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CONTENTS

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Speciation of troglobites: studies in the San Antonio cave (Oaxaca, Mexico)

Horst Wilkens, Peter Junge and Thomas G. Langecker*

SUMMARY

The phylogenetically young species community of San Antonio Cave (Oaxaca, Mexico) exemplifies the hypothesis that speciation of troglobites can occur in close contact with epigean predecessors. In a subterranean creek which continues outside with a rich epigean fauna, four troglobitic aquatic crustacean and one fish species (*Rhamdia reddelli*, Pimelodidae) were studied. Today not a single surface specimen can be found in the cave waters although several epigean species are troglophilic and/or are the ancestors of cave forms in other parts of Mexico. The absence of epigean invaders is attributed to the presence of specimens of some of the more aggressive and carnivorous cave species close to the cave entrance.

Contrary to this it can be presumed that at the beginning of the troglobitic evolution the cave ancestral epigean forms were regularly invading the cave. It is assumed that photonegative behavior played a role for the initial colonization of the cave but it is not of significance as a separating mechanism for the speciation process.

INTRODUCTION

The speciation of cave animals is still today a matter of controversy. Concerning the initial colonization of the cave biotope, the "refugium model" has been widely accepted in the past (Vandel, 1964). It explains the origin of cave species as being derived from epigean forms which have taken refuge in the cave due to environmental changes. Today the view of an "active colonization" is gaining more and more acceptance (Rouch & Danielopol, 1987). This model implies that troglophilic epigean species actively invade the subterranean biotope while still existing at the surface.

It is generally accepted that the speciation process following an invasion requires the final interruption of the gene flow between the

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newly founded cave population and the epigean ancestor. For this, various mechanisms are considered responsible. Above all the extinction or geographic separation of the ancestral form is thought to be most important (Barr & Holsinger, 1985). Contrary to this, Howarth (1981, 1987) proposed that non-relictual Hawaiian troglobites may evolve by a process of an adaptive shift from species that are frequent accidentals in caves. Similarly it has been found in cave living populations of the fish *Astyanax fasciatus* that speciation may even occur in a narrowly sympatric contact with the epigean form (Wilkens & Hüppop, 1986).

The "San Antonio Cave" (Cueva del Nacimiento del Rio San Antonio) which is located in the Acatlán region of Oaxaca (Mexico) (Reddell, 1981) is an excellent model to study speciation processes in cave animals. This cave is characterized by a continuous aquatic connection between the subterranean creek and the surface river which emerges at the cave entrance. Furthermore the cave portion is colonized by several aquatic troglobitic species. These species all show intermediate eye and pigment reduction (Wilkens, 1986) and thus are supposed to be recent invaders with still existing epigean ancestors. One of these is the catfish *Rhamdia reddelli* Miller, 1984 (Pimelodidae), which can be derived from the neotropical genus *Rhamdia* which is widely distributed in epigean waters in Southern Mexico and Belize (Miller, 1966, 1984; Greenfield et al., 1983; Robertson, 1983 a, b; Mosier, 1984).

MATERIAL AND METHODS

The field studies in the San Antonio Cave were performed in February 1988. Six cave fish (standard length 75 mm to 130 mm) had been brought alive to our Hamburg laboratory. Their phototactic behavior was investigated and compared with that of 4 specimens of their epigean predecessor *Rhamdia laticauda* (standard length 130 mm to 155 mm) which were captured in Mexico and with six specimens of the related surface fish *Rhamdia guatemalensis* (standard length 70 mm to 110 mm) which were derived from offspring of *R. guatemalensis* from Yucatan (Mexico). All fish were individually tested for their choice-preference behavior to white light of different intensities.

The fish were placed into experimental tanks (25 l) subdivided into a darkened and a lighted compartment. After seven days of acclimation under bright light (620 Lux at the bottom of the lighted half) in a light-dark cycle of 12:12 h, the time the fish spent in the lighted compartment was recorded during a time period of 5 minutes three times the day over 5 days thus giving a total of 30 experiments. Subsequently, the same experiments were performed using lower light intensities (50 Lux and 3 Lux at the bottom of the lighted half).

The authors are greatful to the "Johanna und Fritz Buch Gedächtnisstiftung" and the "Hanseatische Universitätsstiftung" who financially supported these studies. R. Stawikowski (Gelsenkirchen) kindly determined the cichlid species.

TOPOGRAPHIC AND PHYSIOGRAPHIC DESCRIPTION

The San Antonio Cave consists of an accessible slightly sloping main branch with a length of about 500 m. A partially explored upper level passage is found some 300 m from the main cave entrance. The cave creek begins at the end of the main branch forming a little cascade between boulders of breakdown. The breakdown prevents any further human penetration into the main branch of the cave (Fig. 1). From its emergence the creek flows for a distance of about 320 m, and then disappears into a lower passage and is invisible. With the exception of a spacially limited breakdown area, the so-called basin, the creek remains inaccessible until it discharges from the front of the cave.

The creek flows between steep banks of loamy soil. During the dry season the creek is about 0,5 m wide, 10 cm deep and shows rather rapid water flow. Only two sections have less current. One of these (pool 1) is located at the base of the emergence cascade, the second (pool 2) is formed at about 130 m downstream. Absolutely stagnant, isolated pools are situated in the upper level side branch of the cave system. Water temperature is 22°C.

The original cave entrance is blocked by breakdown, and water can pass only through narrow crevices. Due to this the drainage is retarded. Rainfalls may cause a quick rise of the water level in the cave for a short time. In February 1988 the basin was totally flooded for few days. During the rainy season, however, the water level rises

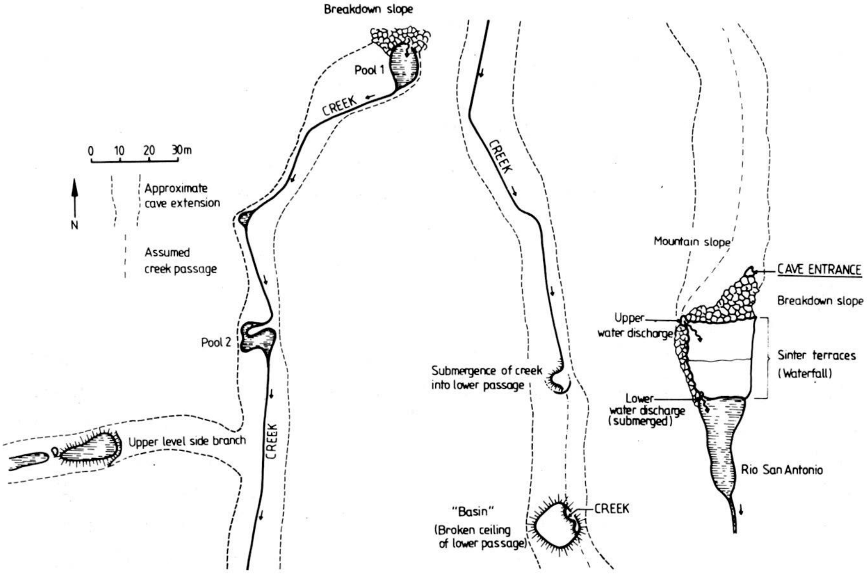

Fig. 1 — The explored section of the Cueva del Nacimiento del Rio San Antonio

even higher. At least in parts, the water body totally fills the cave up to the ceiling. In addition to the discharge within the pool in front of the cave, water then starts streaming out of a second opening in the breakdown slope about 5 m above. The increased water flow causes a considerably sized waterfall to develop. This waterfall has over the years eroded the initial section of the epigean Rio San Antonio for some distance, forming the above mentioned pool.

SPECIES SPECTRUM AND DISTRIBUTION OF THE FISH AND CRUSTACEAN FAUNA

Cave species

- *Procambarus oaxacae reddelli* Hobbs, 1973 a (Cambaridae, Decapoda)

P. oaxacae reddelli has lost the dark body pigmentation. The pigmentation does not regenerate under day light conditions when the crayfish are kept in the laboratory. The complex eye has regressed to a tiny dark spot located on the tip of the eye stalk. It consists of a reduced number of intact ommatidia (Wilkens, 1986). The crayfish therefore cannot merely perceive light but are still able to visualize approaching figures.

P. oaxacae reddelli is the most conspicuous among the crustacean cave species of the San Antonio Cave. It can be found throughout the subterranean creek system, but prefers passages with less current.

- *Macrobrachium villalobosi* Hobbs, 1973 b (Palaemonidae, Natantia)

The shrimp *M. villalobosi* has also totally lost its dark body pigmentation. No darkening can be observed when kept under day light conditions for several months. The compound eye is reduced to a tiny dark pigment spot on the tip of the eye stalk. Several specimens were observed to carry large eggs beneath the pleon. They number about 15 and have a diameter of 1.0 mm. The development takes a time of at least 3 months after which a postlarva of about 2 mm in length hatches.

In the cave *M. villalobosi* is much rarer than *P. oaxacae reddelli*. It occurs in stagnant pools or portions of the creek with very slow water movement. Specimens prefer deeper water bodies as they are found in the upper level passage or in the pool beneath the water fall (Fig. 1).

- *Potamalpheops stygicola* Hobbs, 1973 b (Alpheidae, Decapoda)

P. stygicola shows no body coloration when caught in the cave. In the laboratory, however, stellate erythrophores are developed after some time. This is probably due to the food containing carotinoids. The outer appearance of the eye coincides with that of *M. villalobosi*.

In the cave *P. stygicola* did not occur in the creek but in extremely shallow nearly or completely isolated puddles. Here it was found associated with *Antromysis reddelli* Bowman (Mysidacea).

- *Rhamdia reddelli* Miller, 1984 (Pimelodidae, Pisces)

The specimens of the catfish *R. reddelli* caught in their natural biotope show a light body coloration. When kept in the laboratory they will become darkish grey. There is no considerable interindivi-

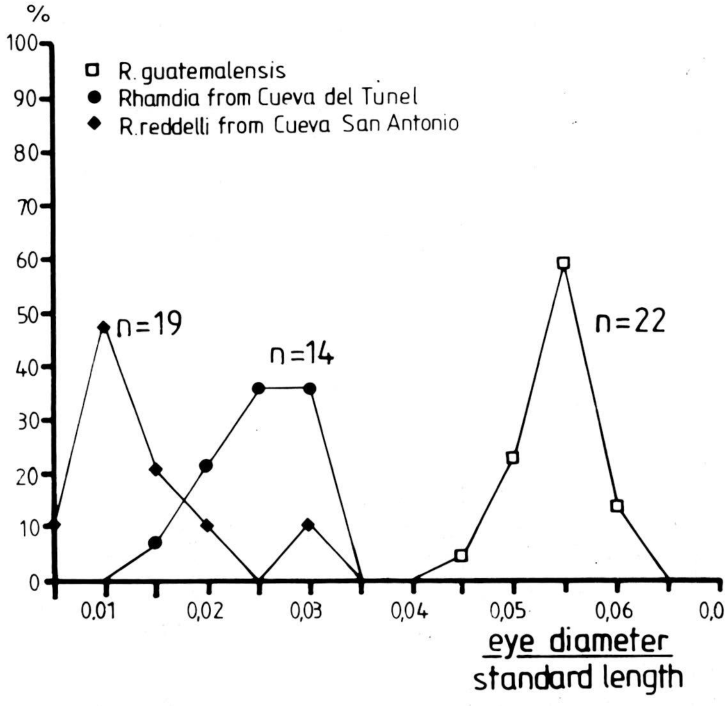

Fig. 2 — Comparison of eye size in the epigean *Rhamdia guatemalensis*, the cave *R. reddelli*, and the undescribed Cueva del Túnel cave population (Samples from 1982, 1986, and 1988)

dual variability of pigmentation. The eyes are reduced and sunk beneath the body surface. They show a bimodal size distribution. The mean eye size is lower than that of another cave-dwelling form of *Rhamdia* (Fig. 2).

The body size of *R. reddelli* ranges from about 6.0 to 15.0 cm (Fig. 3). All specimens were in a good nutritional state and did not show signs of malnutrition, as could be observed in the population of cave-inhabiting *Rhamdia* from the Cueva del Túnel in 1988 (Fig. 4).

In principle *R. reddelli* is distributed throughout the creek of the San Antonio Cave. However, the catfish are usually found in larger numbers in the sections with less rapid current (pool 1 and 2) and in the so-called "basin" (Fig. 1). During the dry season the "basin" only contains water after an occasional rainfall. At such times it is

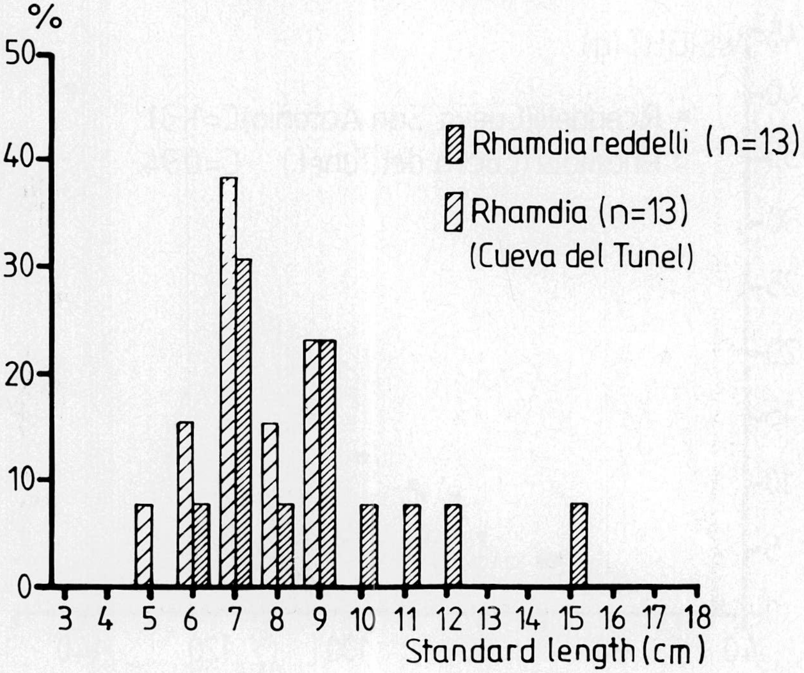

Fig. 3 — Distribution of body size in specimens of *R. reddelli* and the undescribed Cueva del Túnel cave population (Samples from February 1988)

immediately invaded by specimens of *R. reddelli.* They are probably attracted by organic matter which is washed into it from the banks of the subterranean creek and finally sinks to the bottom in this rather slowly streaming section. Presumably these specimens normally stay in the narrow passages between the "basin" and the cave entrance (Fig. 1).

Epigean species

In the subterranean creek no epigean invaders were found. The epigean creek adjacent to the cave entrance, however, is inhabited by a rich fish and crustacean fauna. The most common fish species is *Astyanax fasciatus* (Cuvier, 1819) (Characidae) followed by several species of Cichlidae (*Thorichthys ellioti* Meek, 1904, *Cichlasoma fenestratum* (Günther, 1860), and an introduced African *Oreochromis*

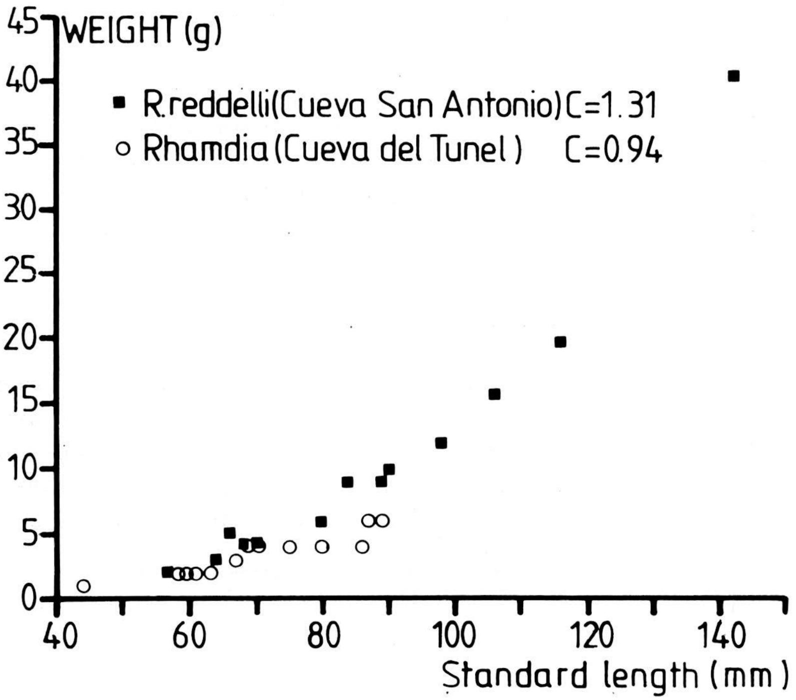

Fig. 4 — Body size and weight of specimens of *R. reddelli* from the San Antonio Cave and of the undescribed Cueva del Túnel cave population (Measurements two days after sampling)

spec.) which all closely approach the submerged area of the lower water discharge of the cave creek. Furthermore *Xiphophorus helleri* Heckel, 1848, *Heterandria bimaculata* (Heckel, 1848), and *Belonesox belizanus* Kner, 1860 (Poeciliidae) occur. At night the active species spectrum changes. Between rocky fissures the heads of some synbranchid eel specimens of the genus *Ophisternon* are protruded. The most conspicuous, however, is a great number of eyed and pigmented *Rhamdia* which can be observed swimming throughout the pool. They have been determined as belonging to the species *R. guatemalensis* (Miller, 1984). These fish show a maximum size of about 200 mm standard length.

THE PHOTOTACTIC BEHAVIOR

Cave Crustacea

Among the cave crustacean species only *P. oaxacae reddelli* shows a light reaction. It is very intense and clearly photonegative. *M. villalobosi* as well as *Potamalpheops stygicola* do not seem to have a photopositive or photonegative response.

Epigean and Cave Rhamdia

The two tested epigean species *R. guatemalensis* and *R. laticauda* as well as the cave-dwelling *R. reddelli* exhibit a significantly photonegative behavior with respect to all three tested light conditions (Fig. 5). There is no correlation between the degree of photonegative response and the used light intensities in any of the tested groups.

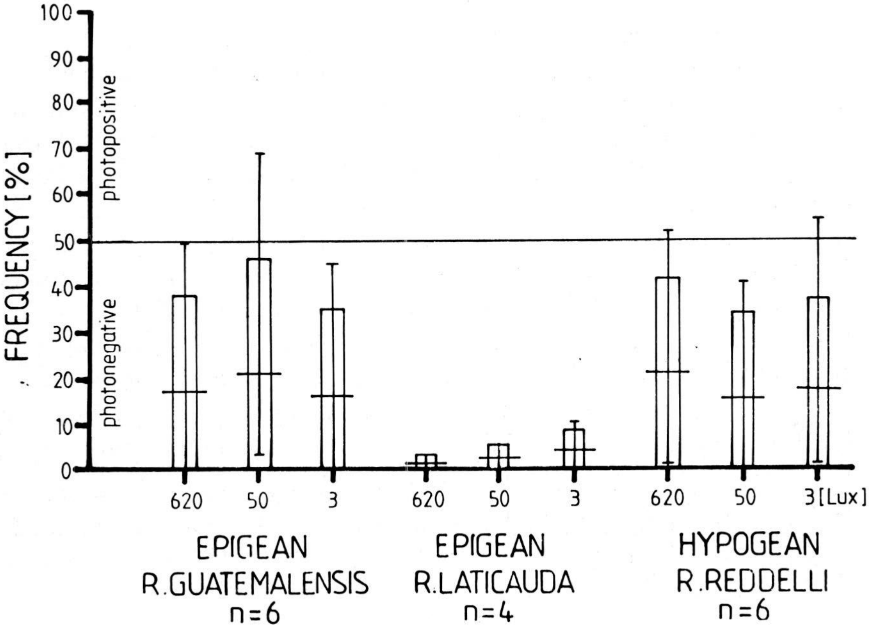

Fig. 5 — Index of light reaction in epigean and cave *Rhamdia*.

The photonegative behavior of the epigean *R. laticauda* differs considerably from that of both *R. guatemalensis* and *R. reddelli*. Contrary to these species, *R. laticauda* exhibits an extreme degree and a low variability of scotophilic behavior. Although only a small number of fish were available for the behavioral experiments (n = 6; 4), the photonegative response of the cave fish *R. reddelli* was found to be significantly decreased under high light intensities (620 Lux) compared tō its epigean predecessor *R. laticauda* (MAN-WHITNEY TEST: $p < 0.025$).

DISCUSSION

The special hydrographic situation in the San Antonio Cave causes a tremendous fluctuation of living conditions and a periodic large extension of the aquatic environment. During the dry season the aquatic organisms mainly occur concentrated in a small, rapidly streaming creek, whereas during the rainy season they can spread over a slowly-moving enlarged water body.

The most remarkable phenomenon of the San Antonio Cave fauna, however, is its clear cut separation from outside although a continuous connection is provided by the river emerging from the cave. Not a single invading epigean specimen was found in the basin which is close to the cave entrance. This situation is particularly demonstrated by the troglophilic *R. guatemalensis* which is abundant outside the cave. According to Miller (1984), the epigean predecessor to the cave fish *R. reddelli* is *R. laticauda* - a species today obviously not occuring outside the San Antonio Cave. This has no relevance, though, because the closely related *R. guatemalensis* seems to be well adapted for the colonization of caves and is known to be a frequent invader into the underground waters of Yucatan (Hubbs, 1938; Wilkens, 1982). Furthermore, laboratory studies have revealed that specimens from outside the San Antonio Cave can successfully hybridize in the laboratory with the cave *R. reddelli*.

The absence of invading specimens of any epigean species might be due to the fact that the narrow water passages near the cave entrance are populated by specimens of the carnivorous and very aggressive species *R. reddelli* and *P. oaxacae reddelli*. These forms probably concentrate at this place because they have the opportunity to feed and prey upon invading specimens. Thus, the absence of any individual of one of the epigean species in the cave could be caused by these aggressive species which form a kind of filter in the entrance region.

Consequently, the location close to the cave entrance is occupied by large and dominating specimens whereas smaller cave fish are found in the more distant regions. In the food poor environment this location is presumably very profitable.

Contrary to the situation today, epigean *Rhamdia* were probably frequent invaders into the San Antonio Cave system at the beginning of their troglobitic evolution. The results on the phototactic behavior of both *R. guatemalensis* and *R. laticauda* are in accordance with the hypothesis that the initial colonization of caves might be supported by a scotophilic behavior. The extremely scotophilic *R. laticauda* seems to be behaviorally much more adapted to cave life than the related epigean *R. guatemalensis*. The greater dependence of the latter species on visual orientation is not only reflected by its highly variable and rather moderately photonegative behavior but also morphologically by its relatively greater eyes. Thus, it is not surprising that *R. laticauda* founded a series of distinct, troglobitic populations in Mexico whereas *R. guatemalensis* evolved a variety of more or less troglophilic and morphologically slightly different populations in Yucatan (Hubbs, 1938) but obviously no true troglobitic form. In the sense of Howarth (1981), *R. guatemalensis* may be characterized as a well-adapted troglophilic species which tends to remain an opportunistic exploiter of the cave environment but not to evolve to a troglobite.

The speciation of *R. reddelli* probably began under the conditions of direct genetic contact between epi- and hypogean populations, as has also been described for a cave population of the characin *Astyanax fasciatus* (Wilkens and Hüppop, 1986). The final separation and speciation of a cave-dwelling population in the San Antonio Cave was certainly not due to factors such as an increased photonegative behavior. Such a segregation mechanism was suggested for the Mexican cave fish *Astyanax fasciatus* by Breder and Rasquin (1947). The phototactic response of *R. reddelli*, however, is significantly less photonegative than that of its epigean ancestor *R. laticauda* and exhibits a high variability (Fig. 5).

All recent studies on the phototactic behavior of cave fish and their epigean relatives gave great evidence against earlier contentions that an increased scotophilia is generally of significance for the speciation of cave fish. A series of investigated cave-dwelling populations of *A. fasciatus* (Romero, 1985; Langecker, 1989) as well as the Brasilian cave fish *Pimelodella kronei* (Trajano, 1987) show a greatly reduced photonegative behavior in comparison to their epigean ancestors just as *Rhamdia reddelli*. Further evidence against such a significance of scotophilia is given by its differential expression during ontogeny. Young specimens of the African cave fish *Caecobarbus geertsi* and of cave-dwelling *A. fasciatus* were shown to react almost indifferently to light (Thines, 1958; Romero, 1985). The failing of the photonegative behavior in stages when it proves to be most useful (Thines, 1958) is not in accordance with its suggested function as a separating mechanism.

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Metabolic efficiency and regulation of body weight: a comparison between life in hypogean and epigean ecosystems

Jayant Biswas *

SUMMARY

In the present study metabolic efficiency in the epigean and hypogean populations of *Nemacheilus evezardi* (Day) was examined. Different experiments were conducted, in both populations, by keeping them either in restricted oxygen or restricted feeding conditions, including starvation. Results clearly show that the rate of oxygen consumption for the hypogean population was significantly less as compared to its epigean counterpart. Further, results also suggest that the hypogean population has a tremendous capacity to maintain its metabolic activity and regulate its body weight under severe conditions characterized by an absence or a limited supply of food.

INTRODUCTION

Kotumsar cave, an ideal and simplified subterranean cave is situated at the bank of the river Kanger in Kanger valley National Park, India, (Lat.: 18°52'09" N; Long.: 81°56'05" E). It has a remarkable constancy in various geophysical and chemical characteristics, (Biswas, 1990). Several true cavernicoles have been reported from this cave (Sinha and Agarwal, 1977; Biswas, 1990; Biswas et al., 1990 a,b).

The subterranean organisms are usually familiar with the situations characterized by decreased and erratic food supply. The reduction in respiratory intensity and a general decrease in activity pattern in many cavernicoles reflect their physiological adaptation in food-limited environment. This phenomenon is often referred as metabolic economy (Poulson, 1963; 1964).

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In the present study the epigean and hypogean populations of *Nemacheilus evezardi* (Day) were used. The former inhabits in the Kanger river system, whereas the latter has successfully colonized the Kotumsar cave. It has already been established that the hypogean population exhibit several morphological, behavioural and physiological divergence (Biswas, 1990; Biswas et al., 1990a, b, c; Biswas and Pati, 1991). The object of the present investigation is to compare the metabolic efficiency between the epigean and hypogean populations.

MATERIALS AND METHODS

Live specimens of *Nemacheilus evezardi* belonging to epigean and hypogean populations were collected from their natural habitat. The former inhabits fast flowing hill streams and the latter is a cave dweller. All fishes were brought to the laboratory and allow to adapt separately in two identical aquaria (75 × 30 × 30 cm). The cave fishes were transported in a light tight container and kept inside a dark room throughout the course of the study. A dim red light was used inside the dark room in order to perform different manipulations on the fish. The water temperature varied between 26±1°C during all experiments. The stock aquarium containing the river fish was kept in the animal quarter, in natural daylenght conditions and in the ambient temperature at Raipur (Lat.: 21°14'N; Long.: 81°38' E).

The fish chosen for different experiments were approximately of the same snout to vent lenght i.e.. 4.0±0,5 cm. Their body weight was 585±10mg (n = 20; 10 each).

Experiment-1. Oxygen consumption by muscle tissue.

Four individuals, each from hypogean and epigean populations, were randomly chosen and starved for a period of one week. On seventh day, the muscle tissue was isolated carefully from each individual and rate of oxygen consumption (μl O_2/g/h) was monitored with the help of an oxygen electrode.

Experiment-2. Feeding diets and body weight.

Sixteen cave or river fish were chosen from the stock aquaria and randomly divided into four groups (Groups - A-D) of four each. Each fish were maintained individually in a separate one liter jar. Prior to each experiment each individual was weighed. Fishes of group 'A' were fed with minced liver *ad libitum*. Fishes of group 'B' and 'C' were fed daily with 3 mg/g and 1 mg/g body weight, respectively. The fishes of group 'D' were starved throughout. The water was changed every fourth day. On day 31 each fish was reweighed and the changes in body weight was compared. An arc-sine transformation was made on each datum. Data were analyzed by analysis of variance (ANOVA) and Duncan's multiple-range test (Bruning and Kintz, 1977; Duncan, 1955).

RESULTS

Results are summarized in figures 1-3.

Oxygen consumption of muscle tissue: the rate of oxygen consumption by muscle tissue of epigean fish was higher as compared to its hypogean counterpart (Fig. 1; $P < 0.05$). Furthermore, hypogean fish survived longer than the epigean fish in an oxygen limited environment (Fig. 2; $P < 0.001$).

Feeding diets and body weight: the results of ANOVA show a statistically significant species effect as well as a diet effect. However, the interaction effect was not statistically significant which shows that both factors are independent (Fig. 3). Body weight of either epigean or hypogean fish declined following starvation as well as restricte feeding. However, the magnitude of decrement was more marked in the epigean fish than in its hypogean counterpart ($P<0.01$).

DISCUSSION

Several direct or indirect techniques have been used to study the metabolism in varieties of cavernicoles (see reviews: Poulson, 1964; Vandel, 1965; Barr, 1968; Culver, 1982; Hüppop, 1985). The first systematic account on the cave adaptive features including the measurement of metabolic rates was published by Poulson (1963), on a series of hypogean Amblyopsid fish of different phylogenetic age. He observed a maximum metabolic rate in the epigean *Chologaster agassizi* over the troglobitic *Typhlichtys subterranea* and *Ampblyopsis spelaea* to the most cave-adapted species *Amblyopsis rosae*. Furthermore, Ercolini et al. (1987) drew identical conclusion in comparing the rate of oxygen consumption among a troglobite

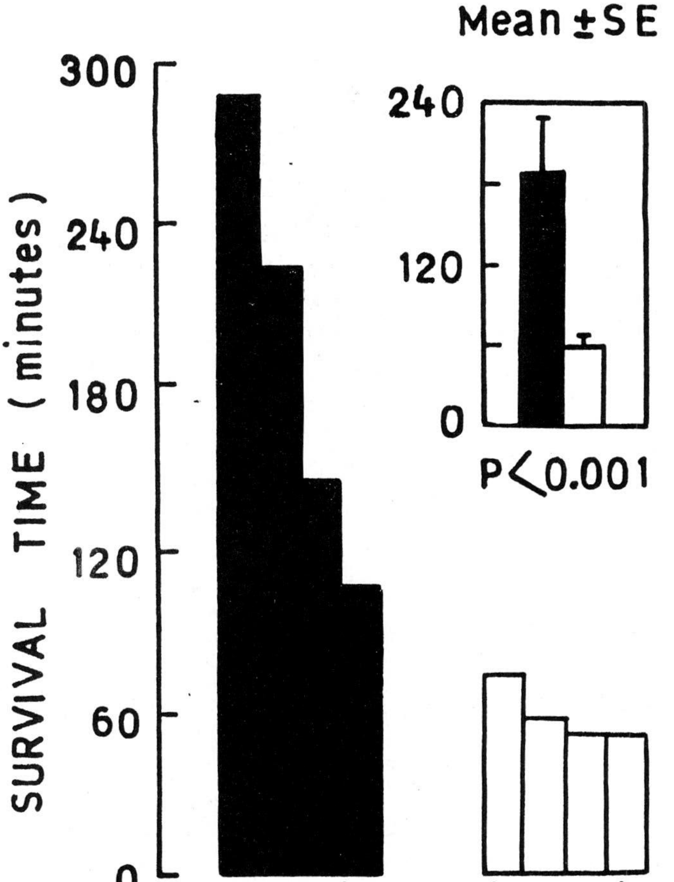

Fig. 1 — Histograms illustrating rate of oxygen consumption by muscle tissue of cave (hypogean) fish & river (epigean) fish. Inset showing the mean ± 1 SE of cave and river fish which differs significantly from each other (P from t-test <0.05).

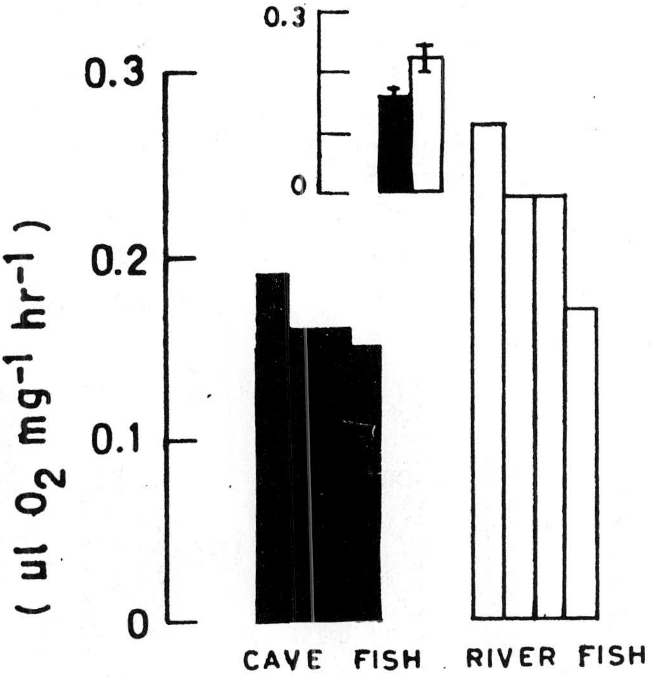

Fig. 2 — Histograms representing survival time of either cave or river fish in a closed bottle. Right inset showing the mean ± 1 SE of cave and river fish wich differs significantly (P from t-test <0.001).

(Barbopsis devecchii), a troglophile *(Phreatichtys andruzzii)* and their closest epigean ancestor *(Puntius lateristriga)*.

As is known, different biological activities may modify the metabolic rate of a living organism, the influence of metabolism modifying factors can be eliminated when the oxygen consumption of a tissue can be monitored *in vitro* (Dickson and Franz, 1980; Biswas, 1990; Biswas and Pati, 1991). In the present study the respiring rate of muscle tissue of starved epigean or hypogean fish was measured *in vitro* and results evidence a lower metabolic rate in the hypogean fish. Further, a period of only one week starvation imposed a marked change in muscle tissue respiration, in the epigean population only, as compared to its oxydative metabolism in full feeding condition, its values being 0.427 ± 0.1 μlO_2/g/h

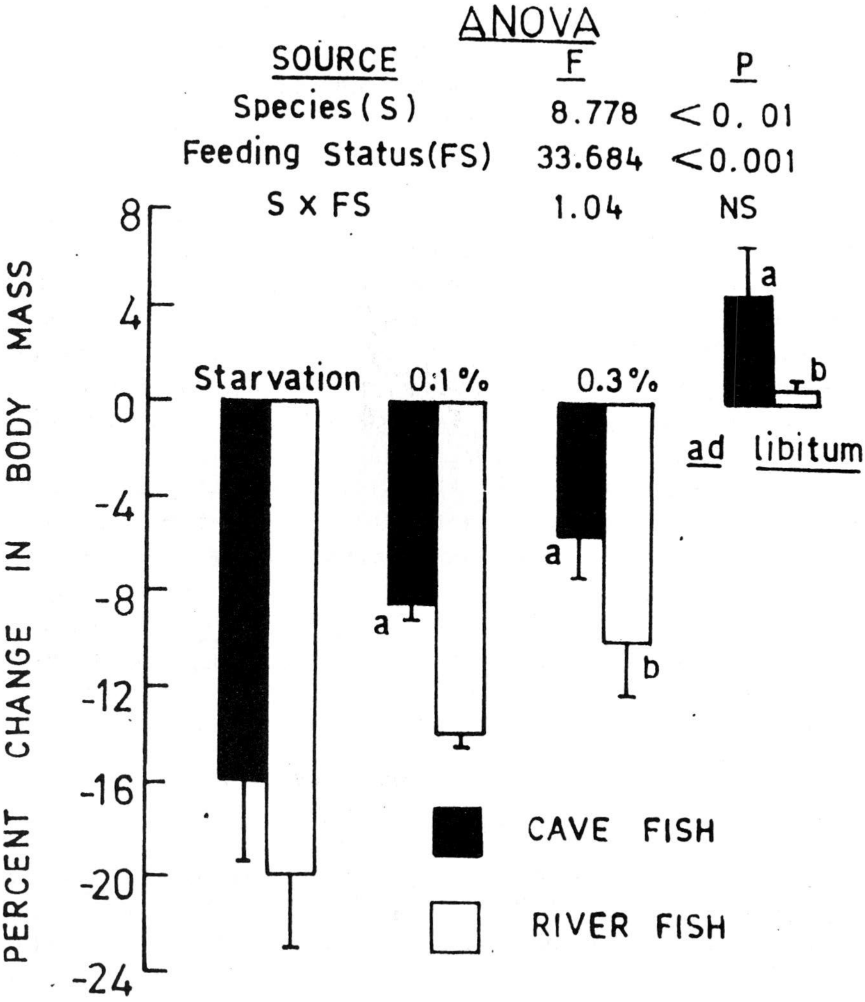

Fig. 3 — Histograms illustrating percent change in body mass of either cave or river fish following starvation or restricted feeding. The percent change in body mass was computed relative to the initial body weight of an individual fish. (a) Differs from the mean value of starved cave fish. (b) Differs from the mean value of starved river fish.

(Biswas and Pati, 1991). These results could be favourably compared with those published earlier (Jeannel, 1929; Burbanck et al., 1948; Dresco-Derouet, 1959). It has been already demonstrated that the fishes belonging to the cave population exhibit an air-gulping behaviour which is completely absent in their epigean counterparts (Biswas et al., 1990a). Upon denied access to atmospheric oxygen, hypogean fish survived 132 minutes longer than its epigean relatives (Fig. 2). Although the method employed was relatively crude, it supports the above findings.

In another experiment, it was found that the reduction in body weight was always greater in epigean fish, irrespective of the feeding diets. Under an *ad libitum* feeding schedule, the hypogean fish gained more weight as compared to its epigean relatives. Hüppop (1986) reported, that during a starvation period of 29 days the body mass loss in the hypogean *Astyanax mexicanus (alias Anoptichthys sp.)* was only 9.5%, whereas a 16.5% bulk loss was recorded in its epigean counterpart *Astyanax fasciatus*.

When food was supplied only at the rate of 1 mg/g body weight, hypogean fish lost less weight as compared to epigean fish. It is thus clear that 1 mg/g body weight diet was as worse as starvation for the epigean fish only. The cave fish with same food regimen (1mg/g) shows statistically significant change from its respective starved group. Further, the food regimen (3mg/g) shows same effect for both the populations (Fig. 3). This suggests that in a food limited environment hypogean *Nemacheilus evezardi* has developed some mechanism(s) to reduce energy expenditure.

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Population size of Pyrenean troglobiont coleopters (Speonomus species) in a cave in Belgium

Raymond Tercafs *,** **and Christine Brouwir** *

SUMMARY

The population size of three troglobitic species of *Speonomus* (Coleoptera Bathysciinae) from the Pyrenees, intentionally introduced in 1969-1970 into the "Grotte de Ramioul" cave (Province of Liège, Belgium) has been studied using the mark-recapture technique. It has been shown that the three cave levels possess large *Speonomus* populations (upper network: 12,718; middle network: 13,902; lower network: 18,249 individuals) and that the superficial underground environment is also colonized, including the schist area. The most abundant species is *Speonomus longicornis* (relative frequency between 0.73 to 0.89). The two other species are present in the relative frequency between 0.04 and 0.23 for *S. diecki*, and between 0.03 and 0.11 for *S. stygius*.

The overall *Speonomus* population size in the cave is estimated at 44,000 individuals.

INTRODUCTION

Three species of troglobiont Bathysciinae Coleopters have been intentionally introduced into the Ramioul cave (Borough of Flémalle, province of Liège, Belgium) by Bouillon and Hubart (1982). They are *Speonomus diecki* Saulcy, *Speonomus stygius* Dieck, from the Surroque mountain mass (Saint-Girons, Ariège, France) and *Speonomus longicornis* Saulcy from the Plantaurel mountain mass (Foix, Ariège). On June 3, 1969, 200 *Speonomus longicornis* were released at a depth of 60 metres below the plateau. On May 8, 1970, 100 *Speonomus stygius* and 80 *Speonomus diecki* were also released at a depth of 30 metres. These proportions between species released were

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chosen by experimenters in so far as, according to knowledge at the time, they corresponded to the proportions generally encountered in the stations of origin. These 380 specimens introduced into the cave seem to have found conditions there favourable for their development and expansion. Trapping carried out some years later revealed hundreds of individuals (Hubart, 1983). It was therefore of interest to study in greater detail the expansion of these transplanted species, evaluating the present population densities in the different levels of the cave and measuring the relative proportions of the three species. It was also useful to verify the expansion of the *Speonomus* towards the superficial subterranean medium near the cave.

MATERIAL AND METHODS

1. Description of the study site

The Ramioul cave is situated at Ivoz-Ramet (coordinates Lambert: 224.97/141.24). It is entirely comprised in the carboniferous limestone which it crosses throughout its width. It is travelled through by an underground stream which enters the soil by sinkholes at the southern end of the limestone. Coal-bearing schists covered with humus are contiguous to the limestone mass and extend northwards (Hubart, 1983; Quinif, 1985). The cave is composed of three levels:

- an upper level, fossile rich in speleothems;
- a middle level, also fossile, poor in concretions;
- a lower level, accessible from the middle level by a 30-metre well. It is an active network about 700 metres long.

The temperature of the cave is fairly stable at around 7 to 9.5°C. Maximum variations are observed in the lower part of the cave, where the underground stream has thermal influence. In winter the air temperature is 7 ± 0.5°C; in June it is 8.2 ± 0.4°C. During the experimental period (15.04.87 - 26.06.87), the following air temperature were recorded: lower network: 8.2-8.6°C.; middle network: 8.4-9.0°C.; upper network: 8.4-9.2°C. The relative humidity, even in the dry period, never decreases below 98%. Trophic resources are unequally distributed (Delhez et al., 1973): - the upper level is poor in alimentary resources apart from roots and woody wastes;

- the middle level encloses a series of hibernating and estival

trogloxene species subsisting in latency for several months;
- the lower level receives a large quantity of organic materials during the water rise.

2. *Marking individuals*

Speonomus longicornis have been captured and marked on the elytrons with a spot of model-making paint, using a fine paint-brush. To test the resistance of the mark to humidity and chafing, the animals were placed in a terrarium the bottom of which is lined with damp plaster covered with clay. The terrarium was kept at 5 ± 1°C, in a dark cold room. Food consists of pieces of cheese. After four months it was found that the individuals still bear a coloured mark. Of the 20 specimens at the beginning of the experiment, four were dead. A second marking was then made on the remaining sixteen individuals. After two months, both marks were still visible and no mortality was observed. Examination by a scanner electron microscope showed that the paint was well localized on the surface of the elytrons, where it was held firm by the thorns covering them. The mark did not spread and did not penetrate under the elytrons. There was no paint on the tergite's cuticles. This technique and the type of paint used therefore seemed suitable for the purpose of the study, since they enable effective long sterm marking. It is analogous to the technique used by Cabidoche (1966) and Delay (1975). For experiments on the terrain, fifteen colours have been used and 2,202 individuals were marked (Table 1).

3. *Captures and recaptures*

The cave studied consists of three levels with different features. That is why several stations have been chosen in each of them (Fig. 1): four in the upper network, eight in the middle one and three in the lower one. A marking colour was chosen for each of them. The first capture was carried out by putting out an organic bait (Shrimp head) for ten days. It has been demonstrated by Juberthie-Jupeau (1982) that the olfactory stimulus does not intervene in the concentration of *Speonomus* around the bait. It is exploratory behaviour of a chancy type which leads these animals to the bait.

Table 1 — Study of the *Speonomus* population size in the "Grotte de Ramioul" cave in the 3 networks: upper, middle and lower.

STATION N°	CAPTURE DATE	NUMBER M	MARKING COLOUR	RECAPTURE DATE	NUMBER n	R	N	S	RELATIVE PROPORTIONS
Upper network									
1	15.04.87	250	GREEN	30.04.87	69	2	5,833	2,853	242 1, 0 d, 8 s
2	15.05.87	69	MAUVE	01.06.87	154	2	3,565	1,770	52 1, 4 d, 12 s
3	05.06.87	152	WHITE	20.06.87	28	1	2,200	1,200	120 1, 12 d, 18 s
4	26.06.87	28	SKY BLUE	09.07.87	80	1	1,120	640	25 1, 0 d, 3 s
Middle network									
5	15.04.87	328	GREY	30.04.87	66	4	4,395	1,726	328 1, 0 d, 0 s
6	15.04.87	44	ORANGE	30.04.87	79	1	1,738	1,000	0 1, 26 d, 18 s
7	15.05.87	69	YELLOW	01.06.87	135	12	690	183	58 1, 3 d, 8 s
8	15.05.87	79	RED	01.06.87	41	0	-	-	62 1, 2 d, 15 s
9	05.06.87	129	TURQUOISE	20.06.87	204	11	2,200	424	95 1, 3 d, 31 s
10	05.06.87	38	PALE GREEN	20.06.87	86	7	413	131	33 1, 2 d, 3 s
11	26.06.87	178	FUCHSIA	09.07.87	210	16	2,209	499	150 1, 3 d, 25 s
12	26.06.87	74	BLACK	09.07.87	183	5	2,257	266	69 1, 1 d, 4 s
Lower network									
13	15.05.87	335	BLUE	01.06.87	298	36	2,707	411	311 1, 12 d, 12 s
14	05.06.87	219	PINK	20.06.87	215	17	2,628	577	126 1, 92 d, 1 s
15	26.06.87	210	SILVERY	09.07.87	153	13	2,487	550	123 1, 75 d, 12 s

The station numbers refer to figure 1. M = total number of individuals captured at the first capture. n = total number of individuals recaptured. N = estimated total population. s = standard deviation. Relative proportions = number of each species in the batch captured (M): 1 = *Speonomus longicornis;* s = *S. stygius*; d = *S. diecki*.

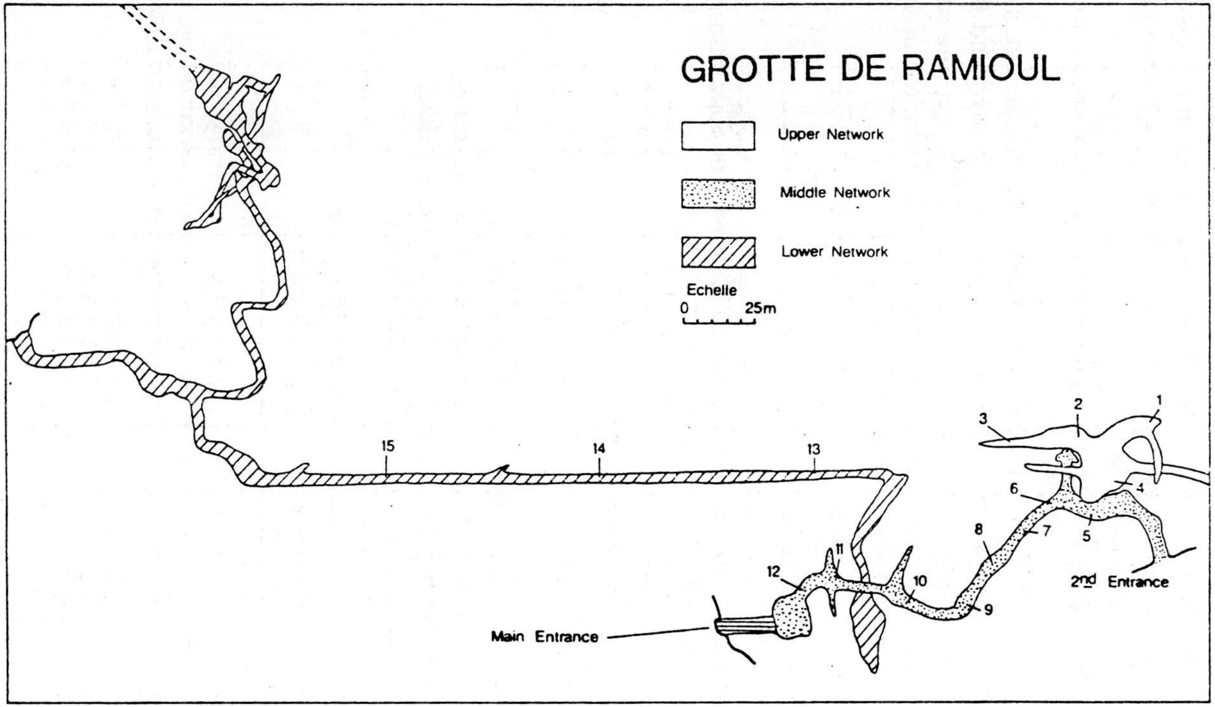

Fig. 1 — Stations of capture and recapture of *Speonomus* species in the "Grotte of Ramioul".

Only a gustative stimulus then keeps them near. The effectiveness of this behaviour through its principal components (movement speed, angulation and lenght of segment between each change of direction) has been studied (Tercafs, 1989).

After being marked in the laboratory, the individuals were released on the site of capture.

5 days later, bait was placed for a further 10-day period. The animals present at the end of the tenth day were captured and the proportion of marked individuals was calculated. The capture and recapture dates are shown in Table 1. No individual marked in one station was found in another one or in the S.S.M.

4. *Mathematical treatment*

The equation used for determining the density of population is that of Petersen, modified by Bayley (Roff, 1973):

$$N = \frac{M\,(n + 1)}{R + 1}$$

where N = estimate of the sizes of the population
M = number of animals marked when first captured
n = total number of animals counted on recaptures
R = number of marked animals retaken

The typical standard deviation of N is given by:

$$S = \sqrt{\frac{M^2\,(n + 1)\,(n - R)}{(R+1)^2\,(R+2)}}$$

The equation used to calculate the standard deviation on the relative frequency (f/n) of each *Speonomus* species is (Cramer, 1954):

$$S = 1.96 \times \frac{\sqrt{f}\,(n\text{-}f)}{n^3}$$

where f = absolute frequency
n = sample size

RESULTS

1. Estimate of population densities in the cave

The results are shown in Table 1. It appears that the effectiveness of the trapping varied from 28 to 250 individuals per station in the upper network, from 38 to 328 in the middle one and from 210 to 335 in the lower one. The number of marked individuals recaptured after fifteen days was still very low in the upper network (1 or 2 individuals), low in the middle network (between 0 and 16) and definitely higher in the lower network (13 to 36 individuals). These recaptures made it possible to estimate the populations in the different sampling stations but still with a very high standard deviation. In the upper network, the four stations studied gave a calculated value from 1,120 ± 640 to 5,833 ± 2,853. In the middle network (8 stations), the calculated values varied from 413 ± 131 to 4,395 ± 1,726. In the lower network (3 stations), they varied from 2,487 ± 550 to 2,707 ± 411.

The relative frequency of the three transplanted species were calculated on the basis of the first captures. Results are shown in Table 2 A. *S. longicornis* is dominant in the three networks, with a relative frequency of 0.89 ± 0.03 in the upper one, 0.85 ± 0.02 in the middle one and 0.73 ± 0.03 in the lower network. *S. diecki* had a relative frequency varying from 0.03 ± 0.02 in the upper network to 0.23 ± 0.03 in the lower one. The relative frequency of *S. stygius* varied from 0.03 ± 0.01 in the lower network to 0.11 ± 0.02 in the middle one.

Table 2A — Relative frequency of *Speonomus* species in the 3 networks. Mean value ± standard deviation.

Network	Species *S. longicornis*	*S. diecki*	*S. stygius*
Upper	0.89 ± 0.03	0.03 ± 0.02	0.08 ± 0.02
Middle	0.85 ± 0.23	0.04 ± 0.01	0.11 ± 0.02
Lower	0.73 ± 0.31	0.23 ± 0.03	0.03 ± 0.01

Table 2B — Chi-square test for *S. longicornis* in the 3 levels

Comparison between	Chi-square	Confidence limits
Upper/middle	3.98	0.05-0.01
Upper/lower	42.3	> 0.01
Middle/lower	33.5	> 0.01

A chi-square test was used to compare the relative frequency of *S. longicornis* in the three levels (Table 2 B). The results showed a high significant difference between the upper network and the lower network, and between the middle one and the lower one. A less significant difference appeared between the upper and the middle one.

The standard error was too high to test the two other species.

2. *Extension of species in the superficial subterranean medium.*

Twenty-eight trappings were made between April and June 1987. Nine stations gave positive results (51 individuals in all). They are all situated in the immediate proximity of the Ramioul cave and always in the limestone mass. No capture was made in the schist area.

DISCUSSION

Quite a lot of work has already been done to determine the number of individuals (N) of cavernicolous populations. The method most used is the one based on the equation of Lincoln-Petersen (Cabidoche, 1966; Mitchell, 1970 a and 1970 b; Peck, 1975; Keith, 1975; Cooper, 1975; Delay, 1975; Mitchell et al., 1977; Sbordoni et al., 1983).

Published results as regards troglobiont coleopters can be summarized in Table 3. The variations found basically stem from the size of the cave studied and the extent of the experiment. For

Table 3 — Population size of troglobiont Coleopters in several caves in France.

Name of cave	Situation	Species	Number	References
Pierre St Martin	Pyrénées (France)	*Aphaenops loubensi*	114-406	Cabidoche (1966)
Ste Catherine	Pyrénées (France)	*Speonomus infernus*	250-317	Juberthie (1960)
Pigailh	Ariège (France)	*Speonomus longicornis*	7,096-130,864	Delay (1975)

instance, the results from the Ste Catherine and Pierre St Martin caves concern only one gallery, whereas those from the Pigailh cave concerned the whole of it. Results obtained at the Ramioul cave show the existence of large populations of *Speonomus* in the three networks, with estimates varying between 413 and 5,833 in the different sample stations but with a high standard deviation, given the small number of recaptures. The lower network of the cave, which was studied for only about a hundred metres is, however, fully colonized as far as the sinkhole (Hubart, in litt.) and a further study would need to be carried out to know the total population of that deep part of the network.

The number of individuals captured in a 10 day trapping were the following (mean ± standard deviation see Table 1 for details):

Network	Capture	Recapture
Upper	124.7 ± 98.2	82.8 ± 52.5
Middle	117.3 ± 96.7	125.5 ± 66.6
Lower	254.6 ± 69.8	222.0 ± 72.7

Marked recaptured individuals are still small in number in the upper and middle levels, more numerous in the lower levels. Successive recaptures are respectively 1.5 ± 0.6, 7.0 ±5.6 and 22.0 ± 12.3. That higher value seems to indicate less scattering of the individuals in the lower level, after a release. The influence of a rather lower temperature in that level, responsible for less locomotory activity, is not be excluded, but another factor may come into it: the geological structure of the galleries. In the lower level, the latter are but little fissured, whereas the middle and upper levels have fissured clayey areas, as well as heaps of speleothems and various deposits which increase the volume of available territory.

To estimate the whole population of the cave, we must considered two hypotheses:

a) all the *Speonomus* of the cave network belong to a single population. In this case the population size of the cave network could be calculated by an application of the Lincoln-Petersen formula, assuming as true parameters R, M and n, the sums of these parameters observed in the sampling stations belonging to the studies cave network.

b) the *Speonomus* are divided in several populations, without exchanges during the sampling time. In this case, the population size of the cave networks is the sum of N calculated from each sampling station by the Lincoln-Petersen formula. Because the marked animals were found exclusively in the sampling station where they were marked, it seems that this second hypothesis is more likely. So the population of the cave network could be estimated in this way. For the upper network (sampling station #1 to #4), the total is 12,718. For the middle network (station #5 to #12), the total is 7,822. In this level, where access is difficult, the number of stations (3), limited to a hundred or so metres in an accessible level of some 700 m, leads to an under-estimate. It is therefore logical to extrapolate using the calculated estimate density of one sampling station (2,607 ± 111), multiplying by 7 (ratio between the whole lower level, 700 m, and the studied section, 100 m) i.e. 18,249 individuals. The total population of the cave would therefore be 44,869 individuals in the accessible levels. There is manifestely scattering in the S.S.M., as sample surveys show presence in the vicinity of the cave (9 positive results in a 50 m area, negative results beyond that). An accurate estimate of the population is impossible here. Bearing in mind that captures take place only during exploratory behaviour, it is necessary for thousands of individuals to be present in the S.S.M. for the results obtained to be accounted for.

The behaviour of the *Speonomus* when seeking food is based on a "Brownian" type of search policy. This fact is an advantage when using the capture-recapture method, as this presupposes that marked individuals quickly mix with the existing population.

Analysis of the relative frequency of the *Speonomus* species shows that *Speonomus longicornis* is largely predominant (between 0.73 to 0.89, depending on the network). This situation is similar to that observed in the stations of origin; perhaps the species has a higher reproduction rate. Also, during the transplantation, 200 individuals were released, as against 80 *Speonomus diecki* and 100 *Speonomus stygius*. The proportions of *Speonomus diecki* and *Speonomus stygius* vary with the networks. *Speonomus diecki* seems dominant in the lower network, whilst *Speonomus stygius* seems dominant in the middle and upper networks. These variations are perhaps to be set in relation with the diversity of trophic resources in the three networks.

Recent capture has been made in the schist area in an artificial gallery at a distance of 120 metres from the cave entrance (Hubart, 1990). Its chemical composition (ampelitic schist calcined not so long for the extraction of alun), is not an obstacle to the expansion of the *Speonomus* species.

CONCLUSIONS

It is important to recall, first of all, the context in which the faunal transplantation took place in 1969 and 1970. The authors (Bouillon and Hubart, 1982) wanted to show that the superficial subterranean medium (S.S.M.) was the major habitat of cavernicoles, caves accessible to man being but a special case. By placing troglobionts in a new-medium - the Ramioul cave -, they desidered to carry out a controlled experiment in the study of expansion of a group of troglobiont species to the S.S.M. The Ramioul cave was chosen because it comprised no species that could compete with the transplanted *Speonomus* (Delhez et al., 1973). Furthermore, it is situated in an area where surface expansion is limited.

This transplantation experiment had already been carried out unintentionally at the Moulis cave (Ariège, France). That cave houses the underground laboratory of the French National Centre of Scientific Research, and numerous specimens belonging to various troglobionts escaped from the breeding places. They were found in the surrounding environment, but as neither the number of individuals that escaped nor their date of departure was known, it was impossible to draw conclusions (Christiansen, 1970). In the case of the Ramioul cave, the experimental conditions were controlled from the start and the following conclusions can be drawn:

- after 18 years the three species of *Speonomus, Speonomus longicornis, Speonomus diecki* and *Speonomus stygius* have developed large populations in the three networks of the cave;
- *Speonomus longicornis* considerably dominates the other two species;
- the nearby superficial subterranean medium (S.S.M.) is also colonized by the three species including the schist area.

ACKNOWLEDGMENTS

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Int. J. Speleol. 20 (1991): 37-45

Revision of the genus Troglophilus (Orthoptera, Rhaphidophoridae) in Crete, Greece

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SUMMARY

The genus *Troglophilus* (Orthoptera, Rhaphidophoridae) from Crete is revised using new data from specimens collected recently. The three previously reported species are considered to be only one, *T. spinulosus*, on the basis of morphological, ecological and distributional similarities. The species is more fully described and notes are given on its ecology.

INTRODUCTION

The genus *Troglophilus* has been considered to be represented in Greece by at least 6 species, 4 of them endemic (Willemse, 1984). *T. cavicola* is known from Austria, northern Italy, western Yugoslavia and central Greece. *T. neglectus* is known from Austria, western Yugoslavia and Greek Makedonia. *T. lagoi* is known only from Rhodos island. *T. spinulosus, T. roeweri* and *T. petrochilosi* are known only from Crete. In addition to these six, a new species of *Troglophilus* has recently been found on Santorini island (Beron, 1986).

As mentioned by Willemse (1985), the systematics and distribution of most cavernicolous orthopteran species in Greece have many problems as very few individuals, and in some cases subadults, have been used in descriptions. This has been pointed out by us in a previous paper (Kollaros et al., 1987) on the Cretan cavernicolous Orthoptera. In the present paper we provide more data on the genus *Troglophilus* in Crete and conclude that it is represented by only one species (*T. spinulosus*). We provide additional description of syste-

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matic characters where needed and make some comments on its ecology.

LITERATURE REVIEW

The first Cretan species of *Troglophilus* was described by Chopard (1921) under the name *T. spinulosus*. The description was based on a subadult male specimen collected by D. Bate in 1904 from cavities near the monastery of Gonia (Chania dept.).

Werner (1927) described a second species, *T. roeweri*, from two males and females (adults?) found in "Arkalospilios" cave in western Crete. The existence of this species was debated by Chopard (1957) who claimed that it was the immature of *T. spinulosus*. Boudou-Saltet (1978) described the female of *T. spinulosus* from a specimen found in "Sendoni" cave (Iraklion dept.) and a third species of *Troglophilus (T. petrochilosi)* from 1 male and 2 females, all adults, found in "Diktaion Andron" cave (Lasithi dept.). She supported the existence of *T. roeweri* and mentioned that the *Troglophilus* species are distributed as follows based on the then available data: *T. roeweri* in western Crete, *T. spinulosus* in central Crete and *T. petrochilosi* in eastern Crete. In our previous paper (Kollaros et al., 1987) we noted that there was a misunderstanding with the *Troglophilus* distribution. Bate had collected in 1905 the *T. roeweri* specimens from the monastery of Gonia (Chania dept. - western Crete) and not from the village of Gonia (Rethymnon dept. - central Crete) (Bate, 1913). Studying 30 characters of 150 samples, we concluded that two species probably exist in Crete, a "small" one and a "big" one, both widely distributed. At all events, the question whether the "small" species, corresponding to *T. roeweri*, was an immature *T. spinulosus* had not been answered.

METHODS

During the last two years, more than 70 caves, cavities and canyons from all over Crete have been visited in search for *Troglophilus* species and some of them have been sampled several times throughout the year. *Troglophilus* specimens were found in 14 localities (Fig. 1). Those without clear sexual characteristics such as

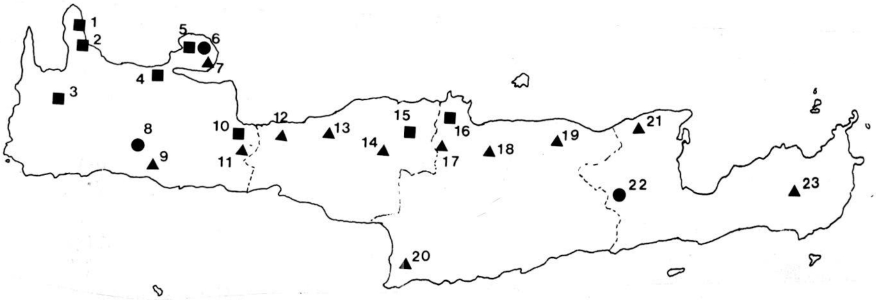

Fig. 1 — Map of Crete showing locations where *Troglophilus* specimens have been collected. (square: unconfirmed old records, circle: confirmed old records, triangle: new records) 1: Ellinospilios, 2: Moni Gonias, 3: Ag. Sofia, 4: Hania, 5: Achyrospilios, 6: Moni Gouvernetou, 7: Farangi Gouvernetou, 8: Tzani, 9: Samaria, 10: Georgioupoli, 11: Kourna, 12: Gerani, 13: Myloi, 14: Psiloritis, 15: Sendoni, 16: Arkalospilios, 17: Gonies, 18: Ag. Irini, 19: Ag. Paraskevi, 20: Agiofarango, 21: Milatos, 22: Diktaion Andron, 23: Mikro Katafygi.

subgenital plates and ovipositors, approximately 20 specimens, were not included in the analysis. Nearly 200 specimens have been collected in total, while for their study, 30 characters were used in total (Table 1). These characters have been used in the past to describe the three species. For statistical analysis we used the SPSS statistics package of the University of Crete Computing Center.

RESULTS AND DISCUSSION

The study of the "big" type of *Troglophilus* showed that we definitely cannot classify it in two different species. The characters used by Chopard and Boudou-Saltet to separate *T. spinulosus* and *T. petrochilosi* are very variable within the same individual. The characters used by Boudou-Saltet to distinguish *T. petrochilosi* were: a. A more light coloration; b. Keel on the 7th and 8th tergite only; c. Ovipositor less acute with only one apical tooth on the inferior valves; d. Subgenital plate of the female not bilobe at the end; e. Proportions between body length, posterior femur and ovipositor 20 mm, 18-19 mm and 8-10 mm for *T. petrochilosi* and 23 mm, 23.5 mm and 12.5 mm for *T. spinulosus*. In the "big" specimens collected by us: a. The coloration was variable within the same population; b. The shape of the keels was also variable within the same population; c. The shape of the ovipositor was similarly acute in all specimens

Table I - Characters used in the identification of *Troglophilus* species. (*: characters used in principal component analysis)

3d to 5th palp segment ratio*
Keel of tergites
Lobes of the 10th tergite
Number of spines on the upper side of the right front tibia
Number of spines on the upper side of the left front tibia
Number of spines on the under side of the right front tibia
Number of spines on the under side of the left front tibia
Number of spines on the under side of the right middle femur
Number of spines on the under side of the left middle femur
Number of spines in the middle part of the inferior internal edge of the hind right femur
Number of spines in the middle part of the inferior internal edge of the hind left femur
Number of spines on the external upper side of the right hind tibia
Number of spines on the external upper side of the left hind tibia
Number of spines on the internal upper side of the right hind tibia
Number of spines on the internal upper side of the left hind tibia
Number of spines on the external under side of the right hind tibia
Number of spines on the external under side of the left hind tibia
Number of spines on the internal under side of the right hind tibia
Number of spines on the internal under side of the left hind tibia
Simple and apical spurs of metatarsus of the hind right leg
Simple and apical spurs of metatarsus of the hind left leg
Apical lobes on the edge of the female subgenital plate
Number of teeth on the internal valves of the ovipositor *
Number and location of the last teeth of the internal valves of the ovipositor
Length of body *
Length of the hind right femur *
Length of the hind left femur *
Length of the hind right tibia *
Length of the hind left tibia *
Length of ovipositor *

and the last two teeth of the inferior valves were either converging, completely separate or forming a bifurcate tooth within the same populations and the same specimens (Fig. 2); d. The subgenital plate's apex of the female varied from monolobe to bilobe; e. The body length of the specimens from caves where *T. spinulosus* had been recorded, varied from 17-22 mm, the posterior femur 19-21 mm and the ovipositor from 8-10 mm. Therefore, the "big" type of *Troglophilus* must belong to one species.

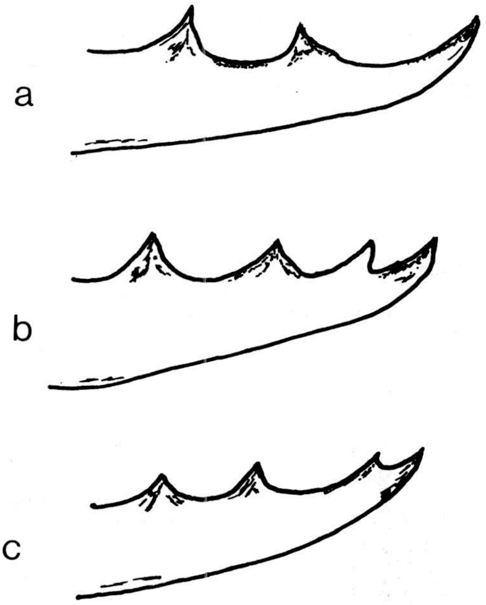

Fig. 2 — Inferior valve of female *T. spinulosus* ovipositor. a: separate apical teeth. b: converging apical teeth. c: bifurcate apex.

In order to analyse quantitatively all the characters from all the specimens, a principal component analysis was carried out. Before this, a Kruskal-Wallis non-parametric analysis of the variance of all characters according to caves was carried out in order to eliminate the characters that were equally variable within populations and between populations. In this way, 22 characters were rejected because they either showed no variation, had similar variation within all populations or were very subjective. The principal component analysis of the remaining characters showed that the three principal axes that accounted for 97.5% of the variation were related to the length of the hind femur, the length of the ovipositor and the number of teeth respectively. According to these three characters all of which are related to length, two types can clearly be distinguished (Fig. 3). One has no teeth on the ovipositor, the length of the ovipositor ranges from 3-4 mm and the length of the hind femur ranges from 15-16 mm. The other has 8-11 teeth on the

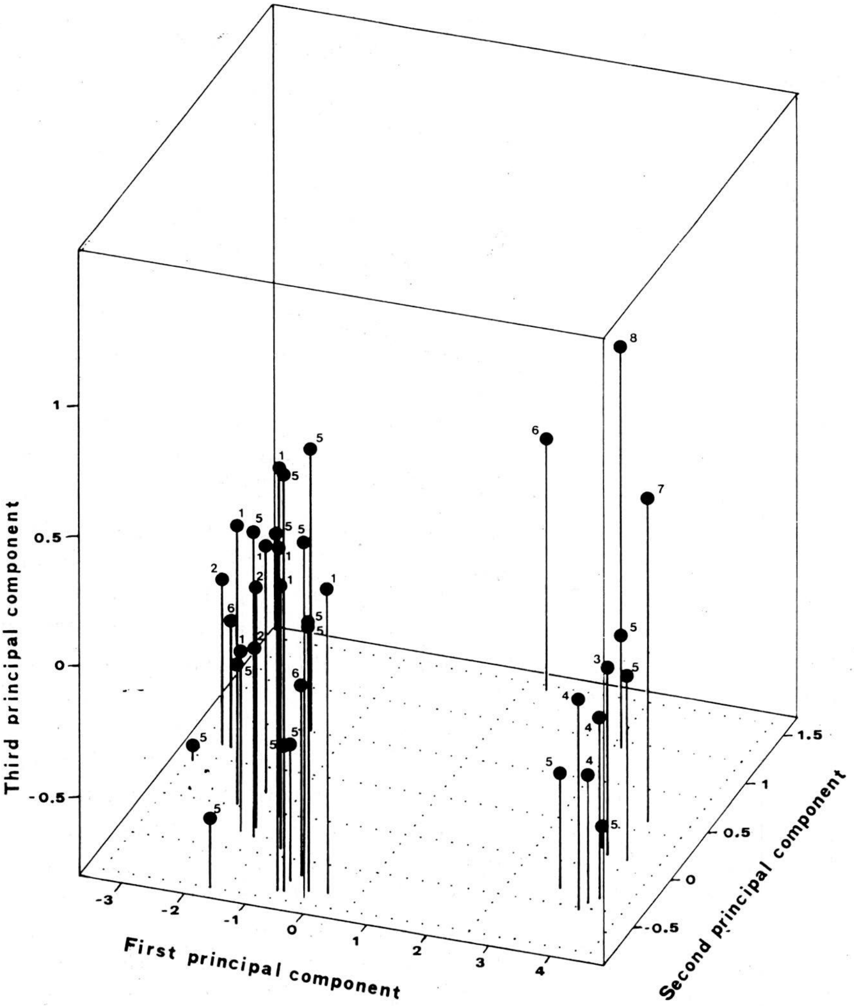

Fig. 3 — Principal component analysis of female *T. spinulosus* specimens. Left group: immatures, right group: adults. (1: Kourna, 2: Farangi Gouvernetou, 3: Samaria, 4: Milatos, 5: Ag. Paraskevi, 6: Ag. Irini, 7: Tzani, 8: Diktaion Andron).

ovipositor, the length of the ovipositor is 8-10 mm and the length of the hind femur ranges from 19-21 mm.

These two types had never been found in the same cave and this supported the two species hypothesis. An interesting point is that in the localities where the "small" type occurred, there were always very small individuals which had been considered as its immatures. In contrast, no such immatures where found in localities were the "big" type occurred.

We recently found both types coexisting in two caves: the cave of Milatos and the cave of Agia Paraskevi near Skoteino. The last cave supports, as far as we know, the largest *Troglophilus* population in Crete.

The gap in some characters between the "small" and the "big" type can be explained by the presence of one or more moults. For example, the 4 mm ovipositors have no teeth, the 7 mm ovipositors have rudimentary teeth and the 8-10 mm ovipositors have fully grown teeth. Also all populations of the "big" type were very small while the "small" type populations were always numerous. The differences between the two types concern characters associated with size. The other characters, such as shape of subgenital plate which is an important character in separating other species, are the same. The toothless ovipositor of the "small" type is unsclerotized, a characteristic that is associated with individuals that have not reached their final moult (Chopard, 1965). The above facts, along with the overlapping distribution and the immature-like characteristics of the "small" type allow us to suggest that there is only one species of *Troglophilus* in Crete: *Troglophilus spinulosus* Chopard, 1921.

SUPPLEMENTARY DESCRIPTION

We provide a supplementary description of *T. spinulosus* in these characters where differences or variation were found. All the other remain as described by Chopard and Boudou-Saltet.

Adult: The length of body, hind femur and hind tibia are 17-22, 19-21, and 21-24 mm respectively. The 3d to 5th palp segments ratio varies from 2.8:3.8 to 3:3.5. Number of spines on the upper side of the front tibia: 9-11. Number of spines on the under side of the middle femur 3-11. Number of spines on the middle part of the inferior internal edge of hind femur: 3-8. Number of spines on the external upper side of the hind tibia: 53-77. Number of spines on the internal upper side of hind tibia: 52-68. Number of spines on the external under side of hind tibia: 18-25. Number of spines on the internal under side of hind tibia: 11-16. Simple and apical spurs of the metatarsus of hind leg.: 4+1 to 8+1. The 6th, 7th and 8th tergites keeled backwards with a more or less angular prolongation in the back edge. Subgenital plate of male big, bilobe with cerca rather short and flattened in the base of the external side. Subgenital plate of the female triangular, monolobe or bilobe on the apex. Shape of ovipositor acute. Length of ovipositor 8-11 mm. The apical teeth of the internal valves can be converging, completely separate or bifurcate, while any combination of these can be found in the same specimen.

ECOLOGICAL NOTES

T. spinulosus is found in the entrances of caves or similar places such as cavities and under big rocks. It is active during the night, remaining hidden in small holes, under stones or among litter during the day. For this we can characterize it as trogloxene. It can coexist with *Dolichopoda paraskevi* and *Discoptila lindbergi* in the same cave because they occupy different niches (Kollaros et al., 1987). Adult individuals are found on the entrance walls while immatures on the floor.

As mentioned before, in only two cases did we find adults and immatures coexisting. This could be a result of the differences in some characteristics of the cave entrances. The entrance of the cave Agia Paraskevi is a doline full of stones and litter with a soft substrate (Paragamian & Legakis, 1986). It is located in a large overgrazed landscape and thus is the only shelter for *Troglophilus* which limited there, develops a large population. In contrast, Milatos and all the other caves where *T. spinulosus* adults were found, have a litterless, stoneless and hard substrate entrance. We might suppose that it lays its eggs in soft substrate and all immatures take advantage of litter and stones to hide themselves during the day. Thus, when these do not occur, adults are forced to search for suitable places away from the entrance for oviposition. This may be one of the reasons for which immature individuals were not found in caves with hard substrate as in the case of Milatos where immatures were found away from the entrance.

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Int. J. Speleol. 20 (1991): 47-55

Observations on the biology of Spelaeiacris tabulae Peringuey (Orthoptera, Rhaphidophoridae), from the Wynberg cave (Capetown, South Africa)

Gianmaria Carchini *, Claudio Di Russo * and Mauro Rampini **

SUMMARY

Data on the age structure, fecundity, egg morphology and feeding habits of the *Spelaeiacris tabulae* population from Wynberg cave are reported and compared with other Rhaphidophoridae species. *S. tabulae* shows a certain degree of adaptation to cave life, as usual in the other temperate species of Rhaphidophoridae

INTRODUCTION

In the whole of Africa the Rhaphidophoridae are represented only by the endemic Macropathinae species: *Spelaeiacris tabulae* Peringuey, 1916 which, as far as we known, is only found in some sandstone caves in the Cape Peninsula. This species is a clear example of Gondwanian relict, because its closest relatives are now present in Patagonia and in the Australian region, showing a clear circum-antartic distribution (Karny, 1931).

Few studies on this species are known, (Peringuey, 1916; Karny, 1929; Hesse, 1929; Grindley, 1956) and at this time there is a scarcity of information on the biology and ecology of this species. In this paper we report the observations carried out in the cave and in

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laboratory on some ecological and morphological traits of this cave cricket.

STUDY AREA AND METHODS

The crickets were collected in the Wynberg cave (Table Mountain, Cape Province, South Africa, 900 m a.s.l.). The cave is located in a mediterranean climate area which is usually dry and hot during the summer. However, during the winter, a part of the cave is flooded (T. Hall, pers. communication). The fauna of the cave is known and includes spiders, isopods and beetles (Craven, in press). Even though the cave was visited by us during summer 1991, the external and internal temperatures of the cave, recorded during the visit, was 12° C and 10° C respectively, and the cave showed noticeable drip both from ceiling and walls.

Forty one specimens of *Spelaeiacris tabulae* were collected in the cave, 50 m from the entrance (G. Carchini, M. Di Domenico and T. Hall leg., 17.02.91). The crickets were mainly observed on the floor and the walls of the cave, where spiders and some isolated bats' and rodents' faecal pellets were also observed. The crickets were captured by hand and kept in a plastic container during the transport out of the cave.

We observed that most of the crickets died during the first hours after capture, when they were all together in the plastic box. In particular, several specimens showed torn off legs. So, each survivor was transferred into a separate box and in this way was transported to Italy without further deaths. The specimens were preserved in alcohol 75%.

To describe the age structure of the cricket population, the metatibial length and pronotum length were recorded from 20 and 30 individuals respectively. The first measure was taken using a vernier caliper, the second using a stereo-microscope with a micrometric eyepiece. In both cases the measurements were to the nearest 0.05 mm. As well as measuring them, we distinguished the nymphs from the adults by the morphology of sexual appendages in the males and by shape and color of the ovipositor in the females (see Fig. 1).

From the dissection of five individuals it was possible to collect five faecal pellets. The faecal pellets were spread on a slide 18 x 18

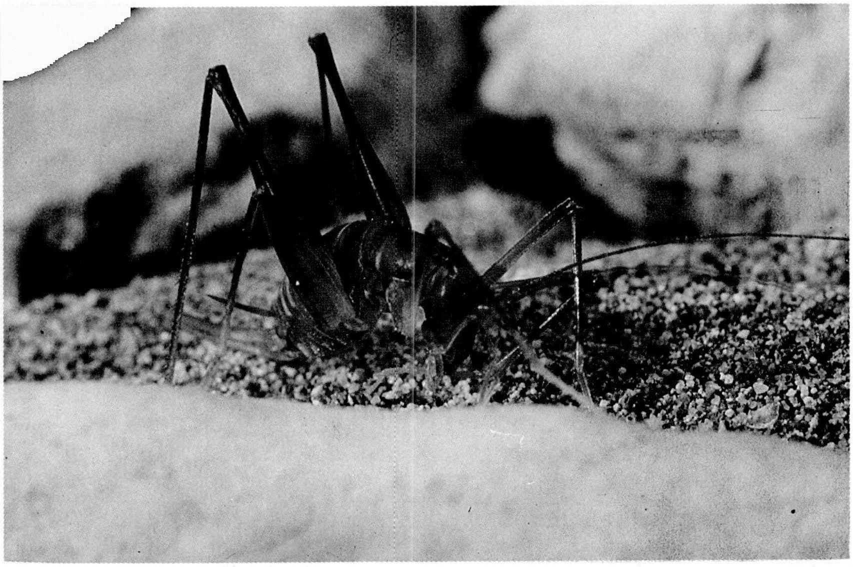


Fig. 1 — Adult female of *Spelaeiacris tabulae*

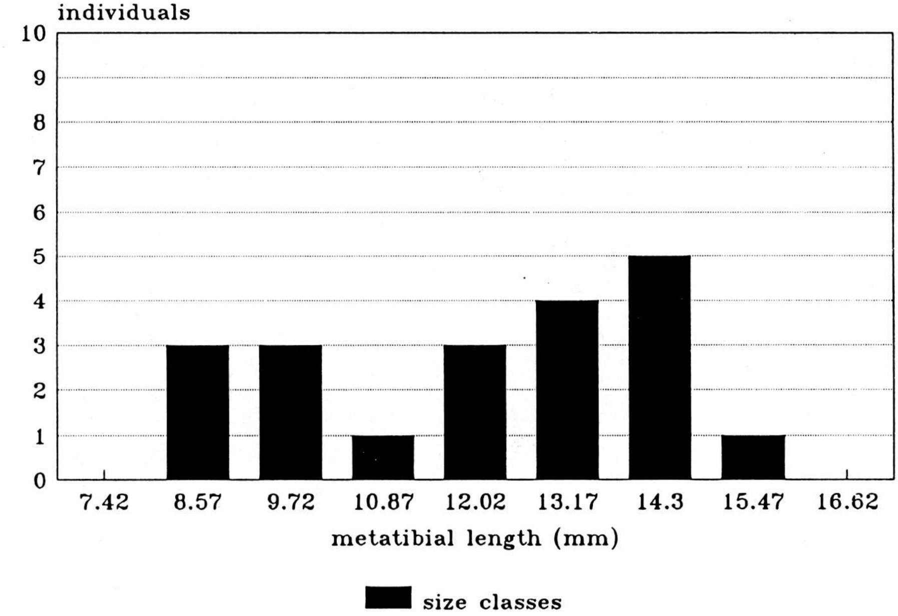
mm and examined through an optical microscope.

Also, from the dissection of three females, 8 mature eggs were isolated. The eggs were measured by stereo-microscope, and, after drying and sputtering, were observed also by S.E.M.

RESULTS AND DISCUSSION

Age structure

Both nymphs and adults were present in the sample. The adult size of the metatibia and pronotum ranges from 14.0 to 15.20 mm and from 3.08 to 3.52 mm respectively. In Fig. 2, the distributions of metatibial and pronotum lengths are reported. This analysis shows a wide distribution of age due to the presence of young and old nymphs together with adults. This large age variation in a single sample may be explained by continuous reproduction, without seasonal timing such as already suggested by Grindley (1956) from the presence of young nymphs throughout the year. This continuous breeding habit is peculiar to life cycles of tropical species (Masaki



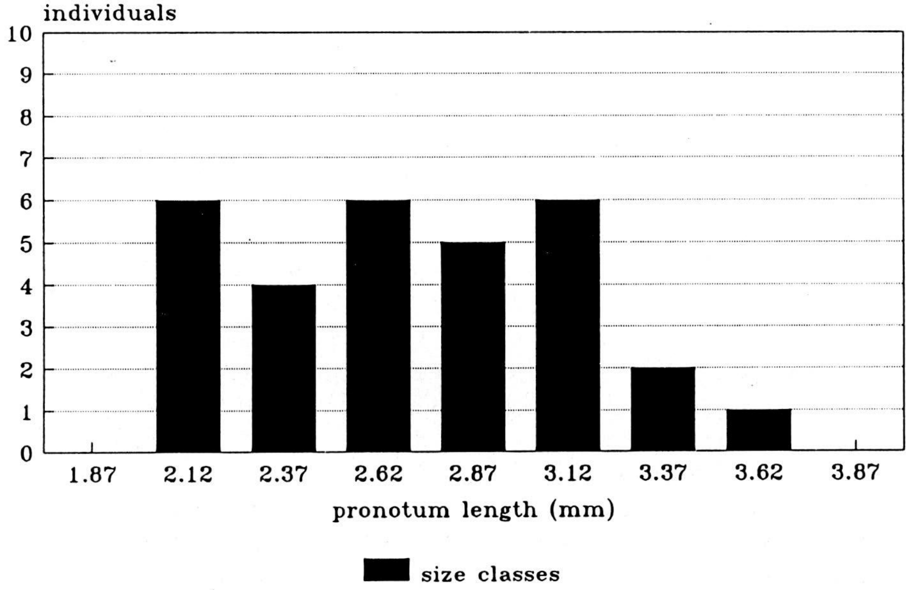


Fig. 2 — Age structure of *S. tabulae* population from Wynberg cave. Size frequency histograms are based on metatibial and pronotum lengths. The values reported on abscissa are the central values of the size classes.

and Walker, 1987) and also to temperate populations and species adapted to the cave habitat (Culver, 1982; Carchini et al., 1991).

On the contrary, the life cycles in temperate epigean crickets are strongly affected by seasonality (Alexander, 1968; Masaki and Walker, 1987) and usually show little age variation between individuals in a sample. Since the climate at the Cape Peninsula is tipically temperate, the observed age structure appears to reflect an adaptation to cave life.

Eggs

The eggs of *S. tabulae* are cylindrical and slightly curved (Fig. 3). The measurements of the 8 eggs, made by optical stereo-microscope, range from 3.20 to 3.36 mm in length and from 1.20 to 1.25 mm in width. Because of damage during the preparation, we were only able to observe two eggs by S.E.M., so the following description is not complete. In particular we were not able to locate the micropiles.

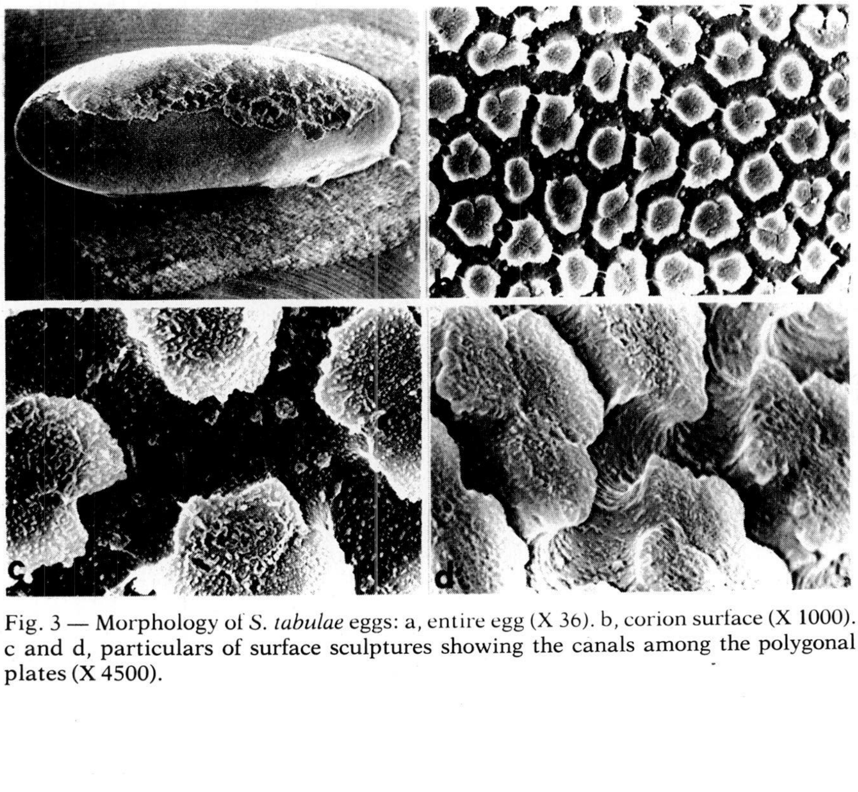


Fig. 3 — Morphology of *S. tabulae* eggs: a, entire egg (X 36). b, corion surface (X 1000). c and d, particulars of surface sculptures showing the canals among the polygonal plates (X 4500).

The corion shows an external surface without cristae, and regularly arranged in polygonal plates separated from each other by canals about 3 nanometer wide. The entire egg surface shows the same pattern. We did not find respiratory orifices either in the plates or in the canals. This fact seems to indicate the absence of specialized respiratory areas.

The general shape of *S. tabulae* egg is similar to those of the other Rhaphidophoridae species, but really this shape is very common in several Orthoptera (Uvarov, 1966; Hinton, 1981). On the contrary, the fine structure of the egg surface appears to be quite different from that shown in other Rhaphidophoridae. Particularly in the Dolichopodinae and Rhaphidophorinae species the egg surface shows a net of hexagonal cells, divided by emerging cristae (Rampini and Saltini, 1988).

Other differences may be observed in the number and in the relative size of the eggs. In Table 1 the number of eggs and the ratio between the egg length and body length of some Rhaphidophoridae species are reported. From these observations it appears that *Spelaeiacris tabulae* produce a small number of eggs, and, by comparing the ratio egg length/body length, it results that it produce

Table 1 — Comparison among egg and body size in several Rhaphidophoridae species. N, average number of eggs for female found in the ovary or (*) layed. All measurements in mm.

Species	N (mean)	egg length	body length	egg/ body	Habitat	Authors
Spelaeiacris tabulae	2.66	3.30	10.5	.314	cave	—
Dolichopoda laetitiae	12.50	4.10	21.0	.195	cave	1
Hadenoecus subterraneus	7.24	4.00	17.5	.23	cave	2
Tachycines asynamorus	100-900*	2.20	13.8	.160	tropical forest	3

(1): Ziccardi, unp. data; (2): Hubbel & Norton, 1978; (3): Sampò & Casale, 1978.

larger eggs than other known Rhaphidophoridae. As in other cave adapted organisms, this feature could be assumed to represent an adaptation to cave life (see Culver, 1982). However, more data on the fecundity will be necessary to confirm this hypothesis.

Feeding habits

Hesse (1929) suggested that *S. tabulae* might feed on *Lecanora* lichens. This supposition was criticized by Grindley (1956) that has not been successful in trying to feed *S. tabulae* on fungi. In our observation, the faecal content showed the presence of six morphologically distinguishable types of items. We have found a total of 385 items in the pellets, including arthropod cuticle (7%), lepidoptera scales (40%), bat hairs (15%), rodent hairs (18%), green vegetables (19%), vegetable fibers (1%). No lichen remains as hyphae or unicellular algae were found.

The occurrence of these categories indicates an omnivorous diet common to those of other Rhaphidophoridae (Remy, 1931; Richards, 1962; Hubbel and Norton, 1978). The presence of arthropods together with bat hairs and lepidoptera scales, commonly found on bat guano deposits, may indicate an origin of this food inside the cave. Because of the presence of vegetable items in the faecal pellets we should assume the occurrence of feeding migrations outside the cave, as is well known in other Rhaphidophoridae (Remy, 1931; Richards, 1962; Richards 1969; Hubbel and Norton, 1978; Di Russo et al., 1991). However, the origin of vegetable items in our case could also be explained by the presence of some plants in the boxes used to transport the crickets.

CONCLUSION

These preliminary observations have allowed us to obtain new information on the little-known biology of *S. tabulae*. Even if further studies on the life cycle, phenology and feeding habits are needed, these preliminary data seem to indicate a certain degree of adaptation of this species to the cave habitat. As far as the origin of this adaptation to the cave habitat, *S. tabulae* could fit well the "refuge" model (Jeannel, 1965) which assumes that the caves are colonized by geographically isolated populations, forced there by unfavourable ecological changes. In fact, the Cape area is now isolated from the main part of the continent by a large barrier of aridity and the climate of the southern part of Africa, changed from wet and cold to arid and hot conditions during the last million years (Leleup, 1956; Darlington, 1968). This situation seem to favour persistence of hygrophilic organisms only in wet refuges as the caves of the Table Mountain area.

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