COMPARATIVE WATER RELATIONS
OF SOME TROPICAL MILLIPEDES

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ABSTRACT. Water content, percentage of total body water lost as a function of time, and cuticular permeability are determined for 10 species of millipedes representing three orders (Polydesmida, Spirobolida and Spirostreptida). Mean water content per cubic centimeter of body mass ranges from 422 mg for *Polydesmopeltis kelaarti* to 886 mg for yet undetermined Species B (Spirostreptida: Harpagophoridae). Mean percentage of total body water ranged from 57.46 for *Orthomorpha coarctata* to 70.21 for *P. kelaarti*. Mean cuticular permeability ranges from 20.28 µg $cm^{-1}h^{-1}$mm Hg^{-1} for *Gonoplectus malayusto* 82.53 µg $cm^{-1}h^{-1}$mm $Hg^{-1}$for *O.coarctata*. Cumulative percentage of total body water lost at 20 hour varied widely ranging from 9.35% in *G. malayus* to 61.64% in *O. coarctata*.
Smaller millipedes (Polydesmida), having lower water reserve, higher CP values and higher rate of percent of TBW lost, are less tolerant to desiccation compared with larger species (Spirobolida and Spirostreptida). Analyzed polydesmids are restricted to hygric environments, whereas, spirobolids and spirostreptids can tolerate desiccation to a large extent and are confined to mesic or xeric habitats.

Key words: water content, total body water (TBW), cuticular permeability (CP), millipedes, habitat type.

INTRODUCTION

Water conservation is of major importance for terrestrial arthropods (CLOUDSLEY-THOMPSON, 1975). In order to prevent desiccation, most arthropods often possess a relatively impervious waxy integument (EDNEY, 1977). However, the frequent opening of respiratory spiracles associated with tracheal breathing leads to a net water loss during gas exchange. Moreover, terrestrial environments associated with soils and leaf litter, vary in moisture content and this may affect the degree to which arthropods experience desiccation stress. As such, soils, which can be classified as hygric (containing a high water content), mesic (containing a moderate amount of water), or xeric (containing a little water), may be associated with arthropods that differ in their water reserves, cuticular permeability and rates of water loss.

The cuticle of most species of millipedes is permeable to the water and this restricts their habitats to areas where the humidity is high (EDNEY, 1977). As such, in these groups water loss by transpiration tends to be proportional to the saturation deficiency of the atmosphere (CLOUDSLEY-THOMPSON, 1960, 1961). Because these arthropods lose water rapidly in dry air at normal ambient temperatures, they tend to be restricted to moist cryptozoic micro habitats such

as those found within soils, under stones, fallen leaves and within crevices (BLIGH *et al.*, 1976). As millipedes vary greatly in size (2mm to 300mm), it is expected that water loss dynamics associated with body size will be evident.

Though water relations in different species of insects have been studied extensively (APPEL *et al.*, 1983; MACK and APPEL, 1986; MACK *et al.*, 1988; APPEL and SPONSLER, 1989; SPONSLER and APPEL, 1990; APPEL *et al.*, 1991), studies on water relations in millipedes are scant (CLOUDSLEY-THOMPSON, 1950; EDNEY, 1951; CRAWFORD, 1972; STEWART and WOODRING, 1973; APPEL, 1988) and there are no comparative studies on water relations in millipedes from different orders.

The objective of this study is to examine different aspects of water relations in 10 species of tropical millipedes including differences in their water content per unit volume, cuticular permeability (CP), total body water (TBW) loss and mortality, in the context of the types of environments they are found in and their overall sizes. In particular, in this study two hypotheses have been tested:

1) that a species' CP values will determine the types of environments they are associated with (hygric, mesic, or xeric); and

2) that differences in millipede body size will influence a millipede's ability to retain and conserve water. If water conservation is affected by water content in an environment, then it is expected that from hygric to xeric environment, CP values will be lowest for species inhabiting drier habitats and the rate of TBW lost also will be lowest for these species. If body size affects susceptibility to desiccation then it is predicted that small individuals will die earlier compared to larger ones.

MATERIALS AND METHODS

In this study, 12 millipede species found across different soil habitats (that varied in moisture content) and seasons were collected from several localities in the district Birbhum ($23^032´30´´N$ to the $24^035´N$, and $87^05´25´´E$ to the $88^01´40´´E$) (West Bengal, India). Among them, 10 species were selected for experimentation as two species are minute (<6 mm) and difficult to handle.

Adult millipedes were collected by hand, randomly from their natural habitats, from June to September. Species A and *Orthomorpha coarctata* (Saussure, 1860) were strictly restricted to the moist decomposed leaf litter in shady areas. Species B was often found in grass fields with decomposed leaf litter or organic matter and within dry soils associated with animal litter, rotten vegetables, etc. *Xenobolus carnifex* (Fabricius, 1775), *Trigoniulus lumbricinus* (Gerstaecker,1873), *Streptogonopus phipsoni* (Pocock, 1892) and *Anoplodesmus saussurii* (Humbert, 1865) were found within grassy fields and open soils rich in organic matter as well as on wall surfaces covered with bryophytes and fungi. These later species were also mostly prevalent at the onset of rainy season. *Polydesmopeltis kelaarti* (Humbert,1865) and *Chondromorpha severini* (Silevestri,1897) were often found in the grass fields rich in organic matter and damp brick as well as in the wall surface rich in bryophytes. For these species, their habitats were strictly in shady areas, such as under the shadow of large trees. *Gonoplectus malayus* (Carl, 1909) was found along the banks of rivers, canals, or high ridge of soil covered with grasses. These species lives within holes and crevices as were strictly nocturnal, active during most months and occurred along a pronounced climatic moisture gradient (high and low moisture gradient in fall and winter respectively).

After collection, millipedes were held within large plastic pots (diameter 30 cm) and maintained in the laboratory on moist soil (30-40% water), decomposed leaves of jack fruit, mango and guava. Each species was placed within a separate pot. The millipedes were also provided daily with fresh water, pieces of cut potato, papaya, or cucumber. The cultures were maintained at about 75-80% Rh and 26-29 ^{0}C. Specimens were used in the experiments within a

week of collection. For each experiment, ten species of millipedes (20 individuals per species) were used (Table 1).

The length and width of live adult millipedes were determined as described by BLOWER and GABBUT (1964), BLOWER and MILLER (1977) and BHAKAT (1987). Surface area and volume of each specimen was estimated by considering the millipede as a cylinder and by using the following formulas:

Surface area = $2\pi rh$ and volume=$\pi r^2 h$, where, r=radius i.e. half of the width and h=length.

Each specimen was weighed separately by an analytical balance with accuracy up to 0.01 mg for estimation of simultaneous weight loss (see below) and final dry weight.

The water content, cuticular permeability (CP), and percentage of total body water (TBW) lost over 24 hour time was determined gravimetrically (APPEL et al., 1983; MACK and APPEL, 1986). For estimation of CP and percentage of TBW lost over time, millipedes were starved for one day prior to the experiment to avoid the variability of gut contents and the dropping of the fecal matter. After starving, individual millipedes were placed in open glass vials having different diameters (2-8 cm) and height (3-6cm), which were then put into a large desiccator maintained at 30 ± 1 ^{0}C and 0-2% Rh. Anhydrous $CaSO_4$ was used in the desiccator as moisture drier which maintained the air in the chamber 0-2% Rh. The desiccator was then placed in an incubator maintained at 30 ± 1 ^{0}C. Over the next 24 hours, at four hour intervals each specimen was taken out of its vial, weighed and then returned to the vial as quickly as possible. After 24 hours weight losses were measured till death for all the specimens. The loss of body mass measures conducted every four hours and percentage of TBW measures (defined as the proportional difference between the initial weight of the live specimen and its successive weights throughout the experiment) were used to calculate percentage of TBW lost over time. After completion of the experiment, dry weight was determined by weighing the oven dried (at 60 ^{0}C) specimen until two successive weighing did not differ. CP was determined using data from the first 4 hours of the desiccation experiment because this period represented the maximum water differential between the millipede and the desiccation chamber and thus the maximum rate of water loss for a given millipede. CP was calculated as the µg of water lost per unit surface area (cm^2) per unit time (h) per unit saturation deficit (mm Hg) in a desiccation chamber.

The data were expressed as means ±S.E. Linear regression analyses were employed to determine percentage of TBW lost over time and these rates were also correlated with millipede size. Q value (body volume to surface area) was calculated for each species and used to quantify the relationship between CP and mortality. t-tests were performed to determine the differences between water content and rates of percent of TBW lost in three millipede orders (polydesmida, spirostreptida and spirobolida).

RESULT AND DISCUSSION

Water content

Length, width and percentage of TBW are listed in Table 1. Initial body water content of the millipedes examined ranged from 57.46±2.04% for *Orthomorpha coarctata* to 70.21±0.89% for *Polydesmopeltis kelaarti*. These were within the range of non-insect arthropods (54–85% TBW) summarized by EDNEY (1977) and in accordance with other millipedes. Among millipedes, for example other studies have shown that *Oxidus gracilis* (C. L. Koch, 1847) (Polydesmida) contained 60% TBW (APPEL, 1988), while *Spirostreptus syriacus* (Spirostreptida) contained 44.5±1.4 to 74.0±1.9% TBW in different geographic locations and seasons (CRAWFORD et al., 1986). DANGERFIELD and MILNER (1993) also reported that water content for *Alloporus uncinatus* (Attems, 1914) (Spirostreptida) was 66.04±0.64%, while for *Odontopyge* sp. (Odontophygidae) was 60.35±0.02% and 59.34±3.57 for *Poratophilus* sp. (Harpagophoridae).

Table 1. Systematic position, measurements, water content, and percent of total body water of ten species of adult millipedes (n=20).

Species	Systematic position		Length (mm)	Width (mm)	Water content (mg/cm^3)	Percentage of water
	Order	Family				
Species A	Polydesmida	Paradoxosomatidae	14.72 ± 0.53	1.62 ± 0.03	711.32 ± 2.86	63.97 ± 2.45
Polydesmopeltis kelaarti	Polydesmida	Paradoxosomatidae	27.09 ± 0.51	3.56±0.09	422.08 ± 2.45	70.21 ± 0.89
Chondromorpha severini	Polydesmida	Paradoxosomatidae	33.23 ± 0.46	4.24±0.13	566.28 ± 6.24	65.97 ± 1.21
Orthomorpha coarctata	Polydesmida	Paradoxosomatidae	17.39 ± 0.20	1.85 ± 0.05	607.28 ± 2.19	57.46 ± 2.04
Anoplodesmus saussurii	Polydesmida	Paradoxosomatidae	35.55 ± 0.40	4.22 ± 0.07	442.49 ± 5.49	66.20 ±1.41
Streptogonopus phipsoni	Polydesmida	Paradoxosomatidae	24.09 ± 0.27	2.81 ± 0.07	512.09 ± 1.85	62.46±1.23
Xenobolus carnifex	Spirobolida	Pachybolidae	55.01 ± 0.62	4.38 ± 0.06	775.78 ± 10.59	60.80 ± 1.52
Trigoniulus lumbricinus	Spirobolida	Trigoniulidae	48.78 ± 0.75	3.82 ± 0.07	743.27 ± 6.28	62.22 ± 2.15
Species B	Spirostreptida	Harpagophoridae	54.50 ± 0.66	3.09 ± 0.06	886.56 ±5.49	59.42 ± 3.08
Genoplectus malayus	Spirostreptida	Harpagophoridae	109.24 ± 1.68	8.00 ± 0.11	832.21±21.54	63.20 ± 4.23

Table 3. Cumulative percent of TBW lost as a function of time in ten species of millipedes (n=20).

Species	Cumulative percent of TBW lost at hour ± SE						% of water lost at death
	4	8	12	16	20	24	
Species A	22.67 ± 1.14	36.03 ± 2.25	45.23 ± 2.30	47.58 ± 1.56	58.49 ± 1.27		58.52 ± 0.92
P. kelaarti	15.11 ± 1.11	24.87 ± 1.95	35.22 ± 2.54	44.16 ± 3.50	47.11 ± 3.26	56.45 ± 3.27	69.14 ± 1.24
C. severini	12.56 ± 0.56	21.50 ± 1.01	29.05 ± 1.32	36.01 ± 1.61	43.91 ± 1.62	51.26 ± 2.10	61.72 ± 0.85
O. coarctata	26.41 ± 1.29	38.66 ±1.93	48.00 ± 2.17	53.52 ± 1.79	61.64 ± 0.83		63.46 ± 1.27
A. saussurii	10.32 ± 0.33	18.05 ± 0.65	24.68 ± 0.90	30.04 ± 1.08	34.68 ±1.15	38.72 ± 1.22	79.66 ± 2.14
S. phipsoni	10.78 ± 0.32	15.48 ± 0.57	20.64 ± 1.10	26.58 ± 1.33	31.79 ± 1.66	36.90 ± 2.23	71.67 ± 1.25
X. carnifex	10.01 ± 0.44	17.16 ± 0.51	24.35 ± 0.62	31.79 ± 0.79	38.90 ± 0.96	49.22 ± 1.14	71.63 ± 0.58
T. lumbricinus	5.60 ± 0.39	9.20 ± 0.56	13.45 ± 0.83	18.03 ± 1.07	22.89 ± 1.15	27.42 ± 1.24	73.29 ± 0.89
Species B	4.82 ±0.33	7.11 ± 0.35	9.49 ± 0.41	10.99 ± 0.46	13.32 ± 0.64	15.81 ± 0.79	68.35 ± 1.27
G. malayus	2.79 ± 0.11	4.66 ± 0.19	6.41 ± 0.24	7.92 ± 0.25	9.35 ± 0.27	10.75 ± 0.32	77.01 ± 1.25

As a general principle, BUXTON (1932) stated that the percentage of water content per mass decreases as an insect increases in size. This, he argued, was the result of a relative increase in the proportion of the total mass contributed by the cuticle in larger animals. BARLOW (1957), however, show no correlation between 'body weight' (presumably fresh weight) and the proportion of dry matter to the water for *Ommatoiulus sabulosus* (Linnaeus, 1758), *Cylindroiulus punctatus* (Leach, 1815), and *Julus scadinavius* Latzel, 1884. He concluded that these millipedes were not in keeping with Buxton's principle. In this study water content in proportion to dry matter were also not correlated (largest millipede *G. malayus* and smallest millipede species A contain 171 mg and 177 mg of water / 100 mg of dry matter respectively). Water content per unit body volume depicts water reservoir of a species better than the total body water (TBW) (Table 1). This shows that *P. kelaarti* contains less water (422 mg/cm^3), relative to Species B (886 mg/cm^3). Moreover, in the polydesmidan (small in size in respect to other analyzed species belonging to other two orders) water content is low (543.59 mg/cm^3) but other larger millipedes (belonging to spirostrepitdan and spirobolidan) contain greater amounts of water (mean value for four species was 809.71 mg/cm^3) (t=870.20, P<0.01). Spirostreptida (*G. malayus* and Species B) contained more water than the two analyzed spirobolidans (*X. carnifex* and *T. lumbricinus*)suggesting that greater water reserves (per unit volume) may be an important adaptation for living in comparatively dry habitats (towards xeric habitat).

Cuticular permeability

For all species, the greatest rate of water loss occurred within the first 4 hr then gradually decreased (Table 3). In insects, decelerating water loss at any given temperature may be due to the overlapping of sclerites or closer packing of cuticle elements as during dehydrates (BURSELL, 1955; LOVERIDGE, 1980).

Table 2 shows the CP of 10 species of millipedes. The greatest mean CP was 82.53±2.78µg cm^{-2} h^{-1}mm Hg^{-1} for *O. coarctata* and lowest mean CP was 20.28±1.23 µg cm^{-2} h^{-1}mm Hg^{-1} for *G. malayus*. When CP values were regressed with the ratio of body volume to area (Q, Table 2) and length (L) across species, CP values were found to decrease with increases in body size (CP=-38.4Q+88.7, r2=0.5592, P<0.01 and CP=0.63L+76.16, r2=0.5401, P<0.05 respectively). These results would suggest that larger species, such as (*G. malayus*) are more desiccation resistant relative to smaller species (*O. coarctata*) and that increase in body size may be an adaptation for more mesic environments. In turn, the negative relationship between CP values and the timing of death when millipedes were placed within desiccation chambers (Mortality=197.17-2.36CP, r2=0.4981, P<0.05) shows that lower CP values provide species with a greater ability to resist desiccation. Millipede having low CP value (20.28 in *G. malayus*) for example, survived for a longer period (303.72 h) compared to the millipede that have high CP values (*O. coarctata*, CP-82.53, died within 21.45 h). Edney (1977) classified the types of habitats that given arthropods may be adapted based on their CP values. Habitats were classified as xeric, mesic, and hygric if they correspond to CP values of <25, 25-40, and >40 respectively. Like other studies that have been found a relationship between CP values and the moisture content associated with their environments (EDNEY, 1951; MEAD-BRIGGS, 1956; CRAWFORD, 1972), this study found that Species A and *O. coarctata* are hygric (with CP values ≥40) and *G. malayus* is truly xeric (CP value ≤25). However most species of millipedes inhabit, at least to some degree, mesic environments. So Edney's classification of habitat will be better fit if we consider CP along with the hour of death, and rate of % of TBW lost. Thus a species may be transitional in between two habitats. On this principle, the habitats of 10 species of millipedes are listed in Table 2. The relationship between values of CP in consideration with long hours of death and minimum rate of % of TBW lost may explain why Species B and *G. malayus* can survive hot and dry conditions with associated low soil moisture and high maximum daily temperatures, while other species of millipedes are restricted to habitats with high moisture content.

Table 2. A species' surface to volume ratio (Q), cuticular permeability (CP), hour of death, and the type habitat it is associated with.

Species	Q	CP[*]	Hour of death	Habitat
Species A	0.405	80.85 ± 1.27	20.35±0.82	Hygric
P. kelaarti	0.89	75.76 ± 2.14	30.51 ± 2.89	Hygric – Mesic
C. severini	1.06	61.76 ± 2.35	40.51±5.11	Hygric – Mesic
O. coarctata	0.463	82.53 ± 2.78	21.45 ± 0.78	Hygric
A. saussurii	1.055	45.21 ± 3.15	80.11 ± 2.70	Mesic – Hygric
S. phipsoni	1.423	30.58 ± 0.83	53.91 ± 4.13	Mesic – Hygric
X. carnifex	1.095	28.74 ± 2.31	40.81 ± 2.22	Mesic – Hygric
T. lumbricinus	0.955	43.80 ± 0.49	70.24 ± 2.32	Mesic – Hygric
Species B	0.773	28. 83 ± 0.89	134.05 ± 5.06	Mesic – Xeric
G. malayus	2.0	20.28 ± 1.23	303.72 ± 15.05	Xeric

*CP in units of $\mu g\ cm^{-1}h^{-1}mm\ Hg^{-1}$

Table 4. Regression equations for cumulative percentage of TBW lost over time (4 to 24 h) for 10 species of millipedes (P<0.01).

Species	Regression equation	r^2
Species A	Y=2.08x+17.04	0.957
P. kelaarti	Y=2.02x+8.99	0.988
C. severini	Y=1.91x+5.64	0.998
O. coarctata	Y=2.13x+20.05	0.980
A. saussurii	Y=1.41x+6.37	0.986
S. phipsoni	Y=1.32x+5.15	0.999
X. carnifex	Y=1.92x+1.70	0.996
T. lumbricinus	Y=1.11x+0.63	0.998
Species B	Y=0.54x+2.50	0.996
G. malayus	Y=0.40x+1.45	0.996

Y = Cumulative percentage of TBW lost and X = Desiccation time in hours: n=6 for all species except Species A and *O. coarctata* (n=5).

Total Body Water loss and Mortality

The mean percentage of TBW lost as a function of desiccation time is shown in Table 3. Rates of cumulative mass loss at 20 h ranged from 9.35±0.27% for *G. malayus* to 61.64±0.83% for *O. coarctata*. All species had a rapid initial rate of water loss within the initial four hours. This rapid loss of water is consistent with a multi-compartment water loss model which assumes that cuticular and extra cellular water is lost more rapidly than tissue or intracellular water (EDNEY, 1977; MACHIN, 1981).

An examination of the mean percentage of TBW lost over time across the species shows that an increase in body length led to a less rapid decline in the percentage of TBW lost over time (Table 5). Smaller species (Species A and *O. coarctata*) for example, rapidly lost their body water reserves and died within 20 h, while larger species, such as *G. malayus* and Species B, lost body water reserves at a slower rate. Cumulative % TBW loss for all species increased linearly with time indicating a constant rate of water loss for a given species (Figs. 1 and 2, Tables 3 and 4). Mean percent of TBW lost per four hours varied widely ranging from 1.592 in *G. malayus* to 8.995 in Species A (order wise Polydesmida 7.446, Spirobolida 6.003, Spirostreptida 1.895) (calculated from Table 3). The mean percent of TBW lost per four hours in Polydesmida differed significantly with that of other two orders (Spirobolida and Spirostreptida) (t=2.643, P<0.05). So

by reducing rate of loss of TBW, spirobolidans and spirostreptidans can tolerate desiccation more efficiently compared to polydesmidans. In other words, smaller millipedes are more susceptible to desiccation compared to larger one. As the percent of TBW lost represents depletion of water reserves, EDNEY (1977) considered the rate of percent TBW loss over time a more accurate reflection of interaction between water reserves and a desiccation environment than does percent wet weight lost over time.
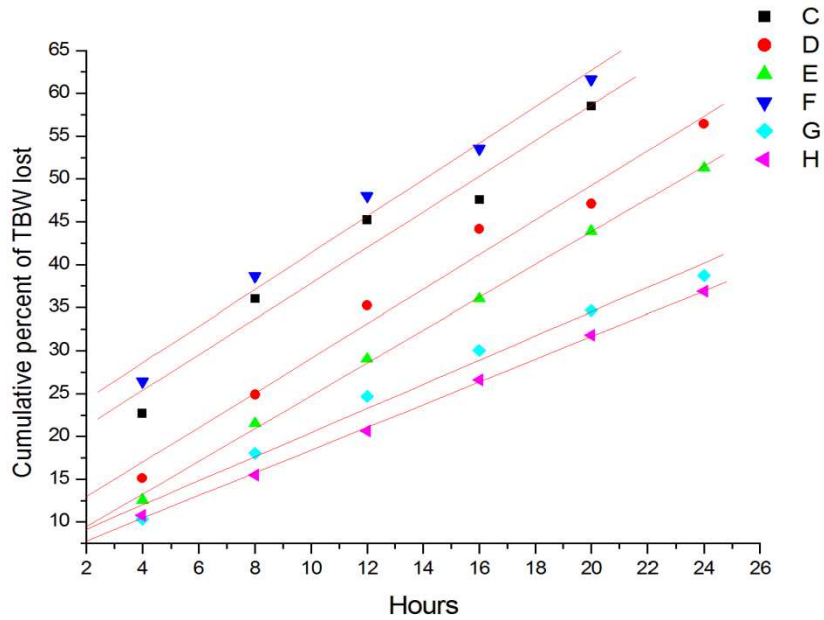

Fig. 1. Cumulative percent of TBW (mean) lost over time (hours) of six species of Polydesmida: C=Species A; D=*P. kelaarti*; E=*C. severini*; F=*O. coarctata*; G=*A. saussurii*; H=*S. phipsoni.*
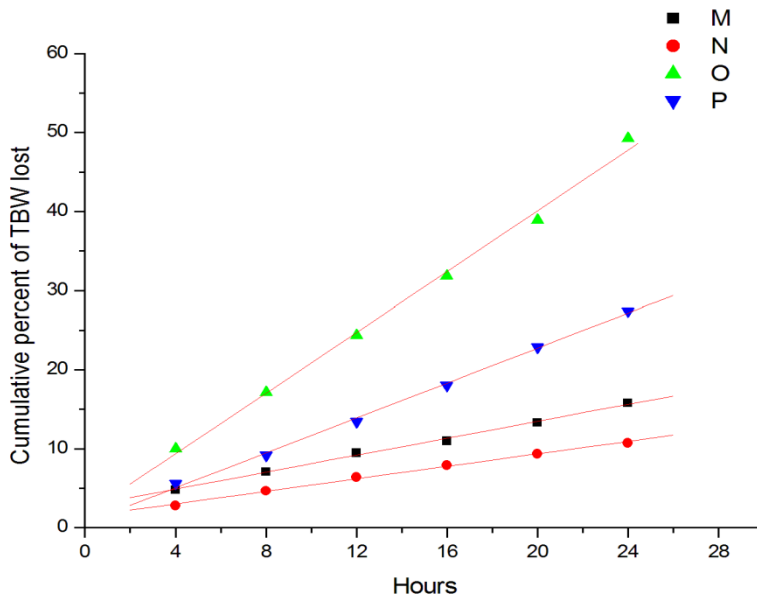

Fig. 2. Cumulative percent of TBW (mean) lost over time (hours) of two species of Spirostreptida: M=Species B; N=*G. malayus* and two species of Spirobolida; O=*X. carnifex*; P=*T. lumbricinus*

In general, the pattern of larger millipedes being less susceptible to water loss than smaller ones (CRAWFORD, 1979) was consistent with the findings of this study (Table 5). Species A and *O. coarctata* are smaller in size and died within 20 h, but the largest one *G. malayus*,

survived more than 300 h (Table 2). Mortality (hour of death) was negatively correlated with species' surface volume ratio (Q) (Mortality=140.75Q-62.59, r2=0.5679, P<0.01).

Table 5. The relationship between millipede species body size (n=10)
and percentage of TBW lost over time (4-24h) (P<0.01).

Hour	Regression equation	r^2
4	Y= 20.92 – 0.21 X	0.5831
8	Y= 32.70 – 0.32 X	0.5916
12	Y= 42.43 – 0.40X	0.6133
16	Y= 49.12 – 0.44X	0.6374
20	Y= 57.61 – 0.51X	0.6480
24	Y= 55.99-0.42X	0.5141

Y= Cumulative percentage of TBW lost and X= Size classes (in mm).

In comparison with spirostreptidans, analyzed spirobolidans and polydesmidans showed more susceptibility to water loss and died earlier. This can be explained by the fact that both these orders (Spirobolida and Polydesmida) do not possess a spiracular closing mechanism (STEWART and WOODRING, 1973) whereas, Spirostreptida can control water loss much more efficiently during movement in the dry surface by regulating the bean shaped structure guarding the spiracle (DWARAKANATH and JOB, 1965).

CONCLUSION

This study showed that within analyzed species smaller forms are mostly restricted to hygric habitat, while larger ones tend to live in xeric habitat. Moreover, smaller species having higher CP value and lower water reserve are more prone to desiccation compared with larger species. Obviously characteristics of millipede (water conservation and desiccation tolerance) determine their distribution in soil environments with variable moisture content (hygric, mesic and xeric). Furthermore, results of this study showed that differences in body size influence a millipede's ability to retain and conserve water, mortality and choice of habitat as well. Moreover, rate of percent of TBW loss over time is higher in analyzed polydesmidans. Hence polydesmidans millipede are less desiccations tolerant and restricted to hygric environments, whereas, spirobolidanss and spirostreptidans millipede species can tolerate desiccation to a large extent and are confined to mesic or xeric habitats.

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