BIOLOGY

THE COCKROACHES OF NORTH QUEENSLAND CAVES AND THE EVOLUTION OF TROPICAL TROGLOBITES

Fred D. Stone

ABSTRACT

Although cockroaches are common and widespread inhabitants of Australian caves, only ten species (one troglobitic) were listed prior to the current biological surveys of North Queensland caves. At least six new cave species in two groups were collected by the Explorers Club Expeditions to Chillagoe and Mt. Garnet regions: two troglophilic/guanobitic species and a related troglobitic species of Paratemnopteryx (Blattellidae), and three troglobitic species of Nocticola (Nocticolidae). Roth (1988) described Nocticola australiensis, from Donna and Trezkinn Caves, Chillagoe and an epigean species, N. babindaensis from Babinda rainforest.

The cockroach species of North Queensland caves are all endemic, and they show close correlation between degree of troglomorphy and the environmental conditions of the five cave zones described by Howarth (this issue). Paratemnopteryx sp. A and B are slightly troglomorphic and are concentrated in twilight and transition zones; Nocticola australiensis shows moderate troglomorphy, and is found in the saturated deep cave zone; N. sp. A is moderately (?) troglomorphic but occurs in the stagnant air zone of Long Shot Cave; the highly troglomorphic Paratemnopteryx and Nocticola relatives are both found in the stagnant air zone of Bayliss Cave. Finally, non-troglomorphic and moderately troglomorphic Nocticola occur in moist epigean rainforest habitats.

INTRODUCTION

Cockroaches (Dictyoptera: Blattaria) are common, widespread inhabitants of Australian caves, and can therefore make important contributions to our understanding of cave ecology and the evolution of cave adapted species.

Richards (1967) listed 10 species of cockroaches from Australian caves, while recognizing that large areas of the country had not been surveyed for cave fauna. Only one troglobitic cockroach was known at that time, the highly troglomorphic Trogloblattella nullarborensis from caves in the Nullarbor (Mackerras, 1967).

Since 1982, the Explorers Club expeditions to the caves of North Queensland, led by Brother Nicholas Sullivan and supported by the Chillagoe Caving Club, have discovered at least six new species of Australian cave cockroaches. Two groups are represented in these collections (as determined by L. Roth):

1. The genus Paratemnopteryx (family Blattellidae), with two troglophilic/guanobitic species and a third related troglobitic species (so far known only from female and immature specimens).

2. The genus Nocticola (family Nocticolidae) with 3 species, all troglobitic; this is the first record of this family in Australian caves. One of the species collected from Donna and Trezkinn caves during the Chillagoe expeditions has recently been described by Roth (1988) as Nocticola australiensis.

It is remarkable, and important for ecological studies, that none of the common cosmopolitan cockroach species, ubiquitous in caves of other tropical regions, have been found so far in the caves of North Queensland. Hamilton-Smith also did not report any alien cockroaches in his 1967 list of Australian cave fauna.

Howarth (this issue) presents a model describing five environmental zones of caves in relation to adaptations of cave species; the **entrance, twilight, transition, deep cave,** and **stagnant** air zones (also see Howarth, 1980; 1983; 1988). In this paper, I will describe the distribution of cave cockroaches of the Chillagoe and Mt. Garnet regions and compare their degree of troglomorphy to their relative occurrence in the five cave zones.

PARATEMNOPTERYX

Distribution: This genus and related genera (Gislenia, Shawella are widespread in caves throughout Australia (Richards, 1967; Hamilton-Smith, 1967). The North Queensland species are medium sized cockroaches (about 8 to 20 mm long). They are abundant as troglophiles and guanobites in twilight and transition zones of caves where food and moisture are available. They are also found in the deep cave and stagnant air zones, but the populations drop rapidly as one moves further into these zones. Roth (Pers. comm.) is currently preparing a paper describing these species, so I will refer to them as P. species A and P. species B.

P. sp. A adults, smaller with either long or short tegmin, were collected from Nasty Cave (Undara lava flow), Tea Tree Cave, Kiwi Cave (Dumpy Tower), and Christmas Pot (Suicide Tower). Immatures, probably of this species, were found in Hercules Cave and Surprise Packet (Markham Tower), Parasol Cave (Katie Breen Tower) and Smeagol's Lair and Here It Is Cave (Mitchell-Palmer).

P. sp. B adults, larger with short tegmin, were collected from Bayliss, Barkers and Pinwell Caves (Undara lava flow), Clam, Spatial and Rhino Caverns (Walkunder Towers), Royal Arch Cave (Royal Arch Tower), Donna and Trezkinn Caves (Donna Tower), and Spring Cave (Spring Tower). Immature specimens were found in additional caves from the same and adjacent towers.

The **third** species, probably in the same or a related genus, is highly troglomorphic, and has been found only in the stagnant air zones of Bayliss and Nasty Caves in the Undara lava flow. It is often glimpsed in cracks (mesocaverns) in the cave walls, and only ventures into large passages when saturation humidity and high carbon dioxide levels are present.

So far, we have never collected both P. sp. A and P. sp. B from the same cave, from caves in the same tower, or even from caves in adjacent limestone towers. In the Chillagoe area, P. sp. A is found in caves east and/or north of the Chillagoe-Mungana road, while P. sp. B is found in caves west and/or south of the road. If it weren't for the Nasty cave population of P. sp. A we might interpret the distribution pattern as showing range boundaries of two allopatric species. However, this apparent pattern could be an artifact of our limited sample of the numerous caves of the region, and of our seasonally restricted field work.

P. sp. A is most often found in hot, humid caves (Tea Tree, Kiwi, Christmas Pot, Hercules, Nasty), often in areas with abundant bat or swiftlet guano. P. sp. B often occurs in the transition zone of large, relatively better ventilated, and less humid cave passages (Royal Arch, Donna, Spring, Clam, Spatial, Pinwill, Barkers and initial section of Bayliss) but it can also be found (with declining frequency) in the saturated deep cave zone of Bayliss and other caves.

Therefore microhabitat preference, possibly with competitive exclusion, could explain the distribution patterns. Further detailed field work is essential in testing such hypotheses, or in rejecting them for alternative hypotheses.

Morphology: Roth is publishing detailed descriptions of these species, so my remarks will be brief. Both species show slight troglomorphy, with considerable variation among individuals both within and between caves. P. sp. A shows variation in wing size (both macropterous and brachypterous forms occur), but lacks pulvilli. Reduction or loss of pulvilli and increased dependence on tarsal claws are adaptations for walking on cave surfaces (Christiansen, 1965; Roth and Willis, 1952). P. sp. B are all brachypterous, but show much variation in pulvilli reduction in populations both within and between caves (Roth, pers. comm.).

The variability among individuals within caves could be due to adaptations to heterogeneous microhabitats at various distances from entrances and on different substrates or food sources, or they might be due to gene flow between epigean and cave populations. Variability between caves could be due to a combination of the above factors plus restricted gene flow over longer distances. Continued field research will be necessary to enable us to sort out these complex patterns of variation.

NOCTICOLIDAE

Cave adapted cockroaches from tropical caves were first collected by Simon in the Philippines nearly 100 years ago. The Philippine cave cockroaches were described in the new genus Nocticola and later they were placed in their own family, Nocticolidae (Bolivar, 1892; Princis, 1966). From rare collections this family was found to be widespread throughout the old world tropics, with cave and surface species found in Africa, India, Southeast Asia, China, and Okinawa (Asahina, 1974; Bolivar, 1892, 1897; Chopard, 1921, 1924, 1932, 1945, 1950, 1966; Gravely, 1910, 1921; Karny, 1924; Roth, 1988; Shelford, 1910; Silvestri, 1946, 1947).

Biological surveys of the caves of Thailand by me (supported in 1986 by the Explorers Club) and of Thailand and Indonesia, by L. Deharveng and colleagues through the Association Pyreneenne de Speleologie, (1986) indicate that Nocticolidae are abundant in suitably humid habitats. In regions that have been intensively surveyed, a range of species occur from non-troglomorphic epigean species to highly troglomorphic species from deep cave and stagnant air zones.

NOCTICOLA: EPIGEAN SPECIES

On the Chillagoe expeditions we were able to find female and immature specimens from a rotting log in Running Creek, Mitchell-Palmer. Roth (1988) includes 2 surface species:

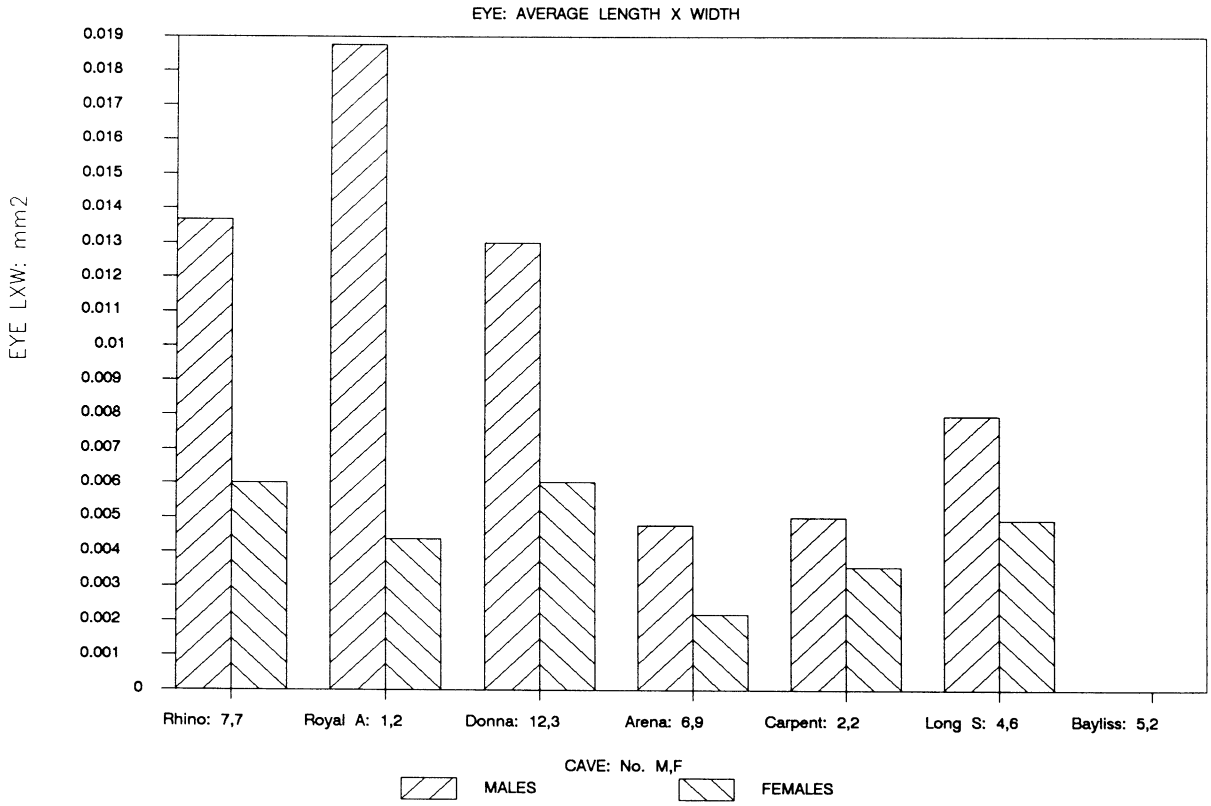
N. babindaensis, collected in a light trap in the rain forest at Babinda, Queensland has fully developed eyes, tegmina and wings. Though in color and lacking ocelli, it can be classified as non-troglomorphic.

The second species **(unnamed)** found under rotting logs at Crater National Park, has reduced eyes and tegmina, and no wings, but a large tergal gland present on the male. This species apparently has moderately troglomorphic characteristics, leading us to question to what extent the mesocavernous habitat extends to holes in the rainforest substrate (holes left by dead roots, holes under or in rotting logs, and termite or other animal burrows).

CAVE NOCTICOLA: DISTRIBUTION AND MORPHOLOGY

N. australiensis adults were collected from Rhino and Pioneer Caves (Walkunder Towers), Royal Arch Cave (Royal Arch Tower), Donna and Trezkinn

GRAPH 1



Caves (Donna Tower), Arena and Spring Caves and The Throne Room (Spring Tower), Kiwi Cave (Dumpy Tower), Carpentaria Cave (Carpentaria Tower) and Hercules Cave (Markham Tower). Immature specimens only were found in Spatial Cavern (Walkunder Towers), Marachoo Cave (Ryan Imperial Tower), Gordale Scar Pot (Spring Tower) and Project 31 Cave (Moffat Tower).

N. australiensis are found in the humid deep cave zones (or in moist microhabitats of transition zones) of caves in the Chillagoe region. They are all moderately troglomorphic, with body color pale yellow, eyes much reduced or absent (smaller in females than males), ocelli absent, tegmin in males reduced, wings in males reduced to scales fused to mesothorax (tegmin and wings absent in females), and 3rd, 4th and 5th tergites modified to glands in males. Individuals show a consistent gradation of forms from relatively less troglomorphic in the south (Walkunder Towers) to more troglomorphic in the north (Carpentaria Tower) (Table 1, Graphs 1, 2).

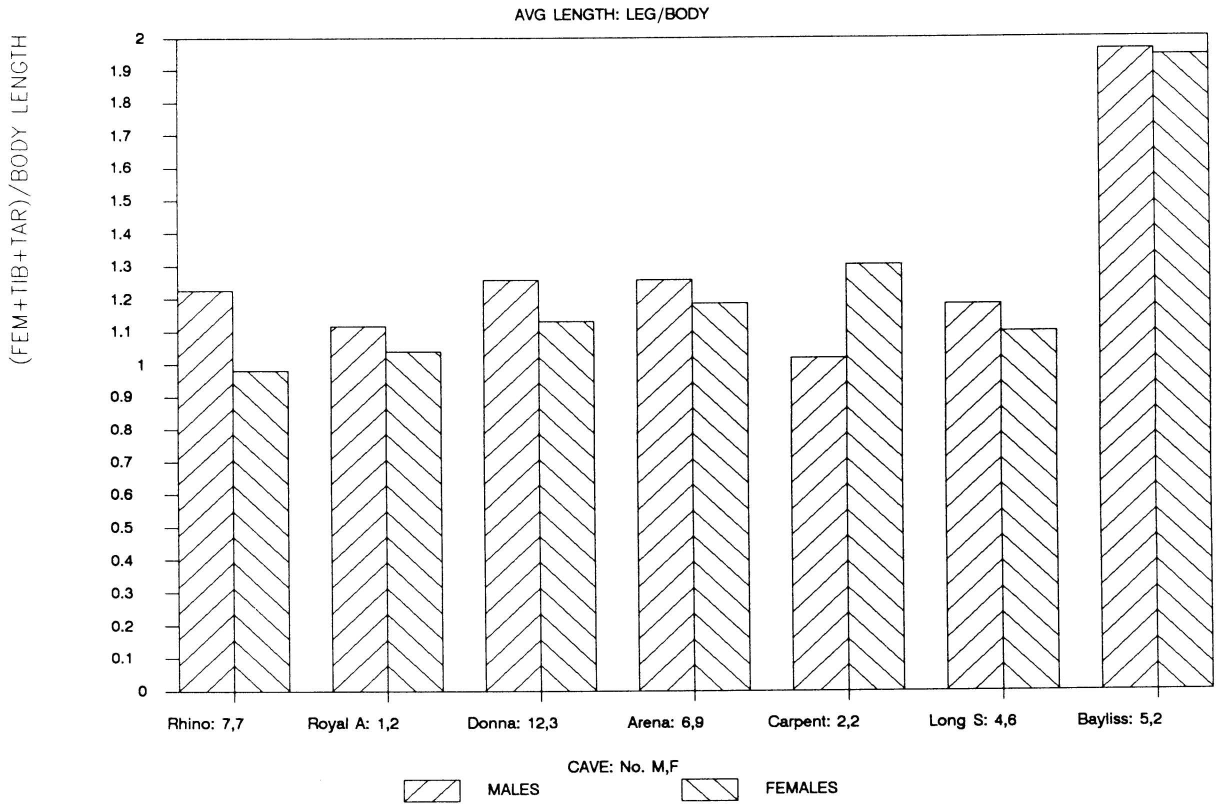
The darkest individuals are from Rhino and Royal Arch Caves, paler from Donna and Arena, and palest from Carpentaria. The eyes of Arena and Carpentaria specimens are much smaller than those from Rhino, Royal Arch and Donna specimens. Body size is also smallest in Carpentaria individuals. Tergal glands also vary consistently among males from different towers. With additional material from Royal Arch and Carpentaria Caves, it will be possible to decide whether geographic races or separate species occur in the separate limestone towers of the Chillagoe region.

The reasons for the regular pattern of variation of N. australiensis are no easier to determine than the reasons for the more complex variation of Paratemnopteryx. Is it possible that deep cave environments are less prevalent in the southerly towers than the northerly ones? Detailed microclimatic data from the caves might provide the answer.

I am currently working on descriptions of two additional species of Nocticola from lava tubes. N. Sp. A from Long Shot Cave is moderately troglomorphic, with leg/body ratio and eye size similar to N. australiensis (Table 1, Graphs 1,2). However, it has the most modified tergal gland of any of the Australian cave Nocticola.

N. sp. B, from Bayliss and Nasty Caves, Undara, is one of the most highly troglomorphic species yet discovered. It is a pale, translucent white color, with eyes, tegmin and wings lacking. It has the smallest body size but the longest legs and cerci of any of the Australian cave Nocticola, and a leg/body ratio nearly twice that of the other species (Table 1, Graphs 1,2). Unlike individuals of N. australiensis, which run rapidly if disturbed, N. sp. B moves slowly. It occurs only in the stagnant air zone of the Bayliss and Nasty caves, and it (along with the highly troglomorphic Paratemnopteryx which occurs in

GRAPH 2



the same locations) provides excellent evidence for the correlation between extreme troglomorphy and the stagnant air zone of these caves.

DISCUSSION

Answers to questions about the ecology and evolution of tropical troglobites can only be gained by careful field studies of relatively undisturbed tropical cave ecosystems, such as those of North Queensland. Although troglobitic species of the Nocticolidae have been known from tropical caves for nearly 100 years, the limited number of specimens from scattered locations mislead cave biologists to believe that true troglobites did not occur in tropical caves (Vandel, 1965)! Now that we know that troglobites are widespread and common in the tropics and probably in Australia where ever the deep cave and stagnant air zones of caves allow us entry into the mesocavernous conditions, it is no longer necessary to invoke special theories of climate change as a cause of presence or absence of troglobites (Barr, 1968; Culver, 1982; Hamilton-Smith, 1967; Holsinger, 1988; Howarth, 1980, 1983, 1988; Moore, 1964; Richards, 1967).

The ability to do long-term, detailed, field work, made possible by the Chillagoe Expeditions, has allowed us to begin to work out the relationships between degrees of cave adaptation and the environmental zones of caves. The cockroaches described in this paper, the planthoppers described by Hoch and Asche (this issue), and other groups yet to be studied in detail (Howarth, this issue) often show a remarkable degree of correlation between levels of troglomorphy and the cave zone where they occur (Howarth and Stone, in prep.). Much additional field and laboratory research remains to be done to test these relationships: will they stand up to more detailed field work, or will new patterns and relationships emerge? Finally, what are the processes at work in tropical caves that commonly produce the adaptive shifts from epigean to troglomorphic species? Only continued field work can lead us to the answers to these questions, or suggest new avenues for investigation.

ACKNOWLEDGEMENTS

I wish to give a heartfelt thanks to The Explorers Club of New York and to Brother Nicholas Sullivan who made the field research on which this paper is based, and its delivery at this meeting, possible. Thanks also to the many members of the Chillagoe Caving Club and the Chillagoe Expeditions who patiently helped us search for the cave creatures, to F.G. Howarth who provided much stimulus and encouragement, and to D. Irvin whose logistic support made the research not only possible but also pleasant. Also, thanks to the Chillagoe National Parks and Wildlife Service for permission to survey the Park caves, and to the Pinwill and Collins families for allowing us to work in their caves.

Dr. Fred D. Stone
Biology Department, Natural Sciences Division
College of Arts and Sciences
University of Hawaii at Hilo
Hilo, Hawaii 96720 USA.

REFERENCES

ASAHINA, S. 1974. The cavernicolous cockroaches of the Ryukyu Islands. **Mem. Natn. Sci. Mus.**, (Tokyo), 7: 145-156.

ASSOCIATION PYRENEENNE DE SPELEOLOGIE. 1986. **Thai-Maros 85**. A. P. S., Toulouse, France. pp 1-215.

BARR, T.C. 1968. Cave ecology and the evolution of troglobites. **Evol. Biol.** 2: 35-102.

BOLIVAR, I. 1892. Etudes sur les Arthropodes cavernicoles de l'ile de Luzon. Orthopteres. **Annls. Soc. Ent. Fr.** 61: 29-34.

BOLIVAR, I. 1897. Viagio di Lenardo Fea in Birmanie e regioni vicine, LXXVIII. Nouvelle espece cavernicole de la famille des blattaires. **Annali Mus. civ. Stor. Nat. "Giacomo Doria"**, ser. 2, 18: 32-36.

CHOPARD, L. 1921. XXVII. On some cavernicolous Dermaptera and Orthoptera from Assam. **Rec. Indian Mus.** 22: 511-527.

CHOPARD, L. 1924. On some cavernicolous Orthoptera and Dermaptera from Assam and Burma. **Rec. Indian Mus.** 26: 81-92.

CHOPARD, L. 1932. Un cas de micropthalmie liee a l'atrophie des ailes chez une blatte cavernicole. **Soc. Ent. Fr., Livre du Centenaire** (Paris), pp. 485-496.

CHOPARD, L. 1945. Note sur quelques Orthopteres cavernicoles de Madagascar. **Revue Fr. Ent.** 12: 146-155.

CHOPARD, L. 1950. Les blattes cavernicoles du genre Nocticola. Bol. **Eos. Tomo extraordinaire** (Madrid). pp.301-310.

CHOPARD, L. 1966. Une espece nouvelle de Nocticola provenant d'une grotte du Transvaal (Dictyopteres, Nocticolidae), **Bull. Sol. Ent. Fr.** 71: 307-310.

CHRISTIANSEN, K. 1965. Behavior and form in the evolution of cave collembola. **Evol.** 19: 529-537.

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

GRAVELY, F.H. 1910. XXIX. Alluaudella himalayensis, a new species of degenerate cockroach. **Rec. Indian Mus.** 5: 307-311.

GRAVELY, F.H. 1920. IV. The female of the cockroach Alluaudella. **Rec. Indian Mus.** 19: 17-18.

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

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

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

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

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

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

HOWARTH, F.G. 1988. Environmental ecology of North Queensland caves, or why there are so many troglobites in Australia. **(This issue).**

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

JEANNEL, R. 1943. Les fossiles vivants des caverns. **L'avenir de la Science,** n.s. No. 1, **Gallimard,** 321pp.

KARNY, H.H. 1924. Beitrage zur Malayischen Orthopteren fauna. **Treubia** 5: 1-234.

MACKERRAS, M. 1967. A blind cockroach from caves of the Nullarbor Plain (Blattodea: Blattellidae). **J. Aust. Ent. Soc.** 6: 39-44.

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

PRINCIS, K. 1954. Report from Professor T. Gislen's expedition to Australia in 1951-1952. Australian Blattariae. **Lunds Univer. Arssk.** N.F.Avd. 2 Bd. 50 Nr. 13. **Kungl. Fysiog. Sallsk. Hand.** N.F. Bd. 65 Nr. 13: 3-49.

RICHARDS, A.M. 1967. Cockroaches (Blattodea) from Australian Caves. **Helictite** 5(2): 35-44.

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

ROTH, L.M. 1988. Some cavernicolous and epigean cockroaches with six new species, and a discussion of the Nocticolidae (Dictyoptera: Blattaria). **Revue Suisse Zool.** 95(1): 297-321.

SHELFORD, R. 1910. A new cavernicolous cockroach. **Ann. Mag. Nat. Hist.** (8) 6: 114-116.

SILVESTRI, F. 1946. Prima nota su alcuni termitofili dell'Indocina. **Boll. Lab. Ent. Agr. Filippo Silvestri** 6: 313-330.

SILVESTRI, F. 1947. Seconda nota su alcuin termitofili dell'Indocina con una appendice sul Macrotermes barneyi Light. **Boll. Lab. Ent. Agr. Filippo Silvestri** 7: 13-40.

SIMON, E. 1896. La faune aveugle des cavernes des iles Philippines et du Transvaal. **Spelunca** 1: 123-5.

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

TABLE 1:

MORPHOLOGICAL COMPARISON OF NOCTICOLA FROM CAVES OF NORTH QUEENSLAND: AVERAGE VALUES FOR SAMPLE SIZES SHOWN

	1	2	3	4	5	6	7	8	9	10
CAVE	SEX	NO.	BODY LGTH mm	LEG: FEM+ TIB+ TAR mm	RATIO LEG/ BODY	RATIO FEM: L/W	CERCI LGTH mm	EYE LXW mm²	TEGM LGTH mm	PRONOT LXW mm²
Rhino	M	7	4.43	5.43	1.23	5.30	1.53	.014	2.18	2.01
Royal A.	M	1	4.65	5.20	1.12	5.00	1.45	.019	2.05	2.10
Donna	M	12	4.19	5.27	1.26	5.27	1.36	.013	2.14	1.95
Arena	M	6	4.28	5.38	1.26	5.61	1.29	.005	2.10	2.03
Carpent.	M	2	4.10	4.18	1.02	4.82	1.00	.005	1.73	1.36
Long S.	M	4	3.88	4.59	1.18	5.52	1.13	.008	2.20	1.64
Bayliss	M	5	3.55	6.95	1.96	9.57	1.67	abs	abs	1.13
Rhino	F	7	5.65	5.54	0.98	4.73	1.46	.006	abs	2.66
Royal A.	F	2	5.10	5.30	1.04	4.24	1.40	.004	abs	2.63
Donna	F	3	4.98	5.63	1.13	5.61	1.30	.006	abs	2.29
Arena	F	9	5.03	5.95	1.18	5.44	1.33	.002	abs	2.54
Carpent.	F	2	4.01	5.23	1.30	4.90	1.15	.004	abs	2.08
Long S.	F	6	4.30	4.72	1.10	5.29	1.11	.005	abs	1.89
Bayliss	F	2	3.85	7.48	1.94	8.17	1.75	abs	abs	1.41

2. Number of individuals measured.
3. Front edge of pronotum to tip of abdomen.
4. Leg length: femur + tibia + tarsus.
5. Ratio of leg length (No. 4) to body length (No. 3).
6. Ratio of femur length to femur width.
7. Cerci length along axis, not including hairs on tip.
8. Maximum length times maximum width of pigmented area of eye.
9. Maximum tegmin length.
10. Maximum length times maximum width of pronotum.

Donna Cave specimens are N. australienses. Nocticola from Rhino Cavern, Royal Arch Cave, Arena Cave and Carpentaria Cave are also from the Chillagoe region, and are either geographic races or closely related species of N. australiensis. The Long Shot and Bayliss specimens are two separate species from lava tubes. One female from Spring Cave and one from The Throne Room are included with the Arena Cave females (all from Spring Tower).