

## WATER LOSS AND RESPIRATION OF CAVE ARTHROPODS FROM CAPE RANGE, WESTERN AUSTRALIA

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**Abstract**—1. Water loss and oxygen consumption were measured from three troglotic (obligate cave dwellers) and one non-troglotic cave species from the tropical but semi-arid Cape Range, Western Australia. The values are compared with those for epigeal species of the same taxa *sensu lato*, measured both *de novo* and from the literature.

2. The species include representatives of the Schizomida (Chelicerata), Araneae, Diplopoda and Isopoda.

3. In ascending order the oxygen consumption ( $\mu\text{l mg}^{-1} \text{hr}^{-1}$ ) was: schizomids (0.24), cave millipedes (0.29), epigeal millipedes (0.29), cave isopods (0.44) and epigeal isopods (0.48).

4. The cave millipedes have a high temperature coefficient for oxygen consumption:  $Q_{10\ 22-30\ ^\circ\text{C}} = 3.26$ .

5. In ascending order the resistance ( $\text{cm sec}^{-1}$ ) to water loss was: cave isopods (22.4), epigeal isopods (31.6), cave millipedes (40.9), schizomids (76.6), cave spiders (132.2) and epigeal millipedes (878.1).

6. The rate of oxygen consumption of the cave species is at the lower end of values taken from the literature for the relevant taxa but are not exceptionally low.

7. The rates of water loss from cave species are high but comparative data are mostly lacking for comparison with epigeal counterparts. Except for isopods the cave species have water loss rates around an order of magnitude greater than epigeal species.

### INTRODUCTION

Until recently troglotes were thought to be rare worldwide in tropical caves due to the small influence of the Pleistocene climatic changes considered necessary to eliminate the surface populations of putative troglotes (Vandel, 1965; Barr, 1968, 1973; Mitchell, 1969; Sbordoni, 1982). Australian caves had been considered to be very deficient in troglotes (obligate cave dwellers). Various explanations for this deficiency have been proposed, emphasizing the aridity of the continent and the lack of pre-adapted moist litter species (Moore, 1964; Hamilton-Smith, 1967; Barr, 1973).

Both of the above presumptions have proved incorrect. Rich troglotic faunas have been found in many tropical areas (Leleup, 1968; Howarth, 1983), including both the wet (Chillagoe in Queensland; Howarth, 1988) and semi-arid (Cape Range; Humphreys *et al.*, 1989; Vine *et al.*, 1988) tropical areas in Australia.

This report is about the fauna of the semi-arid but tropical Cape Range caves on North West Cape peninsula, Western Australia, an area where biopaleontological research has started only recently (Vine *et al.*, 1988; Humphreys *et al.*, 1989). The affinities of the troglotic fauna are with species from wet tropical forest litter; the closest such conditions now occur

is 1200 km to the north across the Great Sandy Desert.

Many cave organisms are food limited and the regressive evolution seen in cave animals involving, *inter alia*, the loss of eyes and pigments, is often considered to have resulted by selection for energy efficiency. There is some indirect support for this hypothesis which is discussed at some length by Culver (1982); the literature usually, but not always, shows low metabolic rate. However, most of the respiration measurements fail to control for temperature, activity and weight; few studies report regressions of metabolic rate on weight. In addition reduced metabolic rate is not universal in cave organisms but is more related to the energy state of the caves; some caves are highly energetic, e.g. bat guano caves.

Furthermore, cave species are often compared with inappropriate surface species. Appropriate species for comparison with troglotes are epigeal species of close taxonomic affinity, ideally the immediate ancestors of the troglotes, or closely related species in caves of different energy density. However, even such comparisons may be problematic as the period since isolation may vary (Poulson, pers. comm. in Culver, 1982) and is usually unknown, and the immediate epigeal ancestors are rarely known, even for troglotes of recent origin.

The approach adopted here is to examine the respiration rate of animals in the dark, straight from culture at the activity level natural under these conditions, and at the temperature of the caves where

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they occur. The cave species considered here all move incessantly and may not therefore be expected to have very low metabolic rates. No categorization into standard, routine or active rates is attempted as these rates form a continuum dependent upon many variables (Humphreys, 1975b, 1977a,b, 1978, 1979). The data are compared with epigeal members of the same broad taxonomic groupings and with the range of values for these groups derived from the literature. No attempt is made to find appropriate species for comparison as the surface populations are arid adapted and far removed taxonomically from the wet tropical litter species from which the troglobites in Cape Range were probably derived (Humphreys, 1989; Humphreys *et al.*, 1989; Vine *et al.*, 1988). Finally, nearly all data on troglobite ecophysiology are for species taken from caves in temperate regions.

### Definitions

The fauna found in caves is traditionally divided amongst: accidentals (species entering caves by chance); troglonemes (sporadic cave dwelling species, e.g. bats); troglonemes (facultative cave dwelling species, often divided into first level troglonemes, found both in cave and epigeal habitats, and second level troglonemes which are found only in caves) and troglobites (obligate cave dwelling species usually with significant eye and pigment reduction and which are of considerable evolutionary interest; Hamilton-Smith, 1967; Culver, 1982). Various other terms and categories are used by different workers (e.g. Vandel, 1965).

The categories are based on the level of dependence on the cave system (Hamilton-Smith, 1971) deduced from their distribution within and without caves and the degree of morphological adaptation presumed to be adaptive to cave life. Second level troglonemes may turn out to have clear adaptations to caves in non-morphological characters, e.g. physiological (Barr, 1963) or reproductive effort (H. Dalens, pers. comm., 1989).

As these are, in essence, functional definitions the classification requires assumptions about the nature of the adaptation or detailed knowledge of the species biology for allocation to these categories. As this knowledge is unavailable for the vast majority of cave fauna, especially in Australia and the newly worked Cape Range area, in this report species are termed troglobites only if they are eyeless and lack pigment in taxa normally possessing these characters.

## MATERIALS AND METHODS

### Materials

The cave animals were collected from a number of caves in Cape Range, North West Cape, Western Australia (detailed in Humphreys *et al.*, 1989). The epigeal isopods and millipedes were collected from gardens in Perth. Species from the caves were compared, where possible, with epigeal species of similar taxonomic groups. Three species of troglobites (*Schizomus vinei*, cave millipedes and "miturgid" spiders) and one non-troglobitic species (*Australophiloscia* sp. nov.) were examined and comparison was made with epigeal millipedes and woodlice. In addition data on the broad taxonomic groups were extracted from the literature. As most of the species are undescribed, we present below details of the material for later comparison.

1. Troglobitic *Schizomus vinei* (Chelicerata: Schizomida) (Harvey, 1988).
2. Troglobitic millipedes (Diplopoda, Craspedosomida: Paradoxosomatidae).
3. Troglobitic "miturgid" spiders (Araneae). The family status of this species is as yet uncertain.
4. Cave isopods (non-troglobitic); *Australophiloscia* sp. nov. (Philosciidae).
5. Epigeal millipedes of the Order Julida.
6. Epigeal isopods (Philosciidae).

### Husbandry

Animals were maintained in the laboratory in either 50 ml vials or small vivaria; in either cases the floor comprised one centimeter or more of soil from the cave of origin. The soil was kept moist with distilled water to maintain near saturated humidity, while preventing the accumulation of solutes. Schizomids were fed weekly on live oniscoid isopods and the "miturgids" on flour moths. Cave isopods and millipedes maintained in leaf litter from the original cave and then supplemented with leaf litter of non-cave origin, heat sterilized to prevent contamination by other species of invertebrates and micro-organisms.

### Water loss

Evaporative water loss (*EWL*) was measured in a dry air stream ( $3 \text{ l hr}^{-1}$  in a 4 mm diameter tube) and the water content of the downstream air determined by means of an electrolytic water detector (CEC 26-303 moisture monitor) at 20°C, at which temperature the animals were housed. The current output of the electrolytic cell was monitored with a Thurlby digital multimeter with an RS-232 interface to a Commodore 128 microcomputer. The computer logged the data at 30 sec intervals, and calculated the *EWL* ( $\text{mg min}^{-1}$ ), surface area specific *EWL* ( $\text{mg cm}^{-2} \text{ sec}^{-1}$ ) and resistance ( $\text{sec cm}^{-1}$ ). The surface area was approximated as Surface area ( $\text{cm}^2$ ) =  $k[\text{Body mass (g)}]^{0.67}$ , where  $k = 12$ , the mean value determined in other studies (e.g. Cloudsley-Thompson, 1957; Davies and Edney, 1952). Resistance to water loss (*R*) was calculated after Nobel (1974) as  $R = dCWV/EWL$ , where *dCWV* is the water vapour concentration deficit ( $\text{mg cm}^{-3}$ ) and *EWL* is the surface area-specific evaporative water loss ( $\text{mg cm}^{-2} \text{ sec}^{-1}$ ). Individuals were placed in the apparatus to equilibrate to remove adsorbed water.

### Respirometry

Oxygen consumption was measured over 24 hr in a Warburg constant volume respirometers using the direct method. A constant temperature was maintained in a water bath fitted with a switching thermometer controlling a circulating heater (Braun Thermomix). Individuals were used straight from culture and, where possible, compared with another species of the same group. The animals were provided with a strip of water soaked filter paper and the carbon dioxide produced was absorbed by 0.2 ml of 5% KOH. Calculations followed Umbreit *et al.* (1964). Respiration was measured at 25°C, temperatures similar to those found in many caves (Humphreys *et al.*, 1989) on animals acclimated to room temperature varying from 19–21°C.

### Statistics

Least squares regression, one-way ANOVA with GT2 multiple comparisons at  $\alpha = 0.05$ , the comparison of the slopes and displacement of regression lines (ANCOVA), correlation and partial correlation follow the algorithms of Sokal and Rohlf (1981). When more than one experimental run was conducted the data for each species were analyzed for consistency between runs using Bartlett's test for homogeneity of variance on the weight specific data. No species showed significant heterogeneity ( $P > 0.05$ ).

Table 1. Analyses of the regression of oxygen consumption ( $\log \mu\text{l hr}^{-1}$ ) on weight ( $\log \text{mg}$ ) for five species determined by Warburg respirometry

Species	<i>b</i>	<i>a</i>	<i>N</i>	<i>r</i>	<i>T</i> <sub>s</sub>	<i>P</i>	Adj. mean <i>Y</i> *	$\mu\text{l mg}^{-1} \text{hr}^{-1}$
<i>S. vinei</i>	1.079	-0.863	24	0.74	5.13	<0.001	0.403a	0.237
Millipedes (cave)	0.769	-0.486	24	0.57	3.27	0.03	0.483a	0.285
Millipedes (not cave)	0.630	-0.223	24	0.71	4.73	<0.001	0.483ab	0.285
Isopods (cave)	0.945	-0.494	13	0.94	9.61	<0.001	0.671b	0.439
Isopods (not cave)	0.643	-0.017	8	0.74	2.73	0.034	0.710b	0.480

\*Adjusted mean *Y* for the common slope of 0.824; rows with common letters are not significantly different at  $\alpha = 0.05$ . The mean masses were respectively 8.6, 12.0, 45.9, 13.1 and 45.8 mg.

## RESULTS

### Respiration

The pooled respiration data for each species were regressed on body weight and the regressions compared using analysis of variance on the slopes and intercepts of the regression lines (Table 1). All species show significant regressions of oxygen consumption on body weight with the slopes (*b*) ranging between 0.63 and 1.08. The slopes of the regressions do not differ significantly ( $F_{s,4,83} = 1.520$ ;  $P = 0.204$ ) and the intercepts were compared for the common slope of 0.824. The intercepts differ significantly ( $F_{s,4,87} = 9.346$ ;  $P < 0.001$ ). Multiple comparison tests (GT2 procedure) show that the adjusted mean *Y* values fall into two main groups (Table 1) with *S. vinei* and the cave millipedes having a lower rate of oxygen consumption than either the cave or epigean isopods, which themselves do not have different rates of oxygen consumption. The epigean millipedes have respiration rates intermediate between these two groups, not differing significantly from either.

### Effect of temperature

For the cave millipedes respiration was also measured at 22°C ( $n = 8$ ), 25.7°C ( $n = 8$ ) and 30°C ( $n = 15$ ). Stepwise regression was conducted to predict oxygen uptake using weight, duration of measurement and temperature as the independent variables. Temperature was the most important variable predicting oxygen consumption ( $F_{s,1,45} = 24.47$ ,

$P < 0.001$ ), accounting for 34% of the variance (adjusted  $r^2$ ). Because of the power function in the relationship between weight and oxygen uptake ( $b = 0.769$ ), weight was also a significant variable, accounting for an additional 6.7% of the variance ( $F_{s,2,44} = 16.68$ ,  $P < 0.001$ ). Duration (47.7–23 hr) had no significant effect on the respiration rate, accounting for only 2.3% of the variance; this suggests the absence of diurnal rhythm. The  $Q_{10,22-30^\circ\text{C}} (= 3.26)$  is high and may indicate a sensitivity to temperature change of a species coming from a relatively uniform thermal environment. Additional work is needed to establish the sensitivity of the troglobitic millipedes, and troglobites in general, to temperature change and to determine whether they acclimate.

Using the data from Poulson (1964), troglobitic isopods have higher  $Q_{10}$  values (Table 2) than less cave adapted and epigean isopods (Kruskal-Wallis Test:  $H_{\text{adj}} = 4.395$ ,  $P = 0.036$ ). While this indicates that troglobites may be more temperature responsive than non-troglobites, these values were obtained by different workers using different techniques. There are no data available from standardized methods which would permit a more definitive statement as to whether troglobites are more responsive to temperature because they have lost the ability to regulate, or are less responsive because they have no need to respond in the short term to temperature changes.

### Water loss

The mean values for water loss and the weights of the six species examined are presented in Table 3, where water loss is presented relative to weight, to surface area and as resistance to water loss. Analysis of variance was conducted on the regressions of water loss ( $\log \mu\text{g hr}^{-1}$ ) on body weight (mg) for all samples of the same species from different caves (millipedes from C162 and C106 and *S. vinei* from C106, C118, C159 and C162). None were found to differ significantly from the others and the samples were pooled.

Table 2. Mean  $Q_{10}$  values of oxygen consumption for six species of Isopoda: Sphaeromidae and Amphipoda: Gammaridae (data from Poulson, 1964, Table 1, where source references are given)

Status	$Q_{10}$	SD	<i>N</i>
Epigean	1.60	0.21	2
Trogophile	1.63	0.40	4
Troglobite	2.26	0.71	6

Table 3. Mean weight and rates of evaporative water loss (EWL) from *S. vinei* and "miturgid" spiders from caves, and millipedes and isopods from cave and non-cave habitats

Species	<i>N</i>	Weight (mg)	Water loss ( $\text{mg g}^{-1} \text{min}^{-1}$ )	Resistance ( $\text{mg cm}^{-2} \text{hr}^{-1}$ )	Resistance ( $\text{cm sec}^{-1}$ )
Cave isopods	19	14.21 (5.59)	2.279 (0.450)	0.742 (0.092)	22.36 (2.83)
Epigean isopods	10	10.54 (11.23)	2.210 (0.962)	0.570 (0.164)	31.61 (8.65)
Cave millipedes	19	10.46 (3.27)	1.668 (0.613)	0.507 (0.205)	40.88 (17.21)
<i>S. vinei</i>	20	8.15 (3.36)	0.836 (0.180)	0.228 (0.039)	76.58 (12.91)
Cave spiders	6	50.68 (69.98)	0.310 (0.319)	0.072 (0.047)	303.99 (132.19)
Epigean millipedes	11	54.47 (22.82)	0.043 (0.013)	0.023 (0.009)	878.13 (284.35)
<i>G. godeffroyi</i>	—	100	0.037	—	—

The data are presented as mass and area-specific rates together with the whole body resistance (*R*). The value in parentheses is the standard deviation of the mean. The data for *Geolycosa godeffroyi* (Araneae: Lycosidae) are taken from Humphreys (1975a; Table 4).

Table 4. Analysis of the regressions of water loss ( $\log \mu\text{g hr}^{-1}$ ) on weight ( $\log \text{mg}$ ) for six species determined by water monitor (see Materials and Methods)

Species		<i>b</i>	<i>a</i>	<i>N</i>	<i>r</i>	<i>Ts</i>	<i>P</i>	Mean <i>Y</i>
"Miturgids"	T	0.500	1.646	6	0.921	4.717	0.009	2.133
<i>S. vinei</i>	T	0.716	1.939	20	0.898	8.651	<0.001	2.630
Millipedes	T	0.826	2.146	19	0.663	3.656	0.002	2.966a
Isopods	N	0.429	2.576	10	0.844	4.451	0.002	3.036ab
Isopods	T	0.559	2.622	19	0.880	7.651	<0.001	3.177b
Millipedes	N	1.437	-0.370	11	0.918	6.962	<0.001	—

## ANOVA

All six species—Slopes:  $F_{5,73} = 4.327$ ;  $P = 0.002$ Minus epigean millipedes—Slopes:  $F_{4,65} = 1.352$ ;  $P = 0.260$ Intercepts:  $F_{5,69} = 120.975$ ;  $P < 0.001$ 

T and N denote troglotic and epigean species respectively. Lines (excluding the epigean millipede) with common letters show that the adjusted mean *Y* values for a common slope of 0.56 are not significantly different.

Comparison of the regressions for the six species showed that the slopes were not parallel. Removal of the epigean millipede data results in parallel lines for the remaining five species with a common slope of 0.555 (Fig. 1), but which are significantly displaced ( $P < 0.001$ , Table 4). The GT2 multiple comparison test shows that the "miturgids" have a lower rate of water loss than *S. vinei* and that both have lower rates than all other species ( $P < 0.05$ ; Table 4). The ratios for "miturgids"—*S. vinei*—millipedes—epigean isopods—cave isopods are 1.0:3.14:6.81:8.00:11.07.

Cave millipedes have water loss rates 41 times that of the epigean millipedes of a given size (ANOVA slopes;  $F_{5,126} = 2.99$ ,  $P = 0.096$ ; intercepts;  $F_{5,127} = 143.17$ ;  $P < 0.001$ ) and the rate of water loss is directly proportional to body weight (common slope = 1.023).

Cave isopods have water loss rates 1.52 times that of epigean isopods of a given size (ANOVA slopes;  $F_{5,125} = 1.17$ ,  $P = 0.289$ ; intercepts  $F_{5,126} = 34.24$ ,  $P < 0.001$ ) and the rate of water loss is proportional to body weight<sup>0.47</sup>.

The regressions for all cave species have a common slope of 0.568 ( $F_{5,3,56} = 1.698$ ;  $P = 0.178$ ) and all four species differ significantly in their rate of water loss, with the ratio "miturgids"—*S. vinei*—millipedes—epigean isopods being 1.0:3.16:6.84:11.07.

## DISCUSSION

## Respiration

The slopes of the regressions (double logarithmic) of oxygen consumption on weight varied between 0.64 and 1.08 with the common slope being 0.82. This compares with a pooled slope of 0.73 in the regression from the pooled data for many species of isopods, spiders and millipedes (Fig. 2). In this pooled data set the individual broad taxonomic groups have slopes of 0.47, 0.06 and 0.64, respectively.

Peters (1983, pp. 245–247) provides a comprehensive analysis of the respiration rate with respect to body mass of 24 groups of arthropods at temperatures between 15 and 30°C. The frequency distribution of these metabolic rates is shown in Fig. 3. These data cover the range of oxygen consumption from 2.2 to 123.7  $\mu\text{l } 10 \text{ mg}^{-1} \text{ hr}^{-1}$ ; the five species considered here all lie to the lower end of this frequency distribution.

A compilation of data for individual species within the same broad taxonomic groupings as the species considered here is presented in Fig. 4. There is clearly no consistency between the respiration levels of the species, both troglotic and epigean, considered here, and the general level of respiration in these groups as reported in the literature (Fig. 4). Both the cave and epigean isopods lie towards the lower end

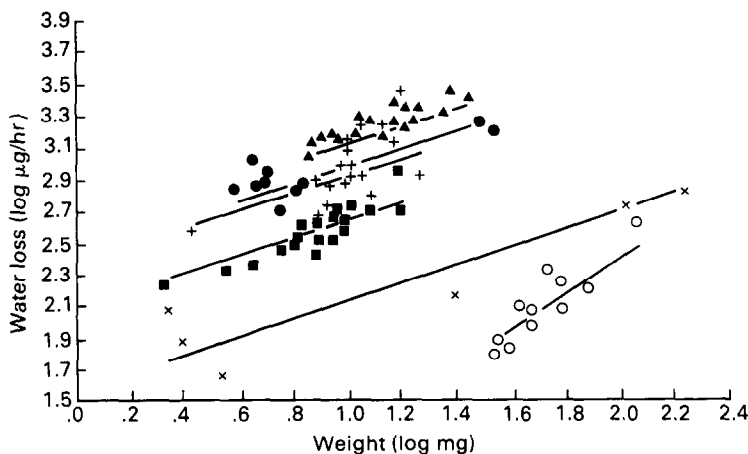


Fig. 1. Regressions of water loss ( $\log \mu\text{g hr}^{-1}$ ) on body weight for six species. The plotted regression lines for all species, except the epigean millipede, have been adjusted to their common slope. "Miturgids" ( $\times$ ), *S. vinei* (squares), cave millipedes ( $\Delta$ ), cave isopods (triangles), epigean isopods (closed circles) and epigean millipede (open circles).

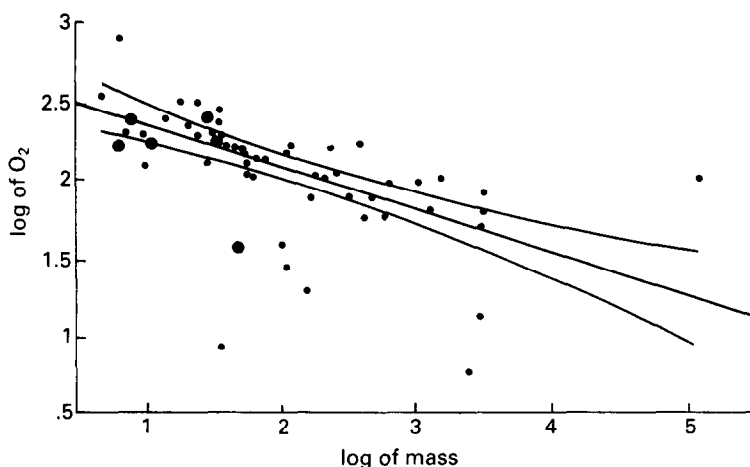


Fig. 2. Graph of respiration rate ( $\log \mu\text{l O}_2 \text{ g}^{-1} \text{ hr}^{-1}$ ) on mass (mg) of many species of millipedes, isopods and spiders. The error bounds enclose the 95% limits of the estimated  $Y$ ;  $Y = 2.65 - 0.275X$ ,  $r^2 = 0.43$ . Large circles denote data from this paper; they are not included in the regression. Data from Al-Dabbagh (1976); Al-Dabbagh and Marina (1986); Byzova (1967); Cloudsley-Thompson (1969); Dwarakanath (1971); Dwarakanath *et al.* (1973); Edney (1964); Hadley *et al.* (1981); McQueen *et al.* (1983); Mispagel (1981); Newell *et al.* (1974); Reichle (1968); Saito (1969); Stewart and Woodring (1973); Wieser (1965); Wooten and Crawford (1974).

of the isopod data (Fig. 4). However, both the epigeal and cave millipedes lie towards the mid-point of the data for millipedes considered in Fig. 4. Although the measured respiration rates were similar, the behaviour of the two species differs in the Warburg apparatus; cave millipedes walk incessantly, as they do in caves, while the epigeal millipedes curl up and remain immobile. The respiration rate of *S. vinei* ( $1.64 \mu\text{l } 10 \text{ mg}^{-1} \text{ hr}^{-1}$ ) lies towards the lower end of data from spiders (Fig. 4) but is greater than that of the cave spider *Lycosa howarthi* ( $1.16 \mu\text{l } 10 \text{ mg}^{-1} \text{ hr}^{-1}$ ; Hadley *et al.*, 1981). In summary, all the species considered here have respiration rates lower than the average for the group shown in Fig. 4. However, the troglitic species do not have lower rates of respiration than do the epigeal species, nor do they have respiration rates especially

low for the broad taxonomic category to which they belong.

#### Water loss

The resistance reported here for *S. vinei* is considerably higher ( $76.6 \text{ cm sec}^{-1}$ ) than that previously reported ( $15.2 \text{ cm sec}^{-1}$ ; Humphreys *et al.*, 1989) for a smaller sample, despite the flow rate used here being *ca* 4.7 times greater ( $7 \text{ cm sec}^{-1}$ ) than that previously used. It probably results from the inclusion of adsorbed water in the earlier study due to a shorter period of equilibration (*ca* 15 min) compared with 33.5 min (SD = 14.7). This is supported by multiplying the rate of water loss during the measurement period by the total time the individual was in the apparatus; this accounted for between 26 and 49% of the gravimetrically determined water loss, with no

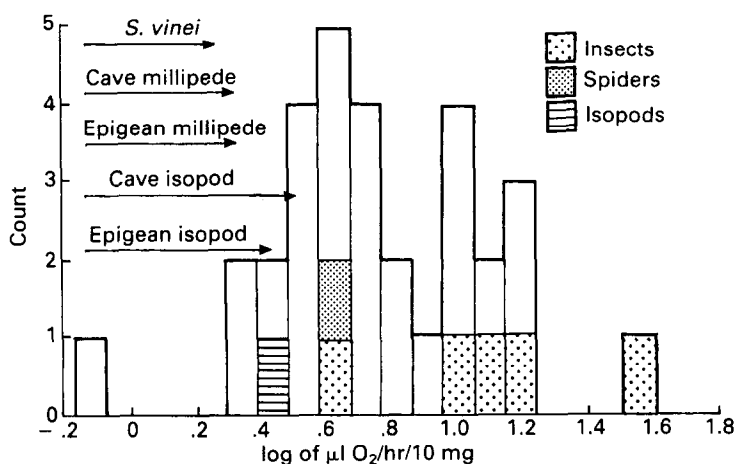


Fig. 3. Histogram of the log frequency distribution of metabolic rates ( $\mu\text{l } 10 \text{ mg}^{-1} \text{ hr}^{-1}$ ) of arthropods calculated from the equations in Peters (1983, pp. 245–247). The arrow tip represents the mean value for the species reported here. Clear bars denote non-isopod crustacea. The data were converted from Watts at 1 kg to oxygen consumption at 10 mg using the same conversion factors as Peters (1983, Appendix 1a).

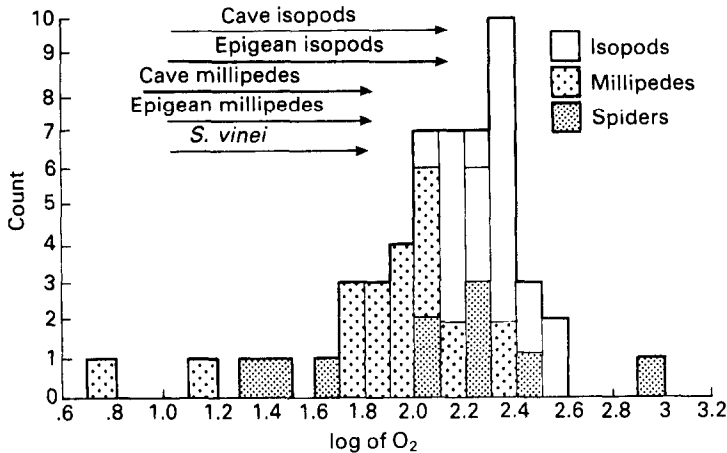


Fig. 4. Histogram of respiration rates ( $\log \mu\text{l O}_2 \text{ g}^{-1} \text{ hr}^{-1}$ ) of many species of millipedes, isopods and spiders (see Fig. 2 for sources of data). The tip of the arrow denotes the mean respiration rate of the species indicated.

significant correlation with individual weight in any species.

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