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Size Allometry in Some Australian Mayfly Nymphs (Insecta: Ephemeroptera)

by

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The relationship between total length and four other dimensions was investigated for seven southeastern Australian species of Ephemeroptera belonging to the families Siphlonuridae, Ameletopsidae Oniscigastridae and Coloburiscidae. Of the twenty-eight relationships investigated, only nine cases of isometry were found. In most cases, there was a change in the allometric relationship late in nymphal life. However, within a given species, this change did not occur at the same total body length for all of the dimensions investigated, indicating that it was not associated with nymphs passing from an immature to a mature stage as suggested by Clifford (1970).
In the case of *Mirawara aapta*, the relationship between pro/mesonotum length and total length was more accurately described by an exponential function than a power function.

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INTRODUCTION

Although ratios of various body measurements of nymphs have been widely used in mayfly taxonomy, only Clifford (1970, b) and Maxwell and Benson (1963) have investigated nymphal allometry. Clifford (1970a) investigated size allometry (sensu Simpson *et al.* 1960) in the leptophlebiid, *Leptophlebia cupida* Say as part of a study of the life history of the species. Maxwell and Benson (1963) studied growth allometry of two species of *Epeorus* in a West Virginia stream. In the present study, size allometry of seven species of Australian mayflies was investigated, in conjunction with life history studies (Campbell 1986), to allow association of changes in size of the structures measured for the life history studies with changes in size of other body parts. The seven species investigated were *Ameletoides* sp. from Chalet Creek, (Victoria); *Mirawara aapta* Harker from the Aberfeldy River, (Victoria); *Tasmanophlebia* sp. from Alpine Creek (New South Wales); *Coloburiscoides giganteus* Tillyard from the Diggers Creek (New South Wales): *Coloburiscoides haleuticus* Eaton from the Goodradigbee River (New South Wales); and an undescribed species of *Coloburiscoides* from Big Pat's Creek (Victoria). All study sites are described in detail elsewhere (Campbell, 1986).

METHODS

Nymphs used for allometric studies were taken from those collected for a life history study (Campbell, 1986). For six of the species, seventy nymphs were measured but for *C. giganteus* eighty were measured. The nymphs measured were selected from nymphs present in several samples using a stratified random sampling method to ensure that a wide size range was included in the measured sample.

The structures measured on each nymph together with the abbreviations which will be utilized are as follows: L - Total length measured from the anterior edge of the head when this was in the normal resting position to the posterior edge of abdominal tergite 10; HW - Head width; MW - Mesonotum width; PL - The length from the anterior edge of the pronotum to the posterior edge of the mesonotum or mesonatal wing buds whichever is the longer. In the genera *Ameletoides, Mirawara* and *Coloburiscoides* the pro and mesonota are fused. For *Tasmanophlebia* the meson length alone was measured; FL - The length of the right foreleg femur. In some cases where this leg was missing the left foreleg was measured. All measurements were made using a Wild M7A stereomicroscope with a measuring eyepiece calibrated against a 200 x .01 mm graticule. Nymphs longer than 2.0 mm were measured to the nearest 0.1 mm at 10 times magnification. Smaller nymphs were measured to the nearest 0.05 mm at 20 times magnification. Within the genera studied sexual dimorphism does not become apparent until late in the nymphal life. As a consequence male and female nymphs could only be differentiated in the large nymphs.

For allometric calculations, arithmetic means were calculated for each of the measurements of the male and female nymphs separately. The data for the remaining nymphs, those of undeterminate sex, were then ranked in order of decreasing total nymphal length (L). Arithmetic means were then calculated and recorded for the measurements of the ten longest nymphs. This procedure was then repeated for the ten longest remaining nymphs and so on to the end of the sample. The means of the groups were then used for further calculations. This procedure reduces the number of points which need to be plotted without an appreciable loss of information (Simpson *et al.*, 1960; Clifford, 1970a).

The means of the groups of measurements of HW, MW, PML, and FL were first plotted against L on a log-log scale which produces a straight line when the allometric relation fits the equation.

$$y = bx^k$$

(Simpson *et al.* 1960). I shall refer to such cases as simple allometry. Isometric relationships, are a special case of simple allometry in which the value of k in the equation is one. (Simpson *et al.* 1960, Gould 1966).

Two other types of allometric relationships were encountered in the present study (Fig. 1). One in which the relationship between dimensions is described by two or more simple allometric relations, I shall refer to as compound allometry, and the other (e.g. curve for PL in Fig. 2) where the relationship cannot be described by the allometry equation (equation 1) or by several simple allometry equations I shall refer to as complex allometric relations.

Where the data, when plotted on log-log scales conformed to either simple or allometry the values of b and k and their 95% confidence intervals were determined by fitting a least squares correlation to the logs of the data (Sokal and Rohlf, 1969). In order to save space only 3 of the data plots are presented here.

RESULTS

Ameletoides sp.

MW displayed simple allometry in *Ameletoides* sp. (Fig. 1) as did HW although the bottom point was below the line possibly indicating a different relationship for small nymphs. Values for b and k were calculated for the total data set for each dimension as well as separately for each of the two lines for PL, HW and FL (Table 1). All of the values of the correlation coefficient were significant at the 0.01 confidence level. Confidence intervals and correlation coefficient could not be calculated for lines with only two points.

Tasmanophlebia sp.

With the exception of HW, all the dimensions of *Tasmanophlebia sp.* displayed simple allometry. Values for b and k were calculated for the whole data set for each dimension (Table 2), as well as separately for the sets of points on each of the two lines for HW.

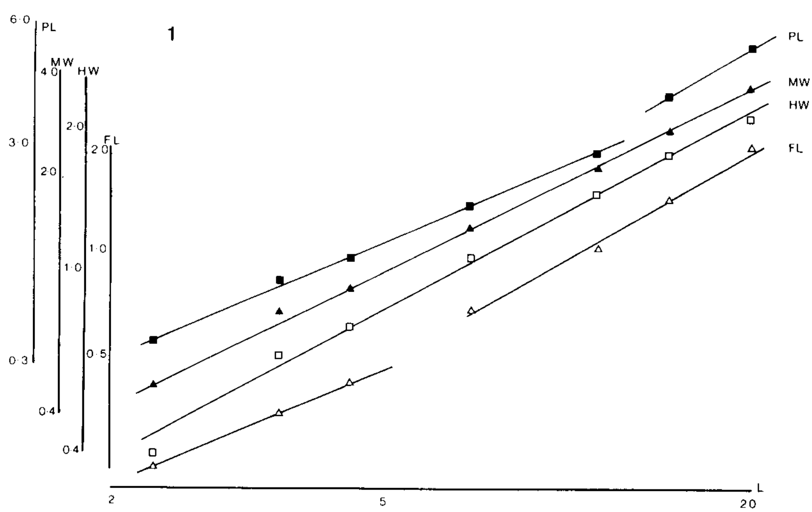

Fig. 1. Pro- and mesonotum length (PL), head width (HW), mesonotum width (MW) and foreleg femur length (FL) plotted against total body length (L) for nymphs of *Ameletoides* sp. All measurements are in millimetres and are plotted on log scales.

Table 1. Values of b and k, 95% confidence limits for k and the correlation coefficient (cc) for the allometric relationship between total length and pro- and mesonotum length (PL), head width (HW), mesonotum width (MW) and foreleg femur length (FL) for Australian Ephemeroptera nymphs.

Dimension	b	k	Upper Limit	Lower Limit	cc	Data Set
Ameletoides sp.						
PL	0.121	1.266	1.367	1.175	0.995	all points
PL	0.061	1.544	-	-	-	upper 2
PL	0.149	1.113	1.163	1.067	0.999	lower 5
HW	0.218	0.817	0.869	0.768	0.997	all points
HW	0.247	0.764	0.788	0.740	0.999	upper 6
HW	0.149	1.177	-	-	-	lower 2
MW	0.216	0.995	1.019	0.970	0.999	all points
FL	0.113	1.027	1.085	0.971	0.997	all points
FL	0.0924	1.109	1.163	1.058	0.999	upper 5
FL	0.150	0.790	0.813	0.768	1.000	lower 3
Tasmanophlebia sp.						
PL	0.034	1.721	1.797	1.648	0.998	all points
HW	0.174	0.937	0.980	0.895	0.998	all points
HW	0.180	0.917	0.992	0.847	0.998	upper 3
HW	0.151	1.044	1.049	1.039	1.000	lower 4
MW	0.132	1.165	1.235	1.100	0.989	all points
FL	0.152	0.799	0.829	0.770	0.999	all points
Mirawara aapta Harker						
PL	0.140	1.264	1.459	1.098	0.982	all points
PL	0.210	0.993	1.076	0.916	0.995	lower 5
HW	0.264	0.920	0.945	0.895	0.999	all points
MW	0.174	1.071	1.132	1.013	0.997	all points
MW	0.646	0.630	-	-	-	upper 2
FL	0.117	0.962	1.015	0.912	0.997	all points
FL	0.116	0.968	1.028	0.912	0.998	lower 5
Coloburiscoides giganteus Tillyard						
PL	0.193	1.220	1.409	1.061	0.978	all points
PL	0.235	1.089	1.182	1.003	0.995	excluding upper two points
HW	0.309	0.848	0.912	0.787	0.994	all points
HW	0.570	0.622	0.990	0.344	0.870	upper 5
HW	0.310	0.839	0.932	0.714	0.990	lower 3
MW	0.309	1.001	1.095	0.915	0.992	all points
FL	0.224	0.868	0.947	0.794	0.992	all points
FL	0.214	0.895	0.961	0.833	0.996	6 points
FL	0.238	0.826	0.895	0.762	0.995	6 points
Coloburiscoides munionga Tillyard						
PL	0.232	1.170	1.241	1.104	0.996	all points
PL	0.441	0.969	1.432	0.969	0.948[1]	upper 3
PL	0.240	1.114	1.157	1.072	0.999	lower 5
HW	0.211	0.980	1.032	0.931	0.997	all points
HW	0.325	0.801	0.842	0.762	0.998	all points
MW	0.220	1.132	1.161	1.104	0.999	all points
FL	0.117	1.125	1.209	1.048	0.995	all points

Table 1 (continued)

Dimension	b	k	Upper Limit	Lower Limit	cc	Data Set
Coloburiscoides haleuticus Eaton						
PL	0.211	1.232	1.317	1.154	0.996	all points
PL	0.257	1.172	1.459	0.948	0.983	upper 3
PL	0.255	1.115	1.127	1.103	0.999	lower 4
HW	0.314	0.849	0.920	0.783	0.994	all points
HW	0.542	0.629	0.678	0.582	0.996	upper 5
HW	0.255	0.984	1.005	0.964	1.000	lower 3
MW	0.307	1.003	1.045	0.963	0.999	all points
FL	0.218	0.881	0.905	0.858	0.999	all points
Coloburiscoides sp.						
PL	0.217	1.233	1.326	1.147	0.995	all points
PL	0.318	1.102	-	-	-	upper 2
PL	0.249	1.108	1.184	1.036	0.997	lower 5
HW	0.254	0.971	1.032	0.914	0.997	all points
HW	1.048	0.866	-	-	-	upper 2
HW	0.234	1.046	1.066	1.026	1.000	lower 5
FL	0.193	0.906	0.937	0.877	0.999	all points
FL	0.341	0.669	-	-	-	upper 2
FL	0.191	0.913	0.964	0.865	0.998	lower 5

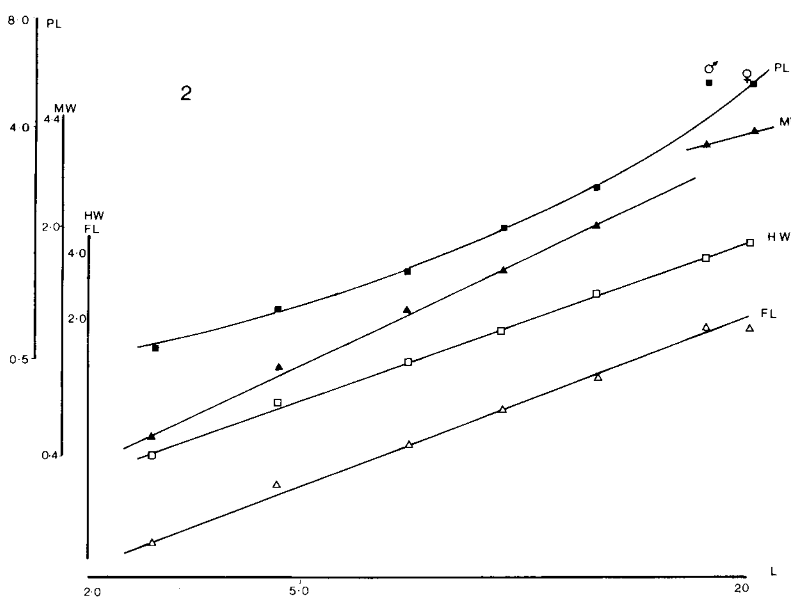

Fig. 2. Pro- and mesonotum length (PL), mesonotum width (MW), head width (HW) and foreleg femur length (FL) plotted against total length (L) for nymphs of *Mirawara aapta*. All measurements are in millimetres and are plotted on log scales.

Mirawara aapta **Harker**

When dimensions of *Mirawara aapta* were plotted against total length on log-log scales two dimensions, HW and FL, displayed simple allometry (Figure 2). However, the line best fitting the data for PL was a curve and the allometric relationship was an exponential rather than a power function, a case of complex allometry. Values of b and k were calculated for all the dimensions, including PL (Table 1). But the expression best describing the relationship for PL was $PL = 0.444\ e^{0.149L.}$

Coloburiscoides giganteus **Tillyard**

Most dimensions of *Coloburiscoides giganteus* conformed to simple allometry (Table 1). The plot for HW, however, produced two lines and the points corresponding to mature male and female nymphs were consistently higher than the lines which fitted the other points. The values for b and k were calculated for the whole set of data for each of the dimensions (Table 1) and for both lines for HW. For PL where the mature male and female nymph values were particularly aberrant the calculation was also carried out with these values excluded. For FL also, where another point also seemed a little high the calculation was carried out for two sets of six points. Only one value of the correlation coefficient was not significant at the 0.01 confidence level.

Coloburiscoides munionga **Tillyard**

Only the data for PL of *Coloburiscoides munionga* did not conform to simple allometry and required two lines. The point for the smallest nymphal size class fell well below the value predicted by the line for HW. Values for b and k were calculated for each complete set of data as well as for the sets corresponding to the two lines for PL and for the set for HW excluding the lowest value (Table 1). The correlation coefficients were significant at the 0.01 confidence level with the exception of that for the upper three points of PL which was not significant.

Coloburiscoides haleuticus **Eaton**

For *Coloburiscoides haleuticus* two dimensions, MW and FL, showed simple allometry, whilst the other two were more complex (Figure 3). Values for b and k were calculated for each complete set of data as well as the sets corresponding to the two lines in Figure 3 for PL and HW (Table 6). All correlation coefficients were significant at the 0.01 confidence level except that for the upper three points of PL.

Coloburiscoides **sp.**

None of the dimensions of *Coloburiscoides sp.* conformed to a simple allometric relationship. In each case the upper two size classes demonstrated a different allometric relationship to the rest. Values of b and k were calculated for each data set as a whole and for the upper two, and lower five sets of points (Table 1). Correlation coefficients and limits could not be calculated for the sets of two points, but the correlation coefficients for all of the other set were significant at the 0.01 level of confidence.

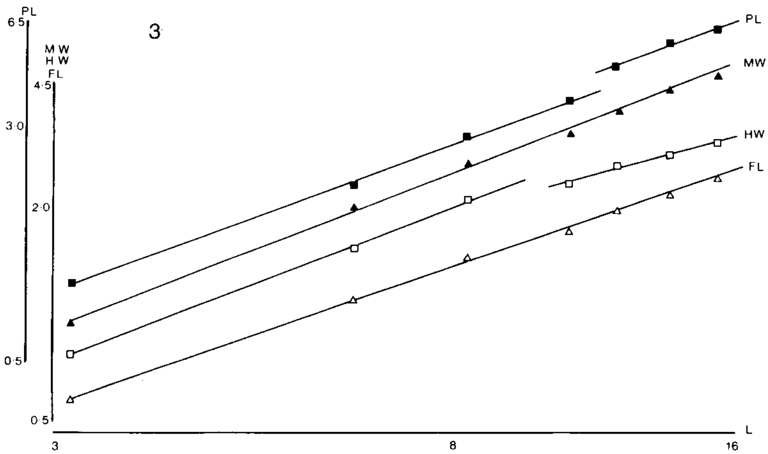

Fig. 3. Pro- and mesonotum length (PL), mesonotum width (MW), head width (HW) and foreleg femur length (FL) plotted against total length (L) for nymphs of *Coloburiscoides haleuticus*. All measurements are in millimetres and are plotted on log scales.

DISCUSSION

If isometry is assumed to occur in each case where k = 1 is within the 95% confidence limits for k, then in the present study complete isometry between length and another dimension occurred only nine times in twenty-eight cases investigated. In another six cases isometry was found to occur over a part of the size range investigated.

Clifford (1970a, b) in his investigation of size allometry of the leptophlebiid *Leptophlebia cupida* failed to find an isometric relationship between total body length and any of the six other parts he investigated. He also found all female dimensions and some male dimensions displayed a compound allometric relationship with total body length. In each case only two simple allometric relationships were compounded. In the present study also no cases of compound allometry were found which involved more than two simple allometric relations.

In a number of other cases in the present study one or two points deviated from the simple allometric relation. There were insufficient data points to determine how systematic the deviations were, but because the points were mean values and the deviations were large, it is not likely that deviations were due to errors.

Clifford (1970a) explained the compound allometric relations he found in his study in terms of the nymphs passing from immature to mature stages. He suggested that the changing ratios of specific growth rates were due to the induction of, or an increasing rate of development of, imaginal structures, Examples of such structures in Clifford's study were the development of the male forceps; the abdomen width in the female nymphs which is associated with egg development, and size of the thorax in both sexes, associated with the development of wing muscles. Furthermore, in Clifford's study the change from one simple allometric relation to another occurred at approximately the same total length for all the other dimensions measured.

In the present study, the same phenomenon was also recorded for one species - *Coloburiscoides* sp. For this species the change from one allometric relation to another occurs between 7 mm and 10 mm total length. No other species showed a similar phenomenon over all the dimensions although PL alone in three other species did show this type of allometric relationship. The change in allometric relationships in PL in each case involved a short period of very rapid growth, which would be associated with the development of wings and flight muscles in the large nymphs. Wenzel *et al.* (1990) also noted that compound allometric relationships occurred between length-length ratios in several European heptageniids and leptophlebiids, but did not provide details of the frequency.

Over the whole size range, as noted above, only nine cases of isometry were recorded in twenty-eight relationships investigated. Of the other nineteen cases, eight had values of k below 1, so the part measured grew relatively less rapidly than total length, while in eleven cases k was greater than 1. PL always had values of k greater than 1, presumably due to the growth of the wingpads especially late in the nymphal life. All of the other dimensions were variable with MW also tending to k values higher than 1 and HW and FL tending to k values lower than 1.

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