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The Trinidad Cave Ant *Erebomyrma*
(=*Spelaeomyrmex*) *urichi* (Wheeler),
With a Comment on
Cavernicolous Ants in General

BY EDWARD O. WILSON

THE TRINIDAD CAVE ANT *EREBOMYRMA*
(= *SPELAEOMYRMEX*) *URICHI* (WHEELER), WITH
A COMMENT ON CAVERNICOLOUS ANTS
IN GENERAL*

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In 1922 W. M. Wheeler described a new pheidologetonine ant, *Spelaeomyrmex urichi*, which he regarded as allied to *Erebomyrma* but sufficiently removed to justify the erection of a separate genus. The eleven syntypes, all minor workers, were collected in "Guacharo Cave," Trinidad, occupied by the oil-bird or "guacharo" (*Steatornis caripensis* Humboldt). Their pale color, minute eyes, and long bristly pilosity suggested to Wheeler that they represent a truly cavernicolous, i.e. troglobitic, species. In addition, Wheeler speculated that "the Texan *E. longi* Wheeler, which is certainly subterranean and has been taken only once (during a nuptial flight), is really a cavernicolous ant." In 1938, however, Wheeler reported the collection of workers of *Spelaeomyrmex urichi* by P. J. Darlington from leafmold in Cuba, thereby casting doubt on the status of the species as a troglobite.

Certainly no more likely troglobite than *S. urichi* has been found among the ants. Further information on its biology has promised to be of exceptional interest. In the course of field work in Trinidad in 1961, the present author undertook to rediscover the species. The first problem was to find the type locality. No fewer than six caves in various parts of the island harbor the guacharo and could correctly be called "Guacharo Cave." The itinerary of the collector, the late Prof. F. M. Urich, was not known. After the author had visited one cave, on the Spring Hill Estate, without success, Dr. David Snow, who was conducting an ecological study of the guacharos, suggested the Oropouche Cave, near Cumaca, as the most likely locality. A single visit to this cave, on April 18, resulted in the immediate finding of two colonies of *Spelaeomyrmex*. Later, a surprising discovery was made: a colony collected from savanna forest at Bernhardsdorp, Surinam, in March 1961 and first identified as *Erebomyrma*, was on second examination determined to be conspecific with *Spelaeomyrmex urichi*. These findings have shed new light on the generic distinctness of

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Spelaeomyrmex, on its status as a troglobite, and on the ecological singularity of cave ants in general.

TAXONOMY

Erebomyrma Wheeler

Erebomyrma Wheeler, 1903, Biol. Bull., 4:137-148, minor worker, queen, male. Type species (monobasic): *Erebomyrma longi* Wheeler.

Spelaeomyrmex Wheeler, 1922, Amer. Mus. Novitates, 45:9, minor workers. Type species (monobasic): *Spelaeomyrmex urichi* Wheeler. NEW SYNONYMY.

Following is a list of the known species of *Erebomyrma*, with attendant bibliography:

eidmanni Menozzi, in H. Eidmann, 1936, Arb. phys. Angew. ent. Berlin-Dahlem, 3:47-48, fig. V (1-4), worker, soldier, queen. Type locality: Mendes, Rio de Janeiro, Brazil.

longi Wheeler, 1903, Biol. Bull., 4:137-148, figs. 1-5, minor worker, queen, male. Type locality: Denton, Texas.

morai Menozzi, 1931, Bull. Lab. Zool. Gen. Agr., Portici, 25:271-272, fig. 7, worker. Original localities: Apaican, Vulcano; and San José (Costa Rica). Borgmeier, 1949, Rev. Brasil. Biol., 9:207-208, figs. 8-9, "ergatogyne" (= soldier), second record from San José, Costa Rica.

nevermanni Mann, 1926, Psyche, 33:103-104, worker. Type locality: Hamburg Farm, Reventazon, Santa Clara, Costa Rica.

peruviana Emery, 1905, Bull. Soc. Ent. Ital., 37:139, nota, queen. Type locality: Marcapata, Peru.

urichi (Wheeler), 1922, Amer. Mus. Novitates, 45:9-11, fig. 1A-B, minor worker. Type locality: "Guacharo Cave," Trinidad. (*Spelaeomyrmex urichi*). Other records: Cuba, Yucatan, Surinam.

The minor-worker characters cited by Wheeler as most strongly separating *urichi* from *longi*, and hence *Spelaeomyrmex* from *Erebomyrma*, are: larger head size; angulate (vs. round) humeri; proportionately larger first gastric segment; and minor features in the shape of the petiole, postpetiole, and legs. These differences probably signify a specific distinction between *urichi* and *longi*, but they are not great enough to justify a generic break, even by liberal standards. The synonymy is supported by the fact that the newly-discovered queen and male of *urichi* are closely similar to these castes in *longi*. One possible difference of generic magnitude, unknown to Wheeler, still remains: *eidmanni*, *morai*, *nevermanni*, and *urichi* are now known to

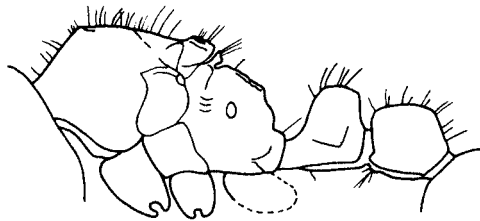
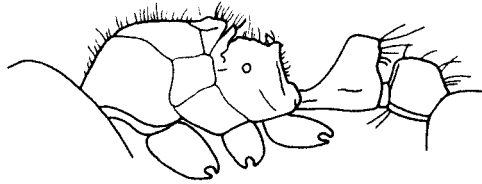
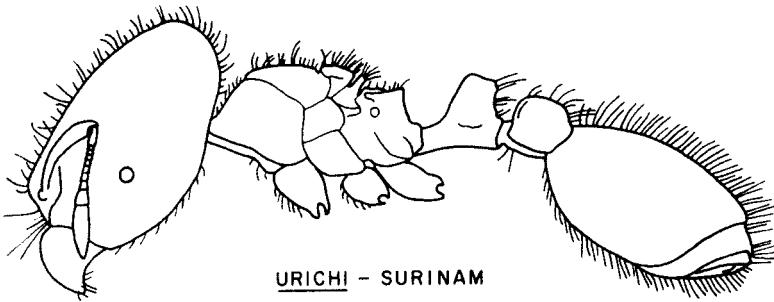


Figure 1. Soldiers of *Erebomyrma urichi* from Bernhardsdorp, Surinam, and Oropouche Cave, Trinidad, and *E. ?nevermanni* from Barro Colorado, Panama, showing variation in thoracic and pedicellar structure in this little known caste.

have a soldier caste, while none has been discovered in *longi*. However, *longi* is known from but a single collection, made under circumstances in which the scarce soldier caste could easily have been overlooked. It

seems a fairly safe conjecture that *longi* soldiers will be discovered when whole colonies of that species are collected.

As just noted, the Oropouche *urichi* and a colony taken at Bernhardsdorp, Surinam, are considered conspecific. The minor workers of the two colonies are virtually identical. In the Oropouche soldier the anterior face of the petiolar node is slightly more inclined posteriorly (thus forming a greater angle with its anterior peduncle), the anterodorsal nodal angle somewhat more rounded, the propodeal angles are more pronounced and acute, and there are some differences in thoracic form and sculpturing (see text-figure). The Oropouche queens have slightly more developed propodeal spines and larger ocelli. In other respects the soldiers and queens appear identical between the two colonies.

Together, the Trinidad and Surinam *urichi* differ markedly from those in a series of *Erebomyrma* collected recently at Barro Colorado (W. L. Brown and E. S. McCluskey *leg.*) and tentatively determined as *nevermanni* Mann. The *urichi* minor worker has distinctly narrower, more erect propodeal spines; while the *urichi* soldier is much smaller and with more pronounced propodeal spines (text-figure).

ECOLOGY

Trinidad. The Oropouche Cave is the source of the Oropouche River, which extends back into the cave as a clear stream several meters in width. A colony of *Erebomyrma urichi* was found approximately 30 meters inside the cave on the bank of the stream, in very feeble light coming from the plainly visible cave mouth. Much of the ground was covered by guano dropped from the large numbers of guacharos nesting overhead. The arthropod fauna at this point was rich and diverse, consisting of ants [*Mesoponera constricta* Mayr, *Odontomachus haematodus* (Linné), and *Solenopsis (Diplorhoptrum) tenuis* Mayr], as well as the *Erebomyrma*, entomobryid collembolans, cave crickets, dermapterans, small flies, and mites. The ant species, other than *Erebomyrma*, have been collected outside caves in Trinidad. *Mesoponera constricta*, which was the most common forager in the vicinity of the *Erebomyrma* nest, was also a dominant ant along the trails through cacao plantations in the Cumaca area. Most of the other insects appeared to be troglaphiles. Fifteen meters farther in, and in almost total darkness, a large *Bufo marinus* was found. In short, at the site of the first *Erebomyrma* nest, troglaphilic (facultatively cavernicolous) animals predominated.

A second group of foraging *Erebomyrma* workers, almost certainly

representing another colony, was encountered between 200 and 300 meters from the cave entrance. This spot was reached only after passing five major twists in the cave and was in apparently total darkness. It was the final outpost of the guacharo nests. Here there were no other ant species; in fact, none of the other three found at the first site ventured beyond the lighted portion of the cave. The arthropod fauna was sparse in species and biomass and consisted wholly of blind, white entomobryids, campodeids, isopods, and snails.

Just past the second site the cave ceiling dipped to within less than a meter of the stream surface, and the passage continued tortuously for another twenty meters or so. Beyond, the cave opened into a final oblong chamber before dipping beneath the stream surface. In this terminal room there were no guacharos; only bats had left a sprinkling of guano on the floor. A careful search revealed no *Ercbomyrma* workers in the terminal chamber.

The nest at the first site, near the cave entrance, was located and excavated. It was enclosed entirely within a large, smooth shale slab partly buried in the cave soil and covered with a thin layer of dense clay. The rock was soft, naturally fractured, and could easily be broken apart with a steel trowel. Columns of workers were observed traveling from the guano piles to two entrance holes twelve centimeters apart on the upper edge of the rock. The holes were each about two millimeters in diameter, and each was surrounded by low, inconspicuous piles of excavated clay. The nest, located only a few centimeters below the surface, consisted of several flat, irregular cavities between five and ten centimeters wide and several millimeters in height. Probably the great majority of workers and all of the other adult castes were collected, both alive and preserved in alcohol. The sample, censused the following day, had the following composition: 547 minor workers, 1 soldier, 10 dealate queens, 10 males. Also present was a large quantity of brood, in all stages of development, including one male pupa. It was estimated that the entire worker population, including that part left foraging or missed in the nest, was not less than 600 and not greater than 1000.

Previous to the excavation, the foraging workers were observed briefly. Workers were found up to $1\frac{1}{2}$ meters from the nest entrances, but the great majority was within a meter's radius. Most were hunting singly or moving in loose files through guacharo guano, just as Urich had found them forty years earlier. Workers returning to the nest converged in two separate files, which, judging from the precision

with which they repeated each twist and turn, must have been following odor trails. Several were carrying objects: a mite, an entomobryid collembolan, and two unidentified arthropod eggs. The mite and entomobryid were freshly killed and had evidently been captured as prey. This conjecture is supported by the fact that *Erebomyrma* workers were most densely concentrated at points where large numbers of entomobryids occurred. Later, in captivity, workers fed readily on a wide variety of larger moths and flies presented to them, but only after these had been killed and cut open. In the original nest over a hundred unidentified globular objects resembling arthropod eggs were found piled with the brood. These were cared for by the captive colony in the artificial nest and may have been used sporadically for food, although direct feeding was not observed. Similar structures were found by Eidmann (1936) in the nests of *Erebomyrma cidmanni*.

Surinam. On March 14 a *urichi* colony was found in open, dry, second growth forest at Bernhardsdorp, near Lelydorp. It was nesting in a small rotting log partly buried in moist leaf litter in a well-shaded part of the forest. The population consisted of a single dealate queen, four soldiers, an estimated 500-1000 minor workers, and a large quantity of brood in every stage of development. Adjacent to the *Erebomyrma* colony was a large colony of the termite *Armitermes minutus* Emerson (det. A. E. Emerson). The *Erebomyrma* colony and a fraction of the *Armitermes* colony were placed alive in separate but interconnected artificial nests. Within a few hours after establishment *Erebomyrma* workers entered the still chaotic termite chamber and began carrying off eggs. They were unopposed by the much larger *Armitermes* adults, and in turn did not molest the *Armitermes* adults or nymphs. While the response of the *Erebomyrma* workers was clear-cut in this instance, it does not necessarily mean that the species is termitolestic on undisturbed *Armitermes* colonies in nature. The colony was kept alive for only a few days and there was no opportunity to extend the experiment. In this connection it is worth noting that Emerson (in Wheeler, 1936) found evidence that *Solenopsis (Diplorhoptrum) laeviceps* Mayr collects and stores eggs of *Nasutitermes cavifrons* (Holmgren) and *N. costalis* Holmgren in British Guiana.

BEHAVIOR

The Trinidad colony was kept under observation in an artificial nest for two months and notes taken on selected aspects of behavior. The ethology of this species is of considerable interest because nothing

has been recorded hitherto on *Ercbomyrma*, and, in fact, very little information is available on the entire tribe Pheidologetonini.

The self-grooming movements of the minor worker are given as follows, according to the classification proposed recently for ants as a whole (Wilson, 1962): (1) oral leg cleaning, (2) antenna wiping, (3) four-leg wiping, (4) three-leg wiping, (5) two-front-leg wiping, (7) head wiping (8) abdomen wiping (front legs). The queen repeated all of these movements and in addition (10) metapleuron wiping, conspicuously missing in the worker. Other-grooming was as frequent as in most other myrmicines. The workers were especially attentive to the large queens, and a populous retinue followed each as it moved about. As many as six were seen riding on one queen's body at the same time.

Worker-to-worker regurgitation was frequent. The queens apparently were fed exclusively by worker regurgitation, and they never approached the prey. In several emigrations studied, adult transport was never observed. In one exceptional instance a worker carried a newly eclosed worker by its left middle and fore legs clumsily and a short distance over the brood pile, as though it were a piece of brood.

DISCUSSION: THE ECOLOGY OF CAVERNICOLOUS ANT SPECIES

Penetration of caves by ants occurs chiefly in the tropics and is limited mostly to the dimly lighted (twilight) zone near entrances. The great majority of records belong to species that are obviously either troglloxenic (penetrating as foragers from nests outside) or troglphilic (facultatively cave-nesting). Further, these species are typically those that are among the most abundant, widespread, and adaptable members of the ant fauna in habitats outside the caves. For instance, a collection of ants made in 1959 in the Batu Caves, Malaya, by Mr. H. E. McClure and studied by the author, consisted primarily of three identifiable species [*Bothroponera tridentata* (Fr. Smith), *Leptogenys diminuta* (Fr. Smith), *Pheidole javana* Mayr] that are among the most widespread and common members of their genera in the Oriental Region. Wheeler (1924) records *Triglyphothrix striatidens* Emery from 400 feet inside the entrance of Siju Cave, Garo Hills, Assam; this ant is a notably adaptable pantropical "tramp" and by far the most widely distributed *Triglyphothrix*. Of 16 species recorded from Yucatan caves by Wheeler (1938), 15 are identifiable, and of these 13 have very extensive ranges in the New World tropics; most are known further to be abundant in various habitats. The remaining two species [*Brachymyrmex cavernicolus* Wheeler, *Paratrechina* (*Nylanderia*) *pearsei* Wheeler] belong to genera whose

taxonomy and ecology are too poorly known to allow further generalization. Kempf (1961) records *Labidus coecus* (Latreille) from "guacharo" caves in northern Peru and Venezuela. Both collections were made in zones of total darkness, at 90 m. and 800 m. respectively from the cave mouths. As Kempf points out, *L. coecus* is one of the commonest and most adaptable army ant species and ranges, at widely varying elevations, from the southern United States to northern Argentina. Santschi (1914) records eight species collected by Ch. Alluaud and R. Jeannel from caves at Tanga and Shimoni, Tanganyika. These can be roughly characterized as follows: *Ponera dulcis* Ford, widespread but known from only a few records; *Leptogenys jeanneli* Santschi, known only from the type collection but an unexceptional member of the epigeic *falcigera* group; *Odontomachus haematoda* L. var. *trogloodytes* Santschi, probably the same as the very widespread, abundant African "*haematoda*" or "*haematoda stanleyi*" (? *nec haematoda* L. of the New World); *Dorylus fimbriatus* (Shuckard), very widespread and abundant; *Monomorium rhopalocerum* Emery subsp. *speluncarum* Santschi, probably equals *rhopalocerum*, a widespread and apparently relatively common species, collected at Shimoni only at a cave entrance; *Strumigenys stygia* Santschi, known only from the type collection but otherwise a morphologically unexceptional species of the *rogeri* group (see Brown, 1954); *Miccostruma marginata* (Santschi), known only from the type collection taken at cave entrance and not morphologically peculiar; *Paratrechina (Nylanderia) jaegerskioldi* (Mayr), very widespread and abundant. Thus this African cave fauna is made up of five more or less common widely distributed species together with three species still known only from the type caves. The latter exceptional group, however, belong to genera (*Leptogenys*, *Strumigenys*, *Miccostruma*) in which rare, local species are usual, so that no particular ecological significance can be attached to the fact that their known range is at present so limited.

Cave ants do not as a group possess the usual morphological modifications found in extreme cave dwellers. For the most part, they show no exceptional pigment or eye reduction when compared with their congeneric relatives, and, in the cases where their habits are known, they are no less epigeic in their foraging behavior. Conversely, the majority of the most highly modified hypogeic and subterranean tropical ant taxa are unknown from caves, e.g., extreme species of *Amblyopone*, *Centromyrmex*, *Solenopsis (Diplorhoptrum)*, *Tranopelta*, *Acropyga*. We may conclude that the troglonexes and troglophiles are characteristically generally adaptable rather than pre-

adapted for cave life. Ants are not exceptional in this regard. Other adventitiously cavernicolous animal taxa are often very varied in their ecology; some other arthropod groups, such as the European copepods, resemble the ants in that the cave species are typically widely distributed on the outside (Hesse, Allee, and Schmidt, 1951).

The question can now be raised, whether there are any ant species that are troglobitic, i.e. limited to caves. *Erebomyrma urichi* is clearly excluded on the basis of information just given, and the accumulated evidence makes it improbable that any other member of the genus is troglobitic. *Paratrechina (Nylanderia) troglodytes* Weber of Cuba, originally recorded from a shallow cave, has been shown to be a junior synonym of *P. (N.) myops* (Mann), which has been found in soil away from caves in two montane localities in Cuba (Brown, 1955). A related species, *microps* M. R. Smith, occurs in places remote from caves on Puerto Rico. *Proceratium cavernicola* (Borgmeier), described from a queen found in the Chilibrillo Caves of Panama, has been recognized as a synonym of *P. micrommatum* (Roger), known from several non-cavernicolous series collected in Central America and Cuba (Borgmeier, 1957; Brown, 1958).

There remain at least four ant species known only from single collections made in caves. *Brachymyrmex cavernicolus* Wheeler (1938) was found beneath a stone near the mouth of Balaam Canche Cave, Chichén Itzá, Yucatan. It is pale yellow in color and has small eyes, which perhaps suggest a normally cavernicolous habit. But it belongs to a genus the taxonomy of which is in outstandingly poor condition, so that the possibility exists that non-cavernicolous series have been recorded in the literature under other names, as in the cases of the *Paratrechina* and *Proceratium* species just mentioned. The African cavernicoles *Leptogenys jeanneli*, *Strumigenys stygia*, and *Smithistruma marginata* have already been discussed. They belong to otherwise non-cavernicolous groups and show no apparent morphological adaptation to cave life themselves. Clearly, until stronger evidence is produced, the existence of troglobitic cave ant species must be considered in great doubt.

Enlarging on this point, let us ask why there are so few (if any) troglobitic ants or, for that matter, troglobitic social insects of any sort. The following hypothesis is proposed. The reproductive unit in social insects is the colony, and it follows that natural selection operates on the colony as a unit. Further, the singly prefertilized mother queen of a monogynous colony ordinarily contains the whole of the transferable genetic material, and, since she stores the sperm of

her mate (or mates), is genetically the equivalent of two or several individuals, the female and sexual consorts in a normal population of non-social animals. Hence, what may be referred to as the "equivalent size" of the reproductive population, N_d , in an idealized deme of social insects outside the nuptial season can be estimated as

$$N_d = \frac{N_t}{N_c} (Q + mQ)$$

where N_t is the total adult population of the deme, including workers, m is the average number of males that fecundated the queens assuming approximately equal sperm contributions, Q is the average number of mother queens assuming approximately equal egg contributions, and N_c is the average mature colony size. Thus in a cave deme containing 10,000 adult individuals with an average mature colony size of 1000 and single fertilizations of single queens, the reproductive population size equivalent would be only 20. We may note that a deme of 10,000 adults, the non-social condition, would perhaps be large enough and contain enough genetic variability to be stable and self-maintaining. Demes of this size are quite common in nature. But a deme-equivalent of 20 adults, the social condition, must be below the critical threshold or dangerously close.

In short, if species of social insects never become truly troglobitic it may be simply because they are unable to maintain sufficiently large cave demes. Due to limited habitable space, the Oropouche Cave could not have contained more than 20 colonies of *Erebomyrma urichi* and probably held considerably fewer. *Erebomyrma* colonies are sometimes polygynous, as we know from the single Oropouche example. If ten queens per colony is accepted as the upper limit, and each were assumed to be singly fertilized, the reproductive-population equivalent of the Oropouche *Erebomyrma* is calculated not to exceed 400. Since the excavated colony was the only obviously populous colony found, the actual equivalent was probably far less.

But let us suppose that social insects do occasionally become troglobitic; what characteristics might they be expected to have? In addition to the well-known morphological changes common to most troglomorphic animals, there are several features of social structure that might be affected. There would likely be one or more of three devices to increase N_d ; namely, (1) decreased colony size, (2) increased polygyny, and (3) increase in m (polygamy). The Oropouche colony of *Erebomyrma urichi* was markedly polygynous, with the added result that the estimated N_d of the colony was large (20). In fact, *urichi*, although not a troglobite, may be pre-adapted for marginal cave exis-

tence. Finally, it is interesting to note that the predicted social modifications are just as likely to be developed in any ant species sufficiently ecologically restricted to be partitioned into very small demes.

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