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Geographical variation in the tropical cave cockroach *Paratemnopteryx stonei* Roth (Blattellidae) in North Queensland, Australia.

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SUMMARY

Observations of cave dwelling organisms in both tropical and temperate caves often reveal morphological modifications, which may reflect various stages of adaptation to cave life. From April 1994 to June 1995 a number of adult *Paratemnopteryx stonei* were collected from 7 caves in tropical North Queensland to investigate the degree of geographical variation in such troglomorphics betwen cave populations. Results of morphometric analyses showed the occurence of a morphological discontinuity between cave populations from the different geographic regions. The body dimensions particularly important in discriminating between each cave population were tegmen length (both sexes), and secondly, tegmen width and tarsus length for males and females respectively. Morphological differences between populations are discussed in relation to stages of adaptation to cave live.

INTRODUCTION

Cave organisms often demostrate degrees of morphological modification (troglomorphy), for example, reduced or lost eyes, wings and bodily pigmentation, and attenuation of appendages (Christiansen, 1961; Barr, 1968; Culver, 1982; Kane and Richardson, 1985). These troglomorphic characters may reflect various stages of adaptation to cave habitats, induced through different regimes of selective pressures, and or genetic factors such as the accumulation of neutral mutations (Poulson, 1985; Wilkens, 1992; Culver et al., 1994). The highest morphological modification occurs in those populations which have been isolated (ie subject to no gene flow) the longest, have experienced stronger selective pressures, or have a greater fixation rate of genetic mutations within a population. Thus, one would expect isolated cave populations to demostrate varying degrees of troglomorphy.

Important factors which determine the degree of isolation or otherwise of cave populations are the presence of geological barriers and/or interstitial

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voids whithin cavernous strata (Barr, 1968; Howarth, 1982; Barr and Holsinger, 1985; Kane and Brunner, 1986). The occurence of such barriers and voids influences the dispersal ability of cave dwelling organisms, and in turn determines the geographic extent and degree of gene flow between cave populations. For example, *Neaphaenops tellkampfi*, a troglobitic (obligately cave dwelling) trechine carabid beetle, in west central Kentucky contains isolated populations which have been allocated subspecies status by Barr (1979). He recognised four subspecies, based on morphological differentiation of the populations which coincides with the presence of faults and rivers between groups of morphological forms.

In contrast, cave populations that are subject to intercave gene flow would have a lower degree of morphological variation. In a study of the distribution and evolution of *Ptomaphagus* beetles in the southeastern United States, Peck (1984) compared 61 separate cave populations. The caves were located in a continuous limestone belt that would be expected to contain abundant subterranean avenues for dispersal. Morphological comparisons between these cave populations showed little variation, although each population was found to contain only one form of spermatheca. Peck suggested that the spermathecal forms are an indicator of species level taxonomic categories, and speciation has occured despite the presence of subterranean dispersal routes.

In North Queensland tropical caves, comparison of two populations of *Undarana*, a cave dwelling cixiid (Hemiptera), from lava tubes 30 km apart, revealed significant differences in external and genital morphology (Hoch and Howarth, 1989). Although the populations were from distant lava tubes of separate origin, individuals may be able to disperse between caves because the lava fields are connected by other basaltic flows. Hoch and Howarth interpreted these differences as indicators of interrupted gene flow between the populations, and therefore surmised the existence of two separate biological entities. In contrast, they found populations of another cixiid, *Solonaima*, to be morphologically similar in the same lava systems.

Early examination of cockroaches we have collected from these lava tubes and other tropical caves in North Queensland indicated that there are morpholo-gical differences between populations of *Paratemnopteryx stonei* Roth (Blatto-dea: Blattellidae). This genus is distributed widely over Australia, with different species living in epigean and cave habitats (Roth, 1990). So far, three of the four cave species whithin the genus have been found only in North Queensland (*P. stonei*, *P. howarthi*, and *P. sp4*). The aim of this study was to investigate the degree of geographic variation in troglomorphies between populations of *P. stonei* in North Queensland caves.

MATERIALS AND METHODS

From April 1994 to June 1995 *P. stonei* adults were collected from 7 caves in North Queensland: Bauhinia (8 males, 5 females) and Clam (16 males, 8 females) caves at Chillagoe, Barkers (16 males, 25 females) and Bayliss (21 males, 27 females) lava tubes at Undara, Frig cave (3 males, 4 females) at Broken River, and Rope Ladder (13 males, 12 females) and Bat cave (3 males, 3 females) at Fanning River (Fig. 1). As cockroaches do not continue to grow once they are adults morphometric analyses were carried out only on adults, avoiding sample bias in the growth stage. In addition, both sexes were analysed separately to investigate sexual dimorphism.

From these collections morphological mesaurements were made on 11 body dimensions using a stereo-dissecting microscope and ocular micrometer. The body dimensions were body length; femur, tibia, and tarsus length of hindleg; cercus length; eye length and width; tegmen length and width; and pronotum length and width.

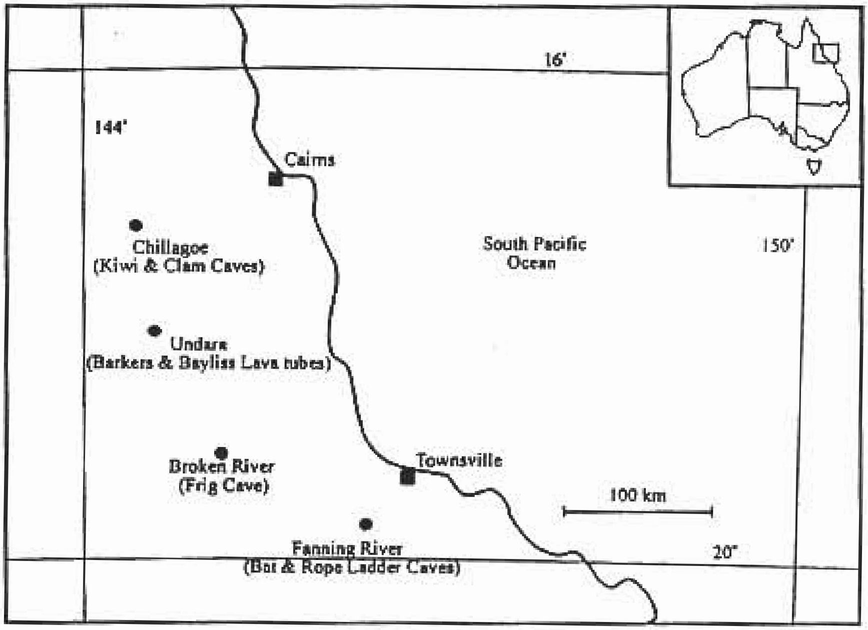

Fig. 1 – Map of North Queensland indicating the four cave regions and cave study sites.

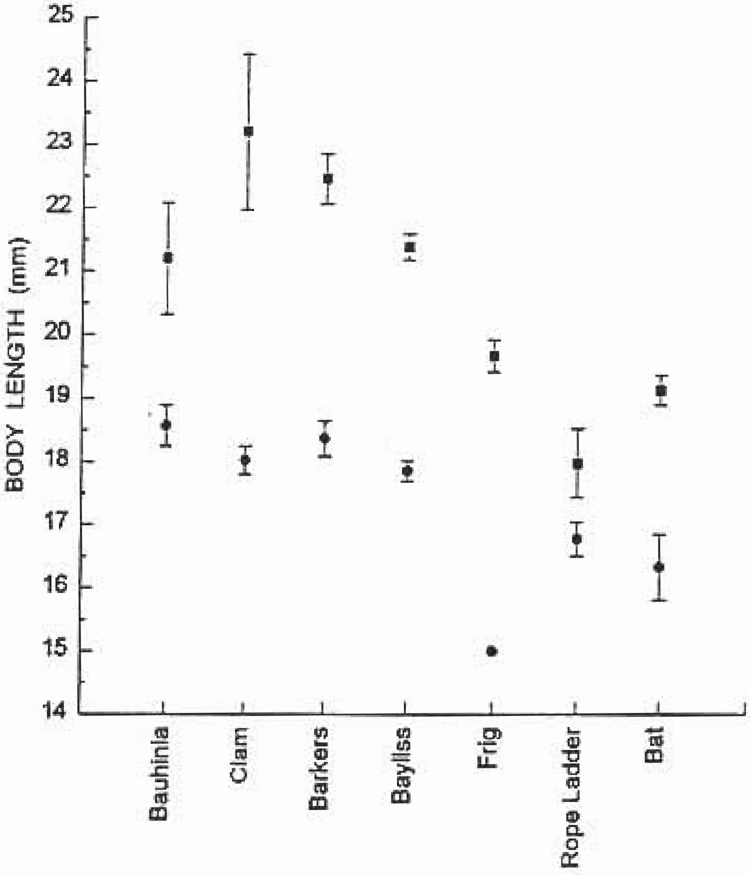

Fig. 2 – Variation in body length (mm) ± SE for males (circles) and females (squares) from the seven cave study sites.

The statistical analysis used to investigate geographic variation between populations was Canonical Discriminant Analysis (CDA), using the SAS program package (SAS Institute, 1987). CDA is an ordination technique for displaying and describing the differences between group centroids, ie for each population, by extracting the eigen vectors from the pooled within-group variance-covariance matrix. The analysis was carried out on ratio transformed data, with respect to body length, to remove the influence of body size on other body characters.

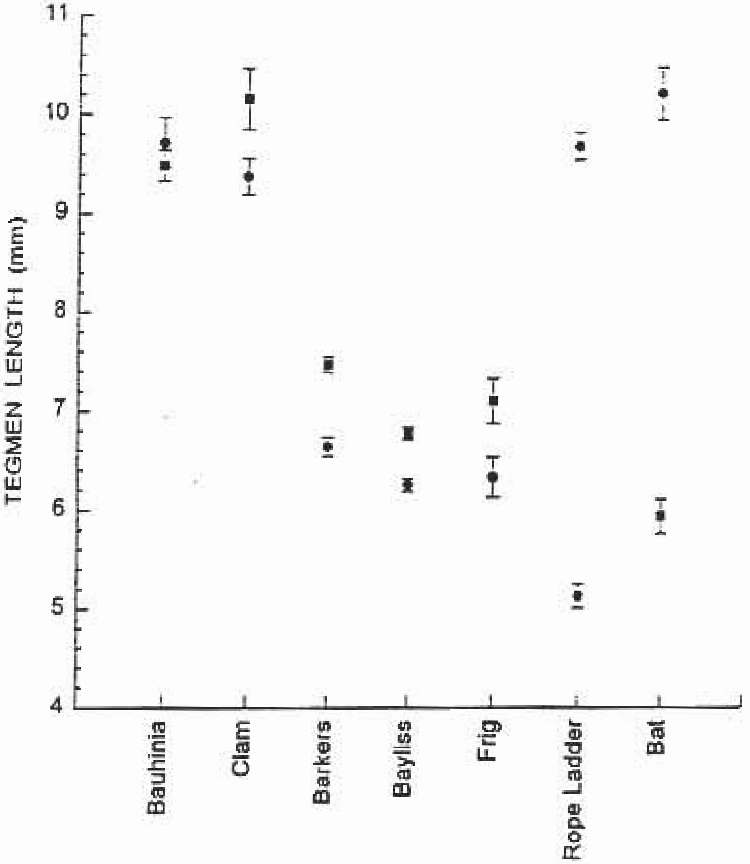

Fig. 3 – Variation in tegmen length (mm) ± SE for males (circles) and females (squares) from the seven cave study sites.

One-way ANOVA's were carried out on body length and the morphological characters defined by the CDA's as being particularly important in discriminating between cave populations. Based on these characters a Tukey Studentized Range (HSD) Test was carried out to define which populations were significantly different from each other (Sokal and Rohlf, 1982).

RESULTS

Initial exploratory data analysis of the raw data using plots of the meam of each of the measured body dimensions indicated that there were 2 main differences between males and females both between and within cave populations. These were body length and tegmen length (Figs. 2 and 3). Figure 2 shows that females had greater body length than males at each of the 7 caves, with populations from Chillagoe and Undara having greater body length than those from Broken River and Fanning River. Figure 3 indicates that females have shorter tegmina than males in populations from Chillagoe, Undara and Broken River.

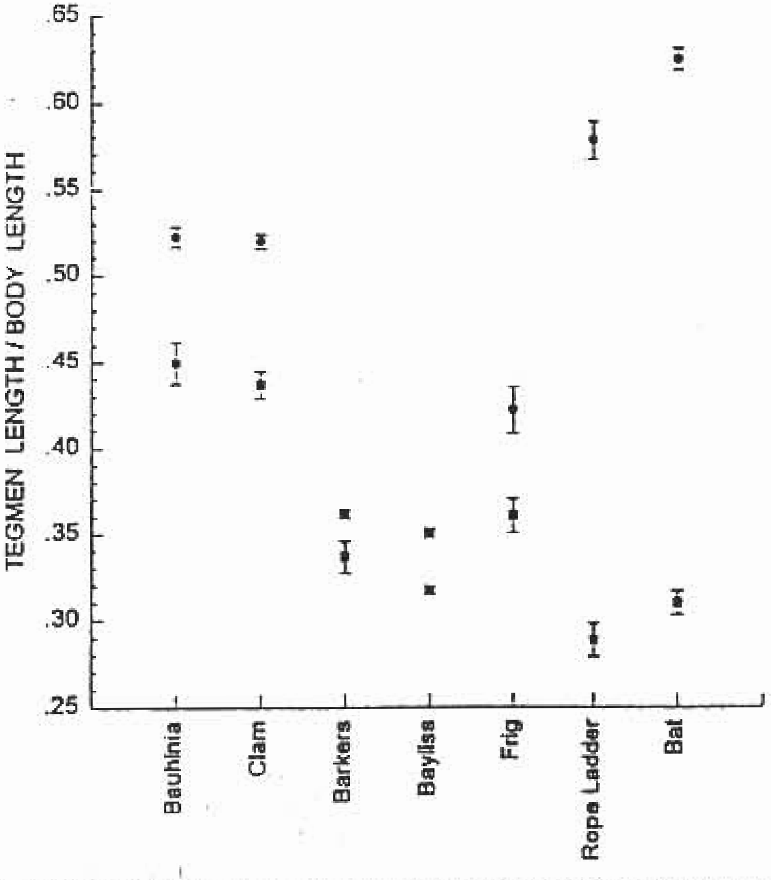

Fig. 4 – Radio transformed tegmen length data ± SE for males (circles) and females (squares) from the seven cave study sites.

Ratio transforming the tegmen length data produced different results to those shown in figure 3 (Fig. 4). In figure 4 females have shorter tegmina than males in populations from Chillagoe, Undara and Broken River, which is opposite to the relationship shown in figure 3. This reversal is due to the effect of body size (females are larger than males) supporting the decision to carry out further statistical analyses on ratio transformed data.

Figure 4 indicates that males had longer tegmina than females, and that sexual dimorphism in tegmen length is most pronounced in the cockroach populations from Fanning River caves. Based on tegmen length, the graph shows 3 morphological groups, these being a long wing morph at Chillagoe (males and females), a short wing morph at Undara and Broken River (males and females), and a long/short wing morph at Fanning River (males and females respectively).

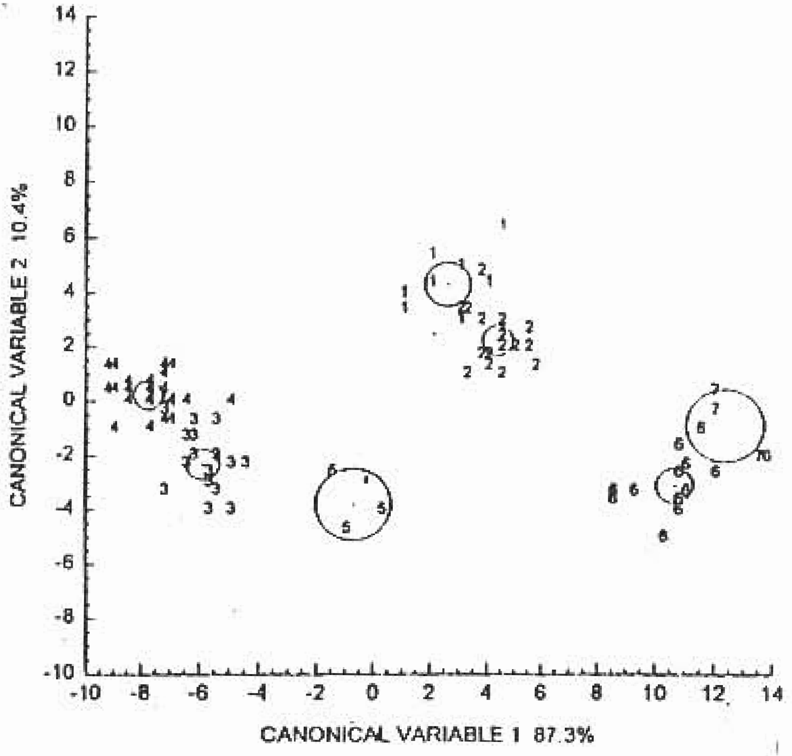

Fig. 5 – Canonical discriminate analysis plots of males with 95% confidence intervals around centroids for Bauhinia (1), Clam (2), Barkers (3), Bayliss (4), Frig (5), Rope Ladder (6), and Bat (7) caves.

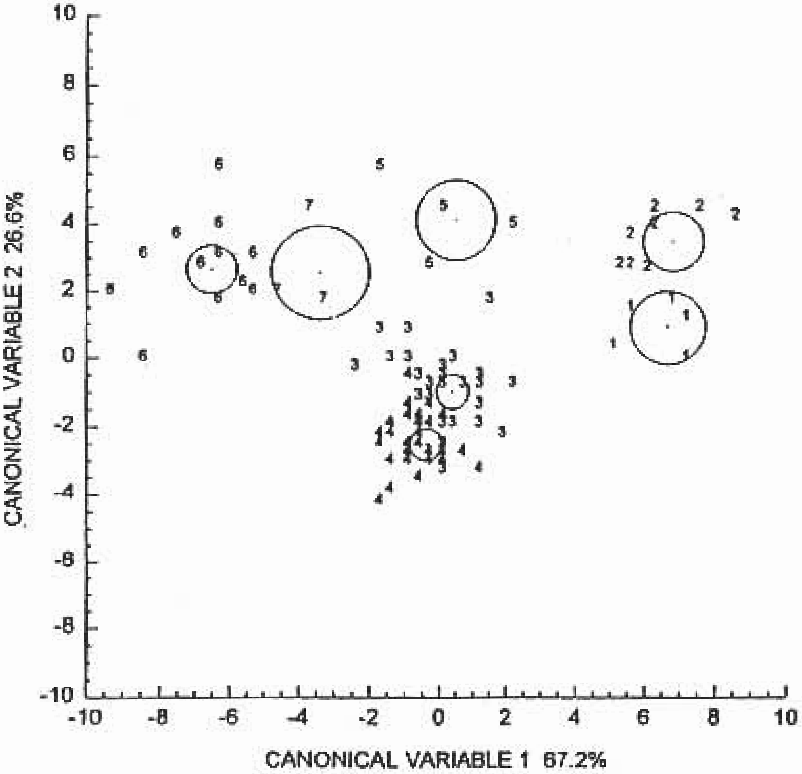

Fig. 6 – Canonical discriminate analysis plots of females with 95% confidence intervals around centroids for Bauhinia (1), Clam (2), Barkers (3), Bayliss (4), Frig (5), Rope Ladder (6), and Bat (7) caves.

Plots of the CDA's for males and females (Figs. 5 and 6 respectively) show a clear separation of the populations with respect to geographic location, and to a lesser degree between caves. For males the canonical variables 1 and 2 summarised 97.7% (87.3% and 10.4% respectively) of the total variation between groups, and 93.8% (67.2% and 26.6% respectively) for the females. Table 1 gives the coefficients for the first canonical variable, and indicates that the body dimensions which are particularly important in discriminating between cave populations are tegmen length (for both sexes), and secondly, tegmen width and tarsus length for males and females respectively. The distinctiveness between populations was confirmed by multivariate F-statistic analysis (Pillai's Trace = 2.860, F = 6.647, p = 0.0001 for males; Pillai's Trace = 2.643, F = 6.376, p = 0.0001 for females).

Table 1 – Coefficients for the first canonical variable from the CDA analyses carried out on males and females, ranked in order of importance in discriminating between cave populations.

MALES		FEMALES	
Tegmen Length	0.976	Tegmen Length	0.788
Tegmen Width	0.574	Tarsus Length	0.344
Eye Width	0.511	Eye Length	-0.326
Pronotum Length	0.496	Tibia Length	0.300
Tibia Length	-0.454	Eye Width	-0.163
Femur Length	-0.434	Femur Length	0.104
Tarsus Length	0.405	Tegmen Width	-0.070
Eye Length	0.353	Pronotum Width	-0.051
Cercus Length	-0.132	Pronotum Length	0.033
Pronotum Width	-0.101	Cercus Length	-0.010

Plots of tegmen width and tarsus length (Figs. 7 and 8 respectively) indicate that male cockroaches from Bat Cave at Fanning River had the widest tegmina and female cockroaches from Bauhinia Cave at Chillagoe had the longest tarsi. Results from the one-way ANOVA's and Tukey Studentized Range (HSD) Tests on body, tegmen and tarsus length, and tegmen width indicated that these characters were significantly different from each other in some populations (Results of which can be obtained from the authors).

DISCUSSION

Previous morphological work on *P. stonei* has been carried out by Roth (1990). He described *P. stonei* from caves at Chillagoe and Undara, but did not carry out any detailed morphometric analyses. He noted that specimens taken from different caves varied in size of tegmina, and reduction in pulvilli. However, comparison of male genitalia were similar enough that he considered the specimens to be races of the same taxon. He classified specimens found in Clam cave at Chillagoe, and those from Bayliss, and Barkers caves as 3 different races. Specimens have not been reported or described from either Broken River or Fanning River caves, and our specimens therefore constitute new locality records for *P. stonei*. Of further interest was the striking sexual dimorphism in tegmen length in individuals from Fanning River caves which has not been found in any other population of *P. stonei*. Sexual dimorphism in wing length is not unique to individuals of *P. stonei*, as it has been recorded in numerous other insects (Thayer, 1992).

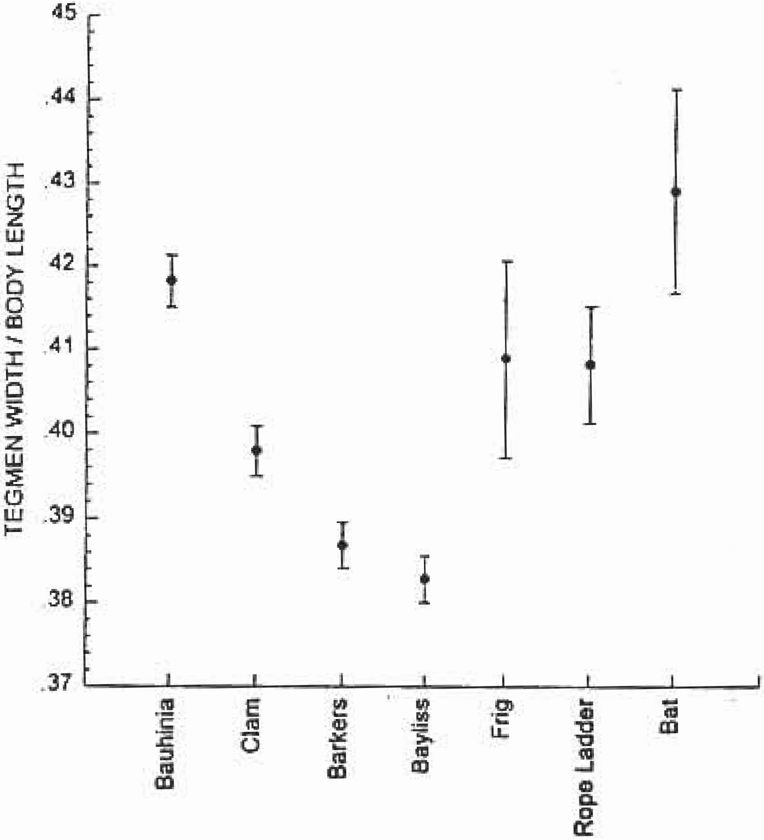

Fig. 7 – Ratio transformed tegmen width data ± SE for males from the seven cave study sites.

The multivariate analyses indicate that there are morphological variations between cave populations which can be resolved into 4 major groups, representing the 4 geographic regions, Chillagoe, Undara, Broken River, and Fanning River (Figs. 5 and 6). There is a degree of variation within each population, where some individuals from caves in the same geographic region, ie Bauhinia and Clam at Chillagoe, Barkers and Bayliss at Undara and Rope Ladder and Bat at Fanning River, fall within each others' data cloud. However, the intracave region variation does not exceed the intercave region variation observed between the four cave regions.

Observations of cave dwelling organisms in both tropical and temperate caves often demonstrate troglomorphy, although the pattern and degree of morphological modification is not universal (Christiansen, 1961; Barr, 1968; Culver, 1982; Kane and Richardson, 1985; Peck, 1990). All individuals of *P. stonei*, except males from Fanning River, were found to have brachypterous tegmina with females having shorter tegmina than males (Fig. 4), and all individuals had vestigial hind wings. Reduction in tegmen width was also noted between males, with both intra and intercave region variation (Fig. 7). Peck and Roth (1992) have documented tegmina and wing reduction in surface dwelling *Chorisoneura* cockroaches from the Galápagos Islands. They concluded that during wing diminution the tegmina are less affected than the hind wings, and within a population the wing is more regressed in females. Wing loss has also been found in a number of other cockroaches, with flightlessness being more frequent among females than males, and there was a higher than average frequency in species inhabiting caves (Roff, 1990). The reduction in wing and tegmen size has been explained as a response to an increased specialisation for a more homogeneous environment, such as caves.

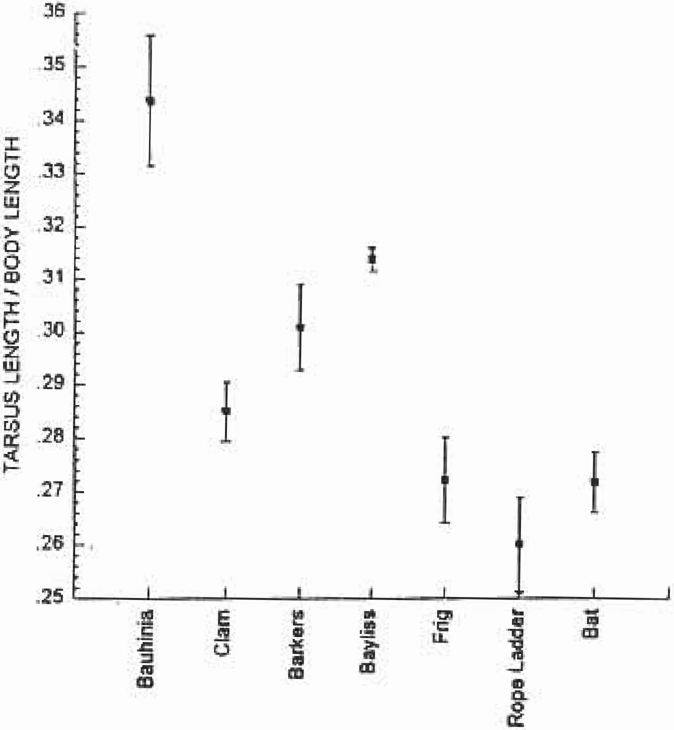

Fig. 8 – Ratio transformed tarsus length data ± SE for females from the seven cave study sites.

Elongation of appendages is a further troglomorphic feature found in cave species. Females from Bauhinia cave at Chillagoe had longer tarsi than females from the other caves (Fig. 8). Leg attenuation in cockroaches has also been reported in species of *Nocticola* from caves at Undara (Stone, 1988). Peck (1986) found a tendency for appendage elongation in cavernicolous *Ptomaphagus* beetles, with *P. cavernicola* having especially long tarsi. Attenuation of legs and antennae may provide a selective advantage by increasing the searching ability of cave organisms in an environment where there is little to no ligth (Peck, 1973).

Tarsal structure in cockroaches is a highly adaptive character, showing distinctive, nonphylogenetic features above the species level (Roth and Willis, 1952; Arnold, 1974). Roth (1990) noted variation in pulvillus reduction in and between populations of *P. stonei* from Chillagoe. Reduction of pulvilli and increased dependance on tarsal claws is an adaptation for walking on muddy cave surfaces (Roth and Willis, 1952; Christiansen, 1961 and 1965). Inter and intraspecific variation in tarsal structure in North Queensland cave *Paratemnopteryx* is currently being investigated by us in populations from caves with different substrate surfaces and humidity levels.

Troglomorphic characters may reflect various stages of adaptation to cave life. The degree of which may be influenced by various factors. Firstly, the selective regimes operating, as body size and allometrically related morphological characters are affected by environmental factors. Thus, variability in morphology between cave populations can be a result of ecological differences between the caves. Secondly, the length of time and degree to which organisms have been isolated can affect morphological variability. Increased variability in troglomorphic characters has been proposed as resulting from intercave gene flow and hybridisation with extant surface species (Avise and Selander, 1972). As the cave regions in this study are over 150 km from each other it is unlikely that there is any gene flow between cave regions, but one would expect intercave connections within regions. Thus, both direct environmental induction, reflecting phenotypic plasticity, and genetic adaptation to current selection pressures may be important in contributing to the observed morphological variation (Atchley, 1983; Allegrucci et al., 1992; Bilton, 1993). Thirdly, non-selectionist origins for troglomorphy have been considered, with morphological variation occuring as a result of the accumulation and fixation of neutral mutations within a cave population (Poulson, 1985; Wilkens, 1992). This also would be influenced by the degree of intercave gene flow. Considering these points, one may expect that populations of one species showing increased troglomorphy, such as the males from Bauhinia Cave at Chillagoe and the females from Barkers Cave at Undara, represent populations that have experienced the greatest isolation or experienced greater selective pressure, and or a greater fixation rate of genetic mutations within a population.

Alternatively morphological variability may reflect phylogenetic differences between cave populations. However, it is important not to rely on morphological characters that may be adaptive for use in inferring phylogeny. To resolve these issues we are currently making microenvironmental comparisons between caves, and molecular, morphological and behavioural studies at the population and species level within *Paratemnopteryx*. Given the similarities of the cave environment in the caves studied, it is difficult to believe that the morphological variations reflect different degrees of troglomorphy resulting from different selection pressures at each site. The morphological differences exhibited by isolated cave populations are more likely to have resulted from the fixation of characters modified by genetic drift.

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