is poorly known. Thus cavernicoles are not usually accorded troglobite status unless they show morphological evidence of a prolonged subterranean evolution (e.g. highly regressed eyes, depigmentation, etc.). This poses special problems in tropical caves (see Discussion).

PHYLUM ANNELIDA

Class Oligochaeta

Family undetermined

1 - 4 Gen. et spp. indet. (4 species)

1. Cueva de Camburales. 2. Cueva de Zarraga. Both from damp clay with largely decomposed patches of flood-deposited detritus. 3. Cueva el Coy-Coy de Uria, from wet decaying palm seed debris. 4. Cueva de Trapichito, from fresh bat guano. All troglaphiles, detritivores.

PHYLUM ARTHROPODA

Class Crustacea

Order Eucopepoda

Family Cyclopidae

5. *Macrocyclops albidus* (Jurine), A. A. Weaver det. Cueva de Camburales, from a slow-flowing muddy canal receiving large quantities of bat guano. This is a cosmopolitan species found in a wide variety of aquatic habitats including: rivers, estuaries, alpine lakes, wells, springs and cave streams. It has been recorded from a number of caves both in Central America (Weaver, pers. comm.) and Mexico (Pearse and Wilson, 1938). Troglaphile, detritivore.

Order Amphipoda

Family Talitridae

6. *Hyalella* prob. *H. meinerti* Stebbing. J. H. Stock det. Cueva del Guarataro, from a sandy pool containing much vegetable detritus and which is isolated except during severe floods. This is a depigmented population of an epigean species. Troglaphile, detritivore.
7. *Hyalella anophthalma* Ruffo, 1957. Hueque cave ("Cueva de Rio Gueque"). Described from a gravid female taken in "Cueva de Rio Gueque" by Nino Sanfilippo in 1956. From the locality data this is almost certainly the "Cueva de Trinidad No. 4" (Hueque cave). Troglobite, detritivore.

Order Isopoda

Family Eubellidae

8. *Neosanfilippia venezuelana* Brian, 1957. Hueque cave ("Cueva de Rio Gueque"). Described from 15 females, 6 males and 4 imm. taken by Nino Sanfilippo in 1956. Troglobite, detritivore.

Family undetermined.

9 - 12. Gen. et spp. indet. (4 species).

- 9, 10. Cueva el Coy-Coy de Uria, on decomposing palm seeds. ?Troglaphiles, detritivores. 11. A white, eyeless species taken on oilbird faeces, Cueva el Coy-Coy de Uria. 12. A white, eyeless species taken on bat guano in Cueva de Camburales and Cueva de Chasea. ?Troglobites, guano scavengers.

Order Decapoda

Family undetermined.

13. Gen. et sp. indet.

- Cueva del Burro, Cueva de Camburales, Cuevas Casas de Piedras, Cueva de los Cuatro Vientos, Cueva del Trueno, Cueva de Zarraga. This crab is found in

practically every cave stream in the Serrania and is also occasionally encountered in sheltered epigeal habitats (e.g. talus in the bottom of dolines). Troglophile, omnivore.

Class Arachnida

Order Scorpionidea

Family Buthidae

14. *Tityus falconensis* Gonzalez, 1974.

Described from males taken in Hueque Cave by O. Ravelo in 1971.

(?) Troglophile, predator.

Order Pseudoscorpionidea

Family Chernetidae, W. B. Muchmore det.

15 - 17. Gen. et spp. nov.? (3 species).

Cueva de Camburales, one female of 15. Cueva el Coy-Coy de Uria, several males and females of 15 and 16 and one male of 17. All taken on decomposing palm seeds. Troglophiles, predators.

18. ?*Lustrochernes* sp. W. B. Muchmore det.

Cueva de Camburales, several males, one female. Taken on bat guano.

L. argentinus (Thorell) has been taken in the Cueva de Guacharo, Monagas state, Venezuela (Beier, 1968). Troglophile, predator.

Order Schizomida

Family Schizomidae

19. *Schizomus* sp. nov. in the *brasiliensis* gp., J. M. Rowland det.

Cueva de Camburales, several females taken on damp bat guano.

Troglophile, predator.

Order Amblypygi

Family Charontidae

20. ?*Speleophrynus tronchonii* Ravelo, 1975. P. Chapman det.

Cueva del Burro, Cueva de Camburales, Cueva de los Cuatro Vientos, Cueva de Macuquita, Cueva del Trueno, Cueva de Zarraga. All taken on damp sticky mud, usually close to a cave stream. This is a pale species with reduced, probably non-functional eyes. *S. tronchonii* is described from 8 adults taken in Cueva 2 del Rio Hueque (very close to Cueva de Trinidad No. 4) by O. Linares and O. Ravelo (Ravelo, 1975). The stream in Cueva del Burro connects with the resurgence of the Rio Hueque, and it is probable that all of the above-mentioned caves are remnants of a formerly interconnected phreatic system. This species is almost certainly a predator on the cave cricket. Troglobite, predator.

Order Araneae

Family Dipluridae

21. *Diplura soricina* Simon, Schiapelli and Pikelin det.

Cueva del Burro, Cueva de Camburales, Cueva el Coy-Coy de Uria, Cueva de Zarraga. Cave entrance talus slopes. Twilight zone only. Liminal, predator.

22. Gen. et sp. indet. (Subfamily Ischnocolinae), Schiapelli and Pikelin det.

Cueva del Burro, Cueva de Camburales, Cueva de los Cuatro Vientos, Cueva de Zarraga. Numerous females, no mature males taken. Confined to the dark zone and common on damp mud banks and guano beds, never far from a stream. Almost certainly a predator on the cave cricket. This species is parasitised by a fungus, *Cordyceps* sp., near *arachneicola* Kobayasi (B. L. Brady det.). Troglophile, predator.

Family Ctenidae

23. *Ctenus* sp. (perhaps *obscurus* (Keyserling) = *Oligoctenus obscurus* Bonnet)

V.R.D. von Eickstedt det.

Cueva el Cou-Coy de Uria. Associated with the decomposing palm seeds.

Troglophile, predator.

24. *Ancylometes* sp. Berktau, V.R.D. von Eickstedt det.

Cueva de Zarraga, floor of entrance chamber. This species is sometimes placed in fam. Pisauridae (subfam. Thalassiinae). Troglophile, predator.

Family Pholcidae.

25. *?Priscula venezuelana* Simon, P. M. Brignoli prelim. det.
Cueva de Camburales, Cueva el Coy-Coy de Uria, Cueva del Guarataro,
Cueva de Zarraga. Troglophile, predator.

Family Oonopidae

26. *Dysderina* sp., P. M. Brignoli det.
Cueva el Coy-Coy de Uria, one male from decomposing palm seeds.
?Troglophile, predator.

Family Caponiidae

27. *Nops* sp., P. M. Brignoli det.
Cueva el Coy-Coy de Uria, one female. ?Troglophile, predator.

Family Argiopidae (Araneidae)

28. *Wendilgarda* sp., M. Hubert det.
Cueva Encanto de Lugo. This genus is also known from Cueva de la Azulita
(Cueva del Pirata), Edo. Merida, Venezuela, and from a Mexican cave
(Archer, 1953). Troglophile, predator.

Family Symphytognathidae, H. W. Levi det.

29. Gen. et spp. indet.
Cueva el Coy-Coy de Uria, taken in both guacharo roost chambers and
in the terminal choke. Troglophile, predator.

Order Opiliones

Family Gonyleptidae

30. *Santinezia albilineata* Roewer, M. Rambla det.
Cueva del Burro, Cueva de Camburales, Cueva el Coy-Coy de Uria,
Cueva de los Cuatro Vientos, Cueva del Guarataro, Cueva de Macuquita,
Cuevas Casas de Pedras, Cueva de Zarraga and many shafts and small
collapsed cave entrances. Twilight zone. Liminal, predator.

Family Phalangodidae

31. *Cynortina tuberculata* (Goodnight) M. Rambla det.
Cueva de Macuquita, one female. The related troglophile *C. goodnighti*
and the troglobite *C. pecki* (Rambla, 1969) are known from caves in
Jamaica. Troglophile, predator.
32. *Pellobunus camburalesi* Rambla, 1978.
Cueva de Camburales (type locality), one male (type), one female.
Cueva el Coy-Coy de Uria, one male, one female. Associated with damp
decomposing palm seeds. Troglophile, predator.
33. *Vima chapmani* Rambla 1978.
Cueva del Trueno (type locality) one male (type). Cueva el Coy-Coy
de Uria, one female. Cueva de Zarraga, one imm. All taken in remote
passages having little apparent energy input. Troglobite, predator.
34. *Vima checkleyi* Rambla 1978.
Cueva el Coy-Coy de Uria (type locality), Cueva del Burro, Cueva de
Camburales, Cueva de los Cuatro Vientos, Cueva del Guarataro,
Cueva de Zarraga. Twilight and dark zones. Troglophile, predator.

Order Acari

Family Ixodidae

35. *Ixodes ?downsi* Kohls, K. H. Hyatt det.
Cueva el Coy-Coy de Uria, males, females, larvae. Taken on decomposing
palm seeds below oilbird roosts. The only other potential host in this
cave is a small rodent (probably *Heteromys anomalus*, C. Naranjo, pers.
comm.). *I. downsi* was described from a cave in Trinidad where the
original host is not known either although bats (at least four species),
oilbirds and a rat were present in the cave. It seems most probable
that the host in Coy-Coy cave is the oilbird *Steatornis caripensis*.

Family Acaridae

36. *Rhizoglyphus* sp., K. Hyatt det.
Cueva de Trapichito, taken on bat guano. Troglophile, guano scavenger.

Family Ascidae, K. H. Hyatt det.

37. Gen. et sp. indet.
Cueva de Trapichito, taken on bat guano. Troglophile, guano scavenger.

Family Dermanyssidae

38. ?*Hypoaspis* sp., K. H. Hyatt det.

Cueva de Trapichito, taken on bat guano. Troglophile, guano scavenger.

39. ?*Hypoaspis* sp., K. H. Hyatt det.

Cueva de Camburales, one female. Cueva el Coy-Coy de Uria, two females.

Troglophile, guano scavenger.

Family Macrochelidae

40. *Macrocheles mexicanus* Evans and Hyatt, K. H. Hyatt det.

Cueva de Trapichito, taken on bat guano. Described originally from a coprid beetle from Mexico. Troglophile, predator.

41. *Macrocheles muscaedomesticae* (Scopoli) (or very close), K. H. Hyatt det.

Cueva de Trapichito, taken on bat guano. This is a cosmopolitan species and there are other species very similar to it that are widely distributed and are found in dung, associated with flies, etc. Troglophile, predator.

Family Uropodidae, K. H. Hyatt det.

42. Gen. et sp. indet.

Cueva de Trapichito, taken on bat guano. Troglophile, Guano scavenger.

Family Trombididae

43. ?*Neotrombidium* sp., K. H. Hyatt det.

Cueva de Camburales, taken on bat guano. Troglophile, predator.

Family indet. (Mesostigmata), K. H. Hyatt det.

44. Gen. et sp. indet.

Cueva el Coy-Coy de Uria, one female. Taken on a harvestman, *Vima checkleyi* Rambla. ?Troglomite, ?ectoparasite.

Class Chilopoda

Order Scutigermorpha

Family Scutigeridae

45. ?*Pseliodes* sp., A. A. Weaver det.

Cueva del Burro, Cueva de Camburales, Cueva de los Cuatro Vientos, Cueva de Trapichito, Cuevas Casas de Piedras, Cueva de Zarraga.

Commonly found in damp muddy passages and on guano beds. An epigeal species also encountered in houses. Troglophile, predator.

Order Geophilomorpha

Family Geophilidae, A. A. Weaver det.

46, 47. Gen. et spp. indet. (2 species).

46. Cueva el Coy-Coy de Uria, taken in wet decaying palm seed debris.

47. Cueva de Camburales, taken in deep, fine cracks in damp clay.

Both species have strikingly lobed posterior legs. Trogliphiles, predator.

Class Diplopoda

Order Polydesmoidea

Family Chelodesmidae

48. *Alcodesmus* sp. nov.?, R. L. Hoffman det.

Cueva de Camburales, one female. Taken on vegetable detritus close to stream. Troglophile, detritivore.

49. ?*Lepturodesmus* sp., R. L. Hoffman det.

Cueva de Camburales, two immatures. Taken on vegetable detritus close to stream. Troglophile, detritivore.

50. Gen. et sp. nov. (close to *Tunochilus*), R. L. Hoffman det.

Cueva de Camburales. Taken on vegetable detritus close to stream.

Troglophile, detritivore.

51. *Trichomorpha* sp., R. L. Hoffman det.

Cueva de Zarraga, females and immatures. Taken on the muddy ceiling and walls above the sump pool. Troglophile, detritivore.

Family Trichopolydesmidae

52. Gen. et sp. nov.?, R. L. Hoffman det.

Cueva del Guarataro, two immatures. Taken on finely triturated detritus on the roof of the low terminal chamber. A depigmented, delicate species.

Morphology and habitat suggest it is a troglobite. If so, it is the first known tropical troglobite of its family, although a few are known in the U.S.A. ?Troglomite, detritivore.

Class Diplura

Order Diplura

Family Campodeidae

53. *Lepidocampa* (s.str.) *juradoi* cf. *seclusa* Condé, 1960. B. Condé det. Cueva el Coy-Coy de Uria, two damaged specimens. Taken from a bed of largely decomposed palm seeds, 1100m. from the entrance, but occur widely throughout the cave. *L.juradoi* was described from Oropuche Oilbird Cave, Trinidad from decaying seed humus. *S.seclusa* is known from Santa Cruz, Galapagos Islands. Condé's suggestion of a close relationship between the two species is based on the position of a sensilla of the third antennal segment (Condé, 1976). ?Troglobite, detritivore.

Class Protura

Order Protura

Family indet.

54. Gen. et sp. indet.

Cueva el Coy-Coy de Uria, taken in decomposing palm seeds. Troglophile, detritivore.

Class Collembola

Order Collembola

Family indet.

55 - 58. Gen. et spp. indet. (4 species).

55, 56. Cueva el Coy-Coy de Uria, taken in decomposing palm seeds.

57, 58. Cueva de Trapichito, taken on bat guano. Troglophiles, guano scavengers / omnivores.

Class Insecta

Order Orthoptera

Family Rhabdophoridae

59. Gen. et sp. indet.

All caves except Cueva de Chasea, Casas de Piedras and Trapichito. This ubiquitous "species" has an extremely variable morphology ranging from a very pale, microphthalmic type to a deeply pigmented, large-eyed type (Plate 4). I would tentatively suggest that two subspecies are represented, with hybridization occurring in some caves. In general the microphthalmic type is found in regions of low food availability, whereas the macrophthalmic type is more abundant where food is plentiful. The macrophthalmic subspecies is probably a troglaxene. The microphthalmic subspecies is probably troglobitic. Both are omnivorous.

Order Dermaptera

Family Labiidae

60. *Marava chapmani* Steinmann, 1979.

Cueva el Coy-Coy de Uria. Taken on decomposing palm seeds. *M.chapmani*'s closest relative is *M.triquetra* which is known from Mexico (and probably also occurs in Honduras, Guatemala and Panama) (Steinmann, 1977). Troglophile, omnivore.

Order Hemiptera

Family Gerridae

61. *Brachymetra furva* Drake, R. C. Froeschner det.

Cueva de Camburales, on stream surface. Troglophile, predator.

Family Cydnidae

62. *Pangaeus docilis* (Walker), R. C. Froeschner det.

Cueva de Camburales. One adult taken from guano/ vegetable detritus, close to stream. This species has been reported from Chilibrillo cave, Panama (Froeschner, 1960) and from Mexican caves (Peck, 1971). It is distributed in non-cave habitats from Guatemala to Peru and Brazil (Froeschner, 1960). Troglophile, omnivore.

63. *Pangaeus piceatus* Stal, R. C. Froeschner det.

Cueva de Camburales. Three adults taken from guano/ vegetable detritus, close to stream. This species has also been reported from the caves of Yucatan, Mexico (Pearse, 1938). Troglophile, omnivore.

64. *Amnestus* sp. nov., R. C. Froeschner det.
Cueva de Camburales. Nine adults taken on bat guano. Several members of this genus have been reported as frequenting caves: in Jamaica (Peck, 1975); in Panama (*A. subferrugineus* see Peck, 1971); and in Guatemala (Froeschner, 1960). Troglophile, guano scavenger.

Order Coleoptera

Family Catopidae

65. *Eucatops* near *glabricollis* Reiteer, S. B. Peck det.
Cueva de Camburales, taken on bat guano throughout the cave. Troglophile, guano scavenger.

66. *Adelopsis brunneus orcinus* Szymczakowski, 1975.

(*Adelopsis* near *linaresi* Szymczakowski, S. B. Peck det.)

Cueva de Camburales, taken on bat guano throughout the cave. Subsequent to the determination by S. B. Peck, Szymczakowski (1975) has revised the status of his species *A. linaresi* (described from Cueva del Guacharo, Monagas state, Venezuela), making it a subspecies of Jeannel's *A. brunneus*: *linaresi*. In the same paper, 2 new subspecies of *A. brunneus* (*orcinus* and *azzalii*) are described from caves in the Serrania de San Luis. *A. brunneus orcinus* is described from 3 males and 1 female taken in Cueva de Camburales by C. Bordon Azzali. My earlier collection from the same cave (determined by S. B. Peck) almost certainly represents the same subspecies. Troglophile, guano scavenger.

67. *Adelopsis brunneus azzalii* Szymczakowski, 1975.

Described from 4 males taken in Cueva de Hueque (Cueva 1) on frugivorous bat guano by C. Bordon Azzali in 1971. Troglophile, guano scavenger.

Family Carabidae

68. *Pachyteles* sp. nov.?. P. M. Hammond det.
Cueva de Camburales. One specimen taken on vegetable detritus close to stream. Troglophile, predator.

69. *Colpodes combayensis* Goud, P. M. Hammond det.
Cueva el Coy-Coy de Uria. Commonly taken on, or close to, areas of decomposing palm seeds. The related *C. cavicola* is known only from St. Claire cave, Jamaica. Like *C. combayensis*, *C. cavicola* shows no cave specializations (Darlington, 1964). Troglophile, predator.

Family Staphylinidae

70. *Belonuchus* sp., P. M. Hammond det.
Cueva el Coy-Coy de Uria. Taken on decomposing palm seeds. One *Belonuchus* (nr. *moquinus*) is widespread in Mexican caves (Reddell 1966, 1967, 1967a). Troglophile, scavenger.

71. Gen. et sp. nov.? (somewhat annectent between the genera *Cryptobium* and *Opithes*), P. M. Hammond det.

Cueva de Camburales. One lightly pigmented specimen taken on bat guano close to the stream. Troglophile, guano scavenger.

72. *Philonthus* sp. (probably *P. serpens* Sharp), P. M. Hammond det.

Cueva de Trapichito, taken on bat guano, Troglophile, guano scavenger.

Family Histeridae

73. *Phelister* sp., Commonwealth Inst. Entomol. det.
Cueva el Coy-Coy de Uria. Taken in great numbers inside decomposing palm seeds. May prey on the numerous Collembola and mites which inhabit these seeds, or even perhaps on the scolytid beetles whose remains are also commonly found inside the decaying seeds. Troglophile, predator.

74. *Bacanius humicola* Mars, Commonwealth Inst. Entomology det.

Cueva el Coy-Coy de Uria. Two adults taken in decomposing palm seeds. Troglophile, predator.

Family Nitidulidae

75. *Stelidota* sp., Commonwealth Inst. Entomol. det.
Cueva el Coy-Coy de Uria. Taken in large numbers on patches of the bright yellow pericarp material which is regurgitated by oilbirds during flight as a defence against intruders. Troglophile, herbivore.

Family Pselaphidae

76. Gen. et sp. indet.

Cueva el Coy-Coy de Uria, one adult taken on decomposing palm seeds.
? Troglophile, predator.

Family Dytiscidae

77. *Trogloguignotus concii* Sanfilippo 1958.

Described from specimens taken in "Cueva de Rio Gueque" (Hueque cave) by Nino Sanfilippo in 1956. Troglobite (phreatobite), predator.

Order Lepidoptera

Family Tineidae

78. *Tinea* sp., D. R. Davis det.

Cueva el Coy-Coy de Uria. Taken on decomposing palm seeds. Cueva de Camburales. Taken on bat guano. Troglophile, guano scavenger

79. *Amydria* sp., D. R. Davis det.

Cueva el Coy-Coy de Uria. Taken on decomposing palm seeds. Troglophile, guano scavenger.

Order Diptera

Family Phoridae

80. *Conicera*(*Hypocerina*) sp., A. Pires do Prado det.

Cueva el Coy-Coy de Uria, Cueva de Camburales, Cueva de los Cuatro Vientos. A total of 133 females were trapped, but no males were taken. This may be due to the use of ripe banana as bait. Ten species are described in the subgenus *Hypocerina* Malloch : 4 from Europe; 1 from Burma; 2 from U.S.A. and 3 from West Indies and Brazil. Troglophile, guano scavenger.

81. *Megaselia* (s.str.) *scalaris* (Loew), A. Pires do Prado det.

Cueva el Coy-Coy de Uria, one male. Cueva de Trapichito, 38 males, 41 females hatched from pupae taken from guano of the bat *Carollia perspicillata*. This is a near cosmopolitan species. Troglophile, guano scavenger.

82. *Dohrniphora cornuta* (Bigot), A. Pires do Prado det.

Cueva de Trapichito, two males and one female hatched from pupae taken from guano of the bat *Carollia perspicillata*. This is a cosmopolitan species. Troglophile, guano scavenger.

Family Empididae, A. Pires do Prado det.

83. Gen. et sp. indet.

Cueva el Coy-Coy de Uria, one female. Troglophile, guano scavenger.

Family Drosophilidae, A. Pires do Prado det.

84. Gen. et sp. indet.

Cueva de Camburales, eleven males, females. Cueva de los Cuatro Vientos, eighteen males, females. Troglophile, guano scavenger.

85. Gen. et sp. indet.

Cueva de Trapichito, two males. Troglophile, guano scavenger.

Family Psychodidae, A. Pires do Prado det.

86. Gen. et sp. indet.

Cueva de Camburales, one male, one female. Troglophile, guano scavenger.

Family Milichiidae, A. Pires do Prado det.

87. Gen. et sp. indet.

Cueva de Camburales, one female. Troglophile, guano scavenger.

Family Chloropidae, A. Pires do Prado det.

88. Gen. et sp. indet.

Cueva de Trapichito, one female. Troglophile, guano scavenger.

Family Muscidae, A. Pires do Prado det.

89. Gen. et sp. indet.

Cueva de Trapichito, one female. Troglophile, guano scavenger.

Family Mycetophilidae

90. Gen. et sp. indet. (perhaps *Orfelina* sp.)

Cueva de Camburales. Mycetophilid larvae, probably of the same species,

occur in : Cueva del Burro, Cueva de Camburales, Cueva de los Cuatro Vientos, Cueva del Guarataro,, Cueva de Zarraga. The larvae are found on ceilings, usually above water. Their characteristic webs consist of a horizontal network from which are hung vertical threads 5-10 cm. long, beaded with sticky droplets which trap small flying insects. Troglophile, predator.

Order Hymenoptera

Family Cynipidae

91, 92. Gen. et spp. indet.

Cueva de Camburales, taken on bat guano. Two species of parasitic wasps with long ovipositors, yellow and black banded abdomens. Almost certainly parasites of larvae of the tineid moth, *Tinea* sp. Troglophiles, predators.

Family Formicidae

93. Gen. et sp. indet.

Cueva de Camburales. Taken in an area of sandy mud containing decomposing leaves and twigs close to stream. Troglophile, omnivore.

PHYLUM MOLLUSCA

Class Gasteropoda

Order Stylommatophora

Family undetermined

94. Gen. et sp. indet.

Cueva el Coy-Coy de Uria. Taken on wet mush of decomposing palm seeds. This is a slender spired gasteropod snail with a translucent shell and delicate leaf green body. Troglophile, guano scavenger?

95. Gen. et sp. indet.

Cueva de Chasea. Taken on bat guano. Similar to 9 but with a longer-spired shell. Troglophile, guano scavenger.

DISCUSSION

A total of 95 species of non-accidental macroscopic invertebrates has been collected in caves of the Serrania de San Luis. Of these only 40 are known by species name or are recognised as being new species. This reflects the chaotic situation of the taxonomy and/or lack of specialists for many groups.

Table 1. Ecological dependency upon caves of the invertebrate species known from caves in the Serrania de San Luis, Edo. Falcon, Venezuela.

Class	Liminals	Trogloxenes	Troglophiles	Troglobites
Oligochaeta			4	
Custacea			5	4
Arachnida	2		25	3
Chilopoda			3	
Diplopoda			4	1
Diplura				1
Protura			1	
Collembola			4	
Insecta		*1	34	*2
Gasteropoda			2	
Totals	<u>2</u>	<u>1</u>	<u>82</u>	<u>11</u>

* crickets are treated as separate troglonexic and troglobitic subspecies.

Table 1 evaluates the ecological cave-specialisation of the 95 species listed above. As used here, the categories are subjective due to inadequate data on the life histories and cave dependency of the species. The data show a preponderance (86%) of troglophiles, with 11% troglobites and 3% troglonexes and liminals. The "troglonexene" category is seldom applicable to invertebrates

inhabiting tropical caves. Only the "macrophthalmic type" of cave crickets are considered to be possible troglloxenes, perhaps leaving the cave at night to feed on green vegetation. The gonyleptid harvestman and diplurid spider are just two of the more conspicuous members of a rich liminal fauna which was not studied in any detail. The 11 species considered to be troglobitic comprise a gammarid amphipod, 3 terrestrial isopods, a diplopod, a campodeid dipluran, a dytiscid beetle, a cricket, an amblypygid, a phalangodid harvestman and a ?parasitic mite. Of these, 9 species are terrestrial and 4 are predators.

Other tropical cave faunas have generally been found to consist largely of troglaphiles, with predatory and terrestrial troglobites being particularly poorly represented (Vandel, 1965; Mitchell, 1969). Examples of such cave faunas in the Caribbean area are those of Panama and Puerto Rico. Peck (1971) listed 67 invertebrate species known from Chilibrillo Cave, Panama. Of these, 60 were troglaphiles and only 3 doubtful terrestrial troglobites. Again, Peck (1974) listed 78 invertebrate species known from the cave of Puerto Rico. Of these, 70 are troglaphiles, with just a single terrestrial troglobite species.

This pattern has prompted much theoretical speculation among biospeleologists. Mitchell (1969) suggested that terrestrial troglobites are unlikely to occur frequently in tropical caves for two principal reasons. Firstly, because the climatic changes associated with the Pleistocene glaciations (which initiated troglobite evolution in temperate zones by removing the epigeal populations of the troglaphile progenitors of present day troglobites) had little effect in lowland tropical or subtropical regions. Secondly, because the generally high energy input into tropical caves lessens selection pressure for features leading to energy economy, and consequently results in a slower rate of troglobite evolution than in the generally energy poor temperate caves. The first argument is weakened by recent evidence which suggests that the lowland tropics did in fact experience profound ecological effects from the alternation of glacial and interglacial stages throughout the Pleistocene (Moreau, 1966; Haffer, 1969). The second argument depends on the debateable premise that troglobite characteristics are adaptive in energy economy (see e.g. Barr, 1968). However, even if this premise is accepted, the argument is largely irrelevant, because such energy-economising adaptations only occur in species which are already cave-limited. A slow rate of troglobite evolution can only produce less adapted troglobites, not fewer troglobites. This poses a problem of how to recognise tropical troglobites, which, although cave-limited, may not possess all the "regressive" features (depigmentation, anophthalmia, etc.) by which most temperate zone troglobites are recognised.

The cavernicolous fauna of the Sierra de San Luis departs from the typical pattern expected in tropical caves in that 9 out of 11 known troglobites are terrestrial species. However, some other recent studies have uncovered far more surprising faunas in tropical caves. Peck (1975) listed 26 troglobites known from Jamaican caves, of which 19 are terrestrial and 17 are predators. Chapman (1976) listed 17 troglobites known from a single cave in Papua New Guinea of which 12 are terrestrial and 8 are predators. A similarly rich troglobitic fauna is known from Cuban caves, although there are fewer terrestrial, and more freshwater species (Orghidan et al. 1973; Taboada, 1974).

In the present state of our knowledge about tropical caves it is probably safest to interpret the development of cave faunas in individual regions by reference to local speleogenesis, and climatic and ecological history. Geomorphological evidence suggests that the tunnel caves of the Serrania are of contemporary origin and were drained rapidly by uplift of the limestone by the early-to-middle Pleistocene. This would have opened up an extensive cave biotope to colonization by a terrestrial troglaphile fauna not unlike the present one. Climatic fluctuations during the Pleistocene initiated troglobite evolution which has produced the few known present day terrestrial troglobites. At least two of these (the amblypygid and the cricket) are widespread and successful.

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THE DESIGN OF SCALING POLES

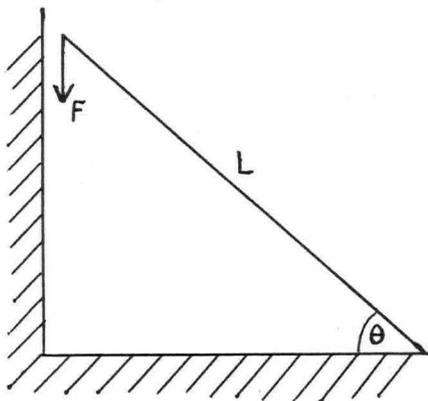
by J. S. Davis

Various covers in the past have used mechanical aids for gaining height in cave exploration, but whether these aids have been designed with safety in mind is debatable. However, the subject is worthy of discussion at the present time with the increase in technical interest in the sport.

The conventional method of bolting can be substantially improved upon in suitable circumstances by the use of a scaling pole, which at first sight seems a very simple piece of equipment. However, the stresses to which a scaling pole may be subjected are far greater than might be expected, with a high risk of failure likely. Consequently, careful design is required to ensure confident safety margins, which as will be seen are very difficult to ensure.

A scaling pole may fail in one of two ways; (1) by bending and (2) by buckling.

In both calculations the top of the pole is able to move on a frictionless wall.



(1) Failure by bending:

for bending the governing equation is (Gordon 1968) :-

$$\sigma_{\max} = \frac{My}{I}$$

where $M = F \cos\theta =$ bending moment

$F =$ load (mass)

$\theta =$ angle of inclination of the pole to the horizontal

$\sigma_{\max} =$ tensile strength of the material (0.2% proof stress)

$y =$ distance (at which maximum stress occurs) from the neutral axis of the section, which for a circular section is equal to the radius i.e. $d/2$

$I =$ second moment of the area of the section and for a solid circular section

$$= \frac{\pi d^4}{64}$$

and for a tube

$$= \frac{\pi(d_2^4 - d_1^4)}{64}$$

d_2 = outside diameter

d_1 = inside diameter

π = 3.142

This equation may be rearranged to give the maximum permissible load, F_{\max} bending, to which a scaling pole could be subjected before failing by bending.

$$F_{\max} \text{ bending} = \frac{\sigma_{\max} (d_2^4 - d_1^4)}{\cos \theta \cdot L \cdot d_2 \cdot 32}$$

where L is the length of the pole.

The angle of inclination θ has an important relationship with F_{\max} bending. As θ increases (i.e. the pole becomes more vertical) F_{\max} increases since $\cos \theta$ decreases, so that failure by bending is a minimum when $\theta = 90^\circ$ when the pole is vertical.

(2) Failure by buckling:

For buckling the equation (Gordon 1978) is governed by the Euler buckling formula which is

$$\text{buckling moment} = F \sin \theta = \frac{\pi^3 E (d_2^4 - d_1^4)}{256 \cdot L^2}$$

where F = load

θ = angle of inclination of the pole to the horizontal

π = 3.142

E = Young's modulus for the material

d_2 = outside diameter of the tube

d_1 = inside diameter of the tube

L = length of the pole

This equation can also be rearranged to give the maximum permissible load (F_{\max} buckling) to which a scaling pole could be subjected before failure by buckling.

$$F_{\max} \text{ buckling} = \frac{\pi^3 E (d_2^4 - d_1^4)}{256 \cdot \sin \theta \cdot L^2}$$

The angle of inclination θ has an important relationship with F_{\max} buckling. As θ increases, $\sin \theta$ increases and therefore F_{\max} buckling decreases, so that as the pole becomes more vertical it is more likely to fail.

It is now clear that the angle of inclination is a very important variable and will have an optimum value for each particular scaling pole.

TABLE I: Relationship between tube length, diameter, wall thickness, mass and maximum bending and buckling loads.

Tube size O.D. (ins.) Tube size I.D. (ins.) Tube gauge ($d_2^4 - d_1^4$) (ins.)	Values of F_{max} for failure by bending and buckling (lbs)									
	bend buckle	bend buckle	buckle	bend buckle	buckle	bend buckle	buckle	bend buckle	buckle	bend buckle
1.906	2.500	2.813	3.000	3.250	4.24	7.41	13.07	12.96	15.20	
1.730	2.372	2.650	2.872	3.122						
7	10	8	10	10						
30	40.0	65.6	69.8	87.4	123.2	136.8	122.1	127.3	143.2	137.9
25	57.6	78.7	100.5	104.9	177.4	164.2	175.8	152.8	206.2	165.5
20	90.0	98.5	157.0	131.1	277.2	205.3	274.7	191.0	322.2	206.9
15	160.0	131.0	279.5	174.4	492.8	273.0	488.4	254.0	572.8	275.2
Mass of poles (lbs)										
30	33.73	33.60	46.86	40.50	44.10					
25	28.13	28.00	39.05	33.75	36.75					
20	22.50	22.40	31.24	27.50	29.40					
15	16.88	16.80	23.43	20.25	22.05					
Mass/unit length of pole (lb/ft)	1.125	1.120	1.502	1.350	1.470					

N.B. The masses of poles do not take overlap of sections into account because this is dependent on the choice of section length.

The optimum value of θ can be derived as follows when
 $F_{\max} \text{ bending} \cdot \cos\theta = F_{\max} \text{ buckling} \cdot \sin\theta$

$$\text{i.e. } \tan\theta = \frac{F_{\max} \text{ bending}}{F_{\max} \text{ buckling}}$$

$$\theta = \tan^{-1} \left(\frac{F_{\max} \text{ bending}}{F_{\max} \text{ buckling}} \right)$$

This relationship is important in relating optimum operating angle and load on the scaling pole.

The above equations can be used to calculate the bending and buckling stresses for poles of different diameter, wall thickness, length and material. However, two important factors should be considered since the use is for caving - (i) weight and (ii) durability.

Possible materials for scaling poles are mild steel, aluminium, duraluminium, stainless steel and titanium. The last three can be eliminated due to lack of availability and/or cost, thus leaving mild steel and aluminium. Aluminium was chosen because of density, availability in overlapping sizes and relatively good resistance to wear and tear. The relative calculations for aluminium poles are shown below in table form. Sizes are imperial as materials are available in this form.

Calculations are based on:

0.2% proof stress (σ_{\max}) for the aluminium alloy

HT30 = 16.5 ton/sq.in.

and Young's modulus (E) = 4500 ton/sq.in.

Values of F_{\max} for bending and buckling have been calculated for respective values of $\cos\theta = 1$ and $\sin\theta = 1$, which represent the worst possible case for failure.

In order to verify the buckling load, a 2ft. length of 2.5 inches outside diameter 10 gauge aluminium tube (HT30 alloy) was tested in a Dennison testing machine (courtesy of Leeds University Mining & Minerals Engineering Department). The tube failed when a load of 8 tons was reached. This was within 5% of the predicted failure load.

The conclusions from the laboratory test and theoretical calculations are that a safety factor in design is not easily attainable where the weight and length of pole are important. Consequently, a compromise between weight of pole, length of pole and weight of caver (+ equipment!) is necessary, erring hopefully in the direction of safety.

In reality, a pole needs to be at least 20-25 ft. long, so that design needs to be kept within the boxed section shown in the table.

The ULSA scaling pole is 25ft. long and is made from a mixture of 3 inches and 3.25 inches 10 gauge HT30TF aluminium tube designed with 9 inches overlapping of sections.

The importance of the angle of inclination has already been shown theoretically, but has not been included in the table because it would complicate it too much. Its effect is shown below in Table II for the ULSA pole.

TABLE II : Relationship between optimum angle of operation θ and maximum permissible load F_{\max} at θ

Length of pole (ft.)	F_{\max} bending (lbs)	F_{\max} buckling (lbs)	θ	F_{\max} at θ (lbs)
30	122.1	127.3	43°48'	176.4
25	175.8	152.8	49°00'	232.9
20	274.7	191.0	55°11'	334.6
15	488.4	254.0	62°31'	550.6

θ can be calculated from the values of F_{\max} bending and buckling and can then be used to obtain a value of F_{\max} at θ which is the maximum load at the optimum value of θ where the risk of failure due to bending or buckling is the same. Values of loads can of course be calculated for any value of θ , but these have no real meaning in terms of safety.

The conclusion from this is that there is an optimum angle at which to operate a pole to obtain the maximum safety margin. In terms of the ULSA pole, an angle of 49° for a 25ft. length with a caver weighing less than 16 stone (224 lbs) would result in use within the calculated safety margin giving a height achievement of 18.9 ft. per bolt (+ reach of caver which may be 5 ft. giving a total of about 24 ft. per bolt). Allowance for the weight of the pole should be included in the total load on the pole. Opinions from cavers who have used scaling poles of different designs is that greater heights can be achieved without failure. This may be true due to the load support provided by the wall and friction of different types of limestone (which has been regarded as friction-less in the theory), but a quantitative evaluation would be irresponsible. The calculations used are based upon sound theory and illustrate the narrow margins of safety which are encountered with scaling poles.

In conclusion, the design of scaling poles is important in order to provide some safety margin, but it should be understood that these are very narrow and nowhere near standards such as those required in civil engineering construction where a safety factor of 6x is quite normal.

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COMMENTS ON LEIF ENGH'S QUESTION

'CAN WE DETERMINE SOLUTIONAL EROSION BY A SIMPLE FORMULA?'

by John Gunn

Engh (1980) has rightly drawn attention to one of the errors in the paper by Lang (1977) in that the formula which Lang provides could not produce the curve shown in his diagram. However, in plotting two points from Sweden on this diagram and then computing a new formula for Lang's curve, Engh has neglected a number of other errors in Lang's paper :

(1) Lang does not indicate how the trend curve was derived and it may well have been fitted by eye.

(2) Lang (1977, p.282) claims that the data used to construct the diagram in question "were collected by ... Dr. D. Balazs from many karstic regions of the world; and some of my own data have been added". However, the position of certain points on the diagram does not correspond to the values given by Balazs (1976). Moreover, the sampling method (1 sample per site) and analytical technique (titration of a 5 ml sample) of Balazs (1976) and, by inference, of Lang (1977), together with their use of the Corbel (1957) formula render the results obtained almost meaningless. As Engh (1980) rightly states the only reliable estimates of solutional erosion are those derived by the hydrochemical method and even here large errors may result (Williams and Dowling, 1979; Gunn, 1981a).

(3) Solutional erosion rates are controlled by water chemistry and runoff so that any attempt to relate world-wide karstic denudation to rainfall without taking into account variations in evapotranspiration must be rejected on logical grounds.

These points are dealt with in greater detail elsewhere (Gunn, 1981b) and it is concluded that for other workers to "put their values of solutional erosion on to the same diagram as Lang" (Engh, 1980, p.32) would be a pointless exercise.

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DISCUSSION OF "PALAEOKARST PHENOMENA IN THE CARBONIFEROUS LIMESTONE
OF ANGLESEY, NORTH WALES", BY D. J. BAUGHEN AND P. T. WALSH

by T. C. Atkinson

The description of sandstone-filled pipes forming palaeokarst surfaces within the Carboniferous Limestone of Anglesey is an important addition to the palaeokarst literature. Baughen and Walsh leave little room for doubt that these features were formed by solution beneath a cover of sand which has been let down by settlement into the growing pipe cavity, the whole process taking place not long after deposition and lithification of the host limestone. The purpose of this note is to suggest a mechanism for the origin of these features.

The shape of the pipes, and the fact that they are sometimes inclined to the vertical, suggests that they formed where groundwater seepage rose steeply or vertically up through the limestone and into the overlying sandstone. The sedimentary features of the sandstone suggest that it was not more than a few tens of centimetres thick except in the pipes themselves, and that its upper surface formed the sea bed. Groundwater flow lines in the limestone would converge upon incipient pipes, leading to greater solutional erosion of the pipe head and growth in an upstream direction along the flow lines. Cave formation in this way was suggested long ago by Rhoades and Sinacori (1941). Few examples of such groundwater exit caves have been reported, however, because diffusely flowing groundwaters in limestones are normally saturated or supersaturated with calcite, and thus solution of the aquifer at the groundwater outflow is impossible. Seepage of groundwater into the sea provides a suitable environment for corrosion, however, because of the possibility of mixing between groundwater and sea water.

Plummer (1975) and Wigley and Plummer (1976) have studied the theoretical behaviour of mixtures of sea water with carbonate groundwaters. In Figure 1 (redrawn from Wigley's and Plummer's Fig. 3) the effect is shown of mixing waters saturated with respect to calcite with different proportions of sea water. If the partial pressure of CO_2 (PCO_2) of the fresh water is 10^{-2} atm (Sample 1), then mixtures containing between 1% and 73% seawater are undersaturated with calcite, even though both groundwater and seawater were initially saturated or supersaturated. For PCO_2 of 10^{-3} atm (Sample 2) mixtures of 1 - 21% seawater are undersaturated.

The sedimentary environment of the Anglesey pipes, in which limestone was overlain by an unconsolidated sand, provides an ideal environment for gradual mixing between seawater and groundwater seeping upwards from the limestone. Provided that the sand was thin and more permeable than the limestone, mixing could take place gradually within the sand layer which would impede flow away from the limestone surface and ensure sufficient contact time for solution to occur. Pipe growth could be expected to begin in local depressions in the sea floor, into which groundwater flow lines would be locally directed, leading to slightly enhanced rates of solution. Once initiated, a pipe would be self-perpetuating as flow lines would be diverted towards it, ensuring that it remained a locus of solution (Fig. 2).

Two corollaries of this proposed mechanism are as follows. First, a thin sand layer is an essential requirement. Where it is not present, the mixing of groundwater with sea water will be rapid with seawater present in great excess and no potential for solution will result. Secondly, as the proportion of seawater in the mixture increases, supersaturation occurs first with dolomite, then with calcite. Thus, there is the possibility that dolomite might be deposited either as euhedral crystals or as fine-grained cement in the sand layer (see shaded quadrant on Fig. 1). This is not necessarily a very likely outcome, as precipitation of dolomite may be inhibited by kinetic or nucleation factors. However, positive

identification of dolomite in minor amounts in the sand layer could be regarded as confirming the hypothesis of pipe origin proposed here.

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REPLY by D. J. Baughen and P. T. Walsh

The Authors are grateful to Dr. Atkinson for drawing their attention to the work of Plummer and Wigley. They find Dr. Atkinson's hypothesis very attractive and, if correct, it obviously neatly explains how sedimentation of the sandy cover and solution of the host limestone could have been interactive processes.

Nonetheless, the Authors are still perplexed that, whereas the piped sandstone Palaeokarsts in the Anglesey Carboniferous Limestone were manifestly strongly developed (the palaeokarsts reported are exposure-dependent and undoubtedly other horizons were also formed there), similar phenomena are so poorly developed elsewhere. One might have considered that the presence of an artesian groundwater flow emerging as submarine seepage through a layer of quartz sand was not so unusual both in time and space. Why was Anglesey so favoured in this respect? Future workers might well address themselves to this problem.

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DETERMINATION OF THE CHARACTER OF THE LONGWOOD SINKS
TO CHEDDAR RESURGENCE CONDUIT USING AN ARTIFICIAL PULSE WAVE

by P.L. Smart & P. Hodge

In May 1978 a pulse wave test was conducted at Bristol Waterworks Charterhouse source, at the head of the Longwood Valley. The test was primarily for Bristol Waterworks to assess the effect of the pumps at Charterhouse shutting down and releasing spring water into the swallet stream entering the August/Longwood Cave System. The pulse also allowed the phreatic volume of the Longwood to Cheddar conduit to be determined.

The water at Charterhouse is derived primarily from the Lower Limestone Shales where it is abstracted by pumpsets in a deep spring chamber. Some water is also collected from springs in the Old Red Sandstone. The water is pumped to supply the areas of Shipham, Yoxter, Charterhouse and Blagdon. This source is important because it yields a large volume (up to 4 Ml/d) of good quality water at a high elevation (reducing pumping costs). Originally the springs would have contributed to the swallet stream entering the August/Longwood Cave System. The depleted flow in this stream is now maintained mainly from higher springs in the Old Red Sandstone and from throughflow on the Blackdown slopes. However, in common with the other Blackdown streams there is a rapid and flashy response to rainfall due to the development of saturation overland flow on the wet peats and a corresponding increase in the channel depth.

The Geography Department liaise with Bristol Waterworks on a regular basis, and it was as a result of a Department gauging station downstream of the Charterhouse sources that a sub-surface leakage of water from the spring chamber became apparent. When Bristol Waterworks pumps were shut-off increases in the discharge of the swallet stream were noted which were independent of rainfall and often in a regular pattern. This water was not in fact recorded by the official Bristol Waterworks overflow gauge. Historically the pumpsets rarely shut off; however, work was being carried out to improve the treatment system at the Station and as a consequence, more frequent and irregular shut-downs could occur. These may cause sudden increases in the volumes of water entering August/Longwood and could therefore cause problems to cavers. In fact, apocryphal accounts of flash floods in the cave with not a cloud in the sky may relate to occasional previous stoppages of the pumps.

THE TEST PROCEDURE

The test was carried out on 23rd May, 1978. At this time there was insufficient water in excess of supply requirements at the spring to provide a flood wave. However, west of Charterhouse there is a Bristol Waterworks borehole in the Lower Limestone Shales. This is not generally used because it degrades the spring. The borehole pump was, however, pressed into service to provide an increment of about 4 Ml/d for one hour in the discharge of the swallet stream.

In order to assess the effects within the cave system and to gauge the pulse in the Lower Longwood streamway, a party of U.B.S.S. cavers were stationed below the junction with Tributary Passage near the climb to the Oxbows. At the Cheddar resurgence the Department gauging station behind the Cliff Hotel was constricted to increase sensitivity and the Geography students monitored the First and Second Feeders and the standing water level in Sayes Hole. An Automatic water sampler was installed on the lake outflow at Cheddar to take samples every 2 hours for tracer dye analysis.

The borehole pump was switched on at 12.30 providing 35.0 l/sec, the discharge at the Department gauging station upstream of the Longwood Sink increasing from 3.1 to 31.7 l/sec in a period of minutes (Fig. 1) (Note, the errors in discharge measurement are probably between 5 and 10%). At 12.45 408 ml of 20% Rhodamine WT solution were injected at the gauging station. Most of the pulse bypassed the Longwood Entrance blockhouse and sank at the timbered flood sink as a spectacular pink cascade. The pump switched off at 13.30 and discharge at the sink returned to its previous level by 14.00.

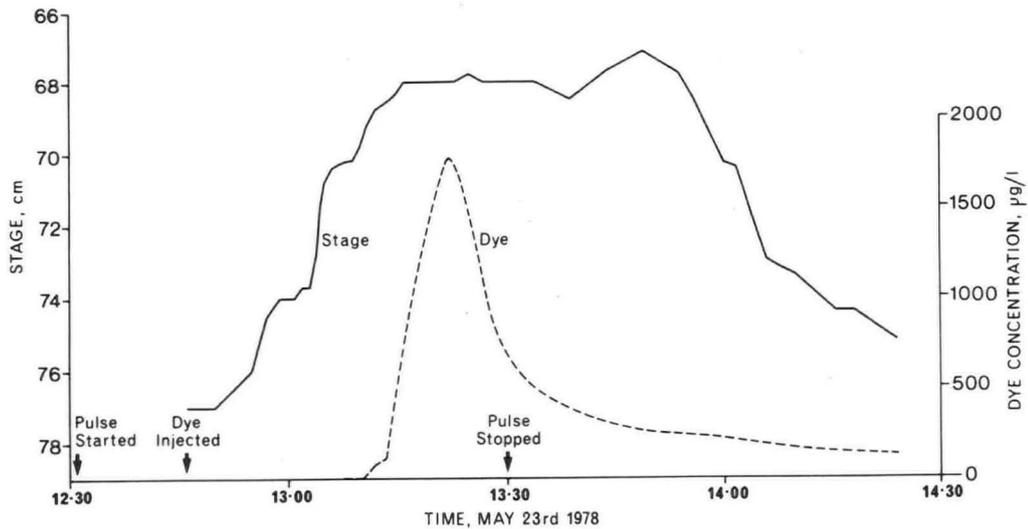


Fig.1 Stage and Dye Concentration at the Lower Streamway Sampling Site; Longwood Swallet

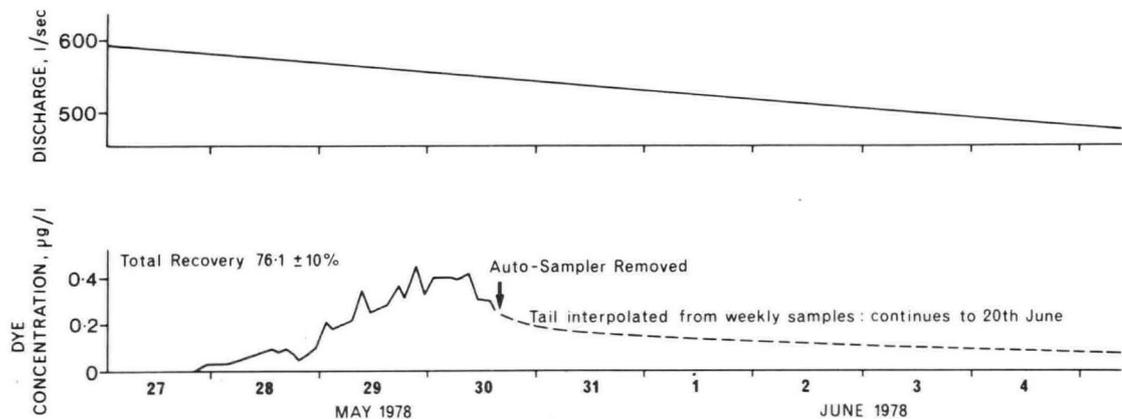


Fig.2 Discharge and Dye Concentration at Cheddar Resurgence

The pulse rapidly passed through the cave system and was detected in the Streamway by the Oxbow at 12.50 (Fig.1). The stage (water depth) increased to a plateau at +0.09m by 13.15. However, after starting to decline at 13.40, the water level rose again to +0.10m at 13.50, before falling exponentially to +0.02m at the end of observations. Tracer concentrations in the pulse at the cave sampling site rose gradually from 13.08 and then steeply to a sharp peak at 13.22 before declining rapidly to yield a very long tail. There was a minor shoulder on the tail at 13.55 following the previously mentioned increase in stage.

At Cheddar observations were continued until 22.30 on 23rd May. No evidence of the arrival of the pulse was detected either in these observations or on the stage recorder during the following weeks. However, dye was detected in the water samples commencing 20.35 27th May (Fig.2). Concentrations increased via a shoulder on the 27th to a plateau by 0.00 on the 30th continuing until the automatic sampler failed during the afternoon of 30th May. Dye was still present in hand samples until 20th June, 1978. Dye recovery was 76.09g + 10% (compared to 81.6g injected) and can be considered complete.

The week prior to the pulse test Bristol Waterworks had test pumped the Charterhouse borehole, discharging pumped outflow into the swallet. A step test commencing 7.00 on 16th May and ending at 19.00 caused a very small stage rise at Cheddar between 12.00 and 14.00 and a fall between 0.00 and 5.00 on 17th May. While on the 18th the pumps were started at 8.00 and switched off at 20.30 resulting in an increase at Cheddar at 12.30 and a decrease at 1.00. The stage increments at Cheddar were less than 0.005m and are consequently at the limit of detection of the installed water level recorder (Munroe IH 109). However, the delay is remarkably consistent between the tests varying between 4.5 and 5.0 hours.

RESULTS

1. The Pulse in the Cave

The pulse was transmitted rapidly through the cave system, as would be expected given the high gradients involved. It was transmitted more rapidly than was the dye (based on first arrival times) as kinematic waves travel faster than the water which produces them. The double form of the wave suggests that there were two major routes through the cave with different travel times. As the Showerbath was dry the slower route may be via the upstream series from the sinks just above the access path to Longwood.

Using the area under the time/concentration curve and the dye mass injected the discharge in the lower streamway can be calculated. It was 38.5 l/sec compared to 31.7 l/sec determined from the swallet gauging station. Some additional inputs may therefore be present, perhaps from leakage upstream of the highest known sink (as indicated by the 3 l/sec difference between the gauging structures) or through the Lower Limestone Shales.

2. The Pulse at Cheddar

The very long dye travel time to Cheddar is of interest. The first arrival travel time was 87 hours, compared to the Mendip Karst Hydrology Project spore travel time of 20 hrs. carried out under high discharge conditions. It is clear that very large differences in travel time between high and low flows will be of considerable importance for the prediction of swallet pollution at springs. The shape of the pulse is very flat indicating considerable dispersion of the input dye pulse. In this test part of this flattening is due to the short duration of the pulse, as can be seen by the presence of a significant tail on the dye curve for the cave sampling site. A second reason for this could be that the total volume of the conduit includes considerable dead space short-circuited by the main flow path. Dispersion into this volume attenuates the dye peak, but the slow release of dye from this temporary storage maintains the dye concentration in the spring. It is intriguing to speculate on the nature of this storage - does it represent solutionally enlarged fissures adjoining the conduit, or merely a large cross-sectional tube with solution pockets? It is even possible that it could be a series of free air surface channels separated by deep large volume sump pools, such as we already know for part of Wookey Hole.

The pulse wave helps in our interpretation here because if there was a significant vadose section in the Longwood to Cheddar conduit the pulse would be only marginally faster than the dye in arriving. This is clearly not the case, the pulse taking only 4.5 to 5 hours to arrive, equivalent to a dye travel time of about 5.50 to 6.25 hours. However, this delay must represent vadose passage otherwise pulse transmission would be instantaneous. If we obtain an estimate of velocity for the stream passage we can determine the amount of vadose passage beyond the Longwood sampling point. The velocity from injection site to the Oxbow's sampling site was 533.5 m/hour using the time to peak of the dye pulse (this is a better estimate of mean travel time than time of first arrival and is used here instead of the pulse centroid because of the unsteady discharge conditions which were partially responsible for the dye tail). The cave continues to fall steeply to an estimated 157m depth and the travel time for this 100m length will thus be about 10 minutes, giving a total mean dye travel time of 47 minutes to the end of the cave. The gradient from here to Cheddar is 0.0118 (using the straight line distance) and, assuming the velocity is proportional to the square root of slope (from the Manning equation) this would give an estimated vadose velocity at this gradient of 95.4m/hour. This estimate is higher than that calculated for the pool sampling site in the cave (using cross sectional area and discharge) of 4.9m/hour, but is greater than the mean travel time to Cheddar of 16.3m/hour (using the dye peak). It is therefore probably a correct order of magnitude figure.

Now given the 5.5 to 6.25 hour lag at Cheddar and subtracting the travel time to the known end of the cave, the length of vadose streamway may be determined as between 453 and 525m. If we now guesstimate that cave passages are twice the straight line distances point to point only some 9% of the conduit to Cheddar is air-filled. The simplest form for this vadose/phreatic ratio would be exactly the sort of thing found in Swildons Streamway and Wookey Hole - a looping tube with the tops of some loops cut off by vadose trenches - Swildons luckily is more vadose than phreatic whereas Wookey is more phreatic, and similar to Longwood.

What sort of passage size does the phreatic segment represent ? As the pulse wave is transmitted instantaneously in the flooded sections, whereas the dye takes the average travel time of the water, the volume of water discharged between arrival of pulse and dye equals the volume of the conduit. Unfortunately we do not know whether the Longwood conduit feeds directly to Cheddar without junctions, or whether the whole of the Cheddar discharge passes through the Longwood conduit. Clearly these are extreme cases and the true volume may be calculated using some intermediate discharge. The Cheddar and Longwood discharges are 590 and 3 l/sec respectively, giving volumes, using 99 hour difference between pulse and dye first arrivals, of $2.10 \times 10^5 \text{ m}^3$ and $1.07 \times 10^3 \text{ m}^3$. These correspond to straight line conduits of 9.98 and 0.72m in diameter. As the Goughs Cave/Long Hole/Great Oones conduits are about half the diameter calculated, then the underground conduit may well be twice the straight line length. The abandoned Longwood conduits are, if anything, larger than the calculated volume, perhaps an indication of the reduction in Longwood flows since the start of abstraction. It is important to remember, however, that conduit diameter is also controlled by the duration of active solution, not just discharge.

CONCLUSIONS

The test showed that the initial vadose movement of water in the swallet caves of the Mendips is very rapid due to the steep gradients. However, much lower velocities are observed in the lower gradient downstream segments leading to the resurgence. The delay in the arrival of the flood pulse at Cheddar indicates that only about 11% of the conduit beyond the known end of August/Longwood Cave is vadose, although this estimate depends strongly on the vadose velocities present in these lower gradient segments. The volume of the Longwood to Cheddar conduit may be estimated within rather wide limits from the results of the test, the figures from Cheddar flows indicating that conduit lengths may well be about twice the straight line sink to rising distance.

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