

ADAPTATIONS TOWARDS FOOD AVAILABILITY AND FORCE OF RIVER FLOW OF THE NYMPHS OF THE GENUS *AFRONURUS* LESTAGE (*EPHEMEROPTERA: HEPTAGENIIDAE*) IN SOUTH AFRICA AS A POSSIBLE EXPLANATION FOR THE DISTRIBUTION OF ITS SPECIES IN RIVERS

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I. Introduction

Since the revision of the genus *Afronurus* LESTAGE in South Africa (SCHOONBEE, 1968), an account was also given on the ecological distribution in rivers of its various species (SCHOONBEE, 1973). In the latter paper it was shown that the species always are distributed in a certain order along the length of rivers. No attempt was made, however, to explain this pattern of distribution of the species.

In this paper a theory is put forward attempting to explain this phenomenon. The relative head width in relation to head length and femur widths, in relation to lengths, of the nymphs are regarded as specific adaptations to availability of food such as algae, and resistance against force of flow, respectively, in the various parts of the rivers, thus allowing for the presence of certain species of *Afronurus* and the absence of others in particular sections of the river systems investigated.

As an introduction, a statistical evaluation is made of these ratios for the various species. Differences and similarities between the species regarding these ratios are discussed.

II. Sampling localities

Material on which the present results are based were collected from various localities in the Natal, Transvaal and Cape provinces of South Africa (Fig. 1). This enabled the author to compare amongst others morphological variation with respect to the head and femurs of nymphs within a species such as *A. barnardi* of material collected at localities of more than a thousand kilometres away from each other.

Sampling sites from where material was collected for this study are the following:

1. *Umgeni river system, Natal*

Dargle Forestry. Head water region of the Umgeni river system

Howick. Upper middle region of Umgeni river

Albert Falls. Lower middle region of Umgeni river

Emolweni river. Small coastal tributary, of Umgeni river, less than 50 km from the sea

2. Vaal river system, Transvaal

Vaal river. Several localities in the catchment area of this river system

Skandinawië drift. At bridge on the Vaal river near the town of Potchefstroom

3. Great Berg river system, Western Cape Province

Several localities as well as from a tributary at a place with the name of Saron, where material of *Afronurus barnardi* was collected for the present study.

Measurements of the lengths and widths of the heads and femora were made on formalin preserved specimens. With the exception of *A. harrisoni*, of which only four nymphs were available for measurements, enough material was collected of the other species namely *oliffi*, *barnardi*, *scotti* and *peringueyi* to enable statistical evaluations on these data obtained.

III. Statistical procedure

Symbols used in the statistical treatment of data are the following:

N, N_1, N_2 : Number of organisms analysed for a certain characteristic;

$\bar{X}, \bar{X}_1, \bar{X}_2$: Mean values

S_x^2, S_1^2, S_2^2 : Variance

S_x, S_1, S_2 : Standard deviation

In comparing the differences between the means of the abovementioned ratios for the various species, Student's t-test was employed (SIMPSON et al, 1960).

The coefficient of variability (*C.V.*) was calculated from the formula

$$C.V. = \frac{100 S_x}{\bar{x}}$$

IV. The ratio head width/length

Results of the measurements of the relative head width/length ratios for the *Afronurus* species, are summarized in Table 1. With the exception of *A. harrisoni*, where the material available, namely 4 specimens, was not considered adequate for statistical treatment, all the species show linear correlation of head width against head length with values closely ground around the lines of regression (Figs 2-5).

This tendency is verified by the extremely low values of the coefficient of variability obtained (Table I) which in the case of one species only, namely *A. peringueyi*, exceeds the value of 4. Attention is also drawn to the fact that as a result of deviations from the typical *barnardi** characteristics by the Western Cape material (SCHOONBEE, 1968) those from the Transvaal and Natal were considered separately from that of the Cape.

V. The ratio femur length/width

A statistical procedure similar to that employed for the head ratios was followed in the comparison of width relative to length of the first, second and third femora of specimens of the same species from the different localities as well as those of the different species respectively (Table II). Some preliminary deductions that can be made from these results obtained are the following:

* The Transvaal and Natal material from the various localities was found not to differ statistically from each other regarding the head and femur ratios and was therefore considered as belonging to the same complex of *barnardi*. Thus, *barnardi* material from any of the localities within the Natal-Transvaal area is considered and treated as representative for the species within this complex.

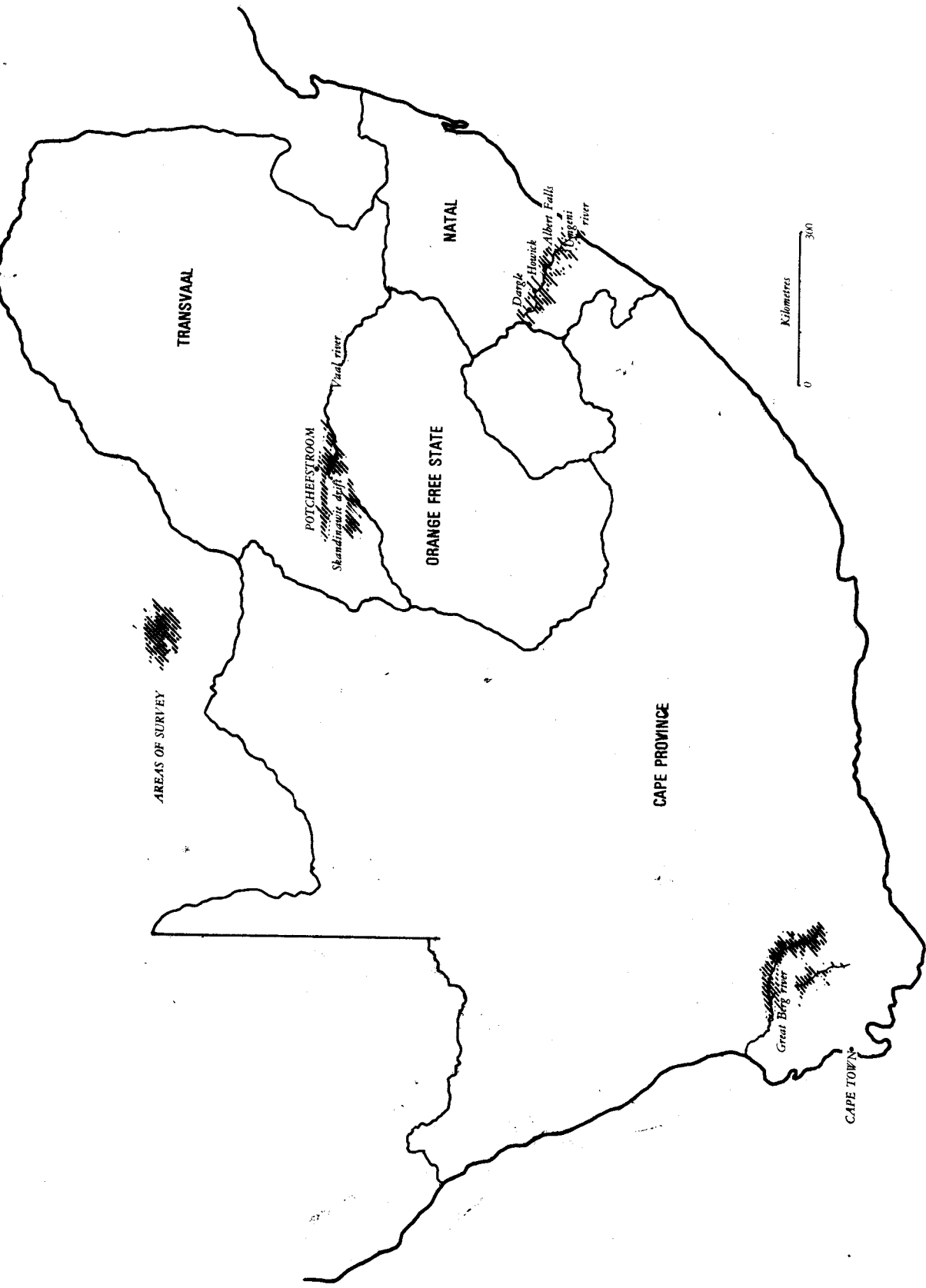


Fig. 1. River systems from where collections were made of *Afronurus*

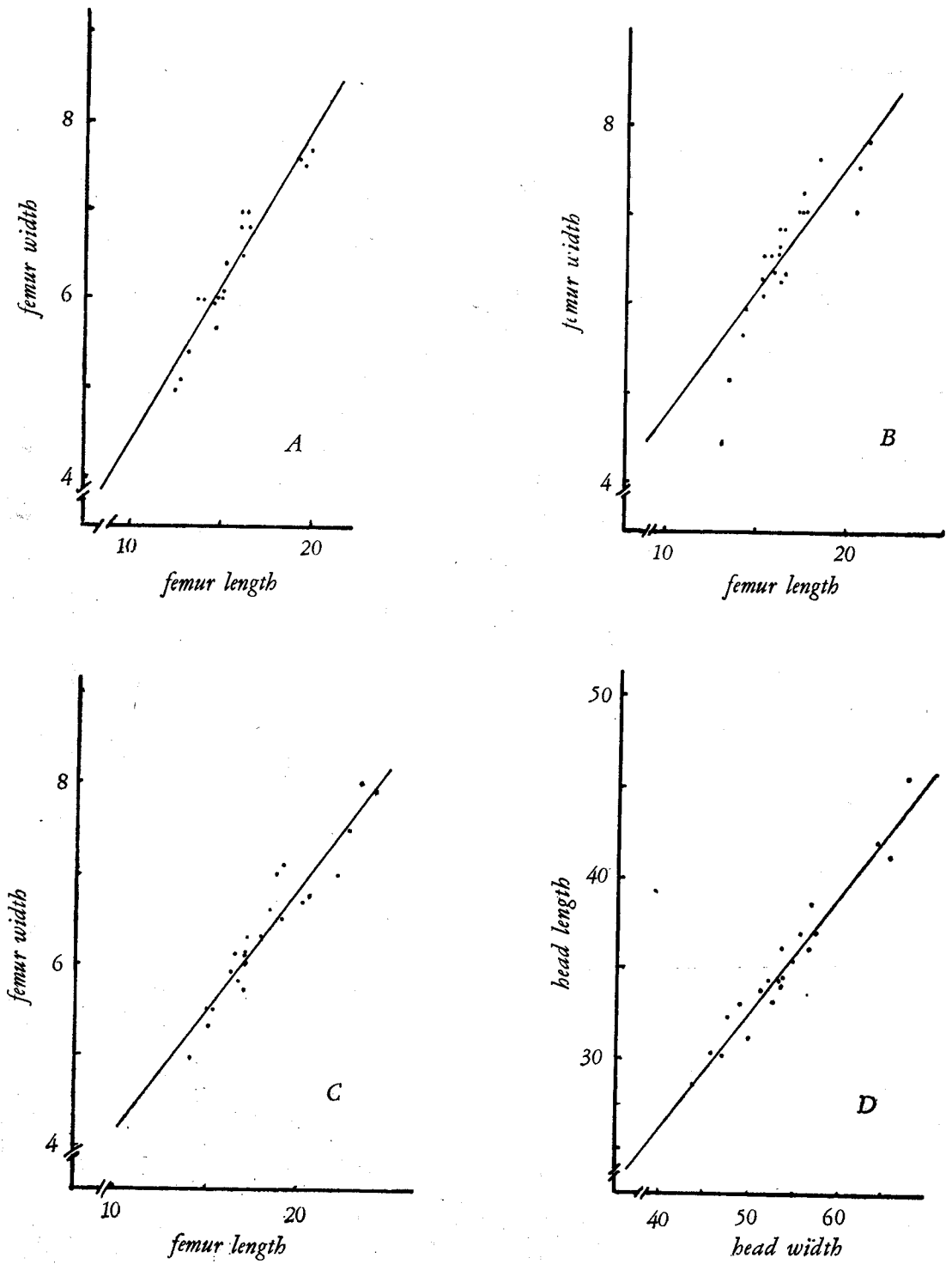


Fig. 2. First, second and third femur ratios (A-C) and head ratio (D) of *A. oliffi*

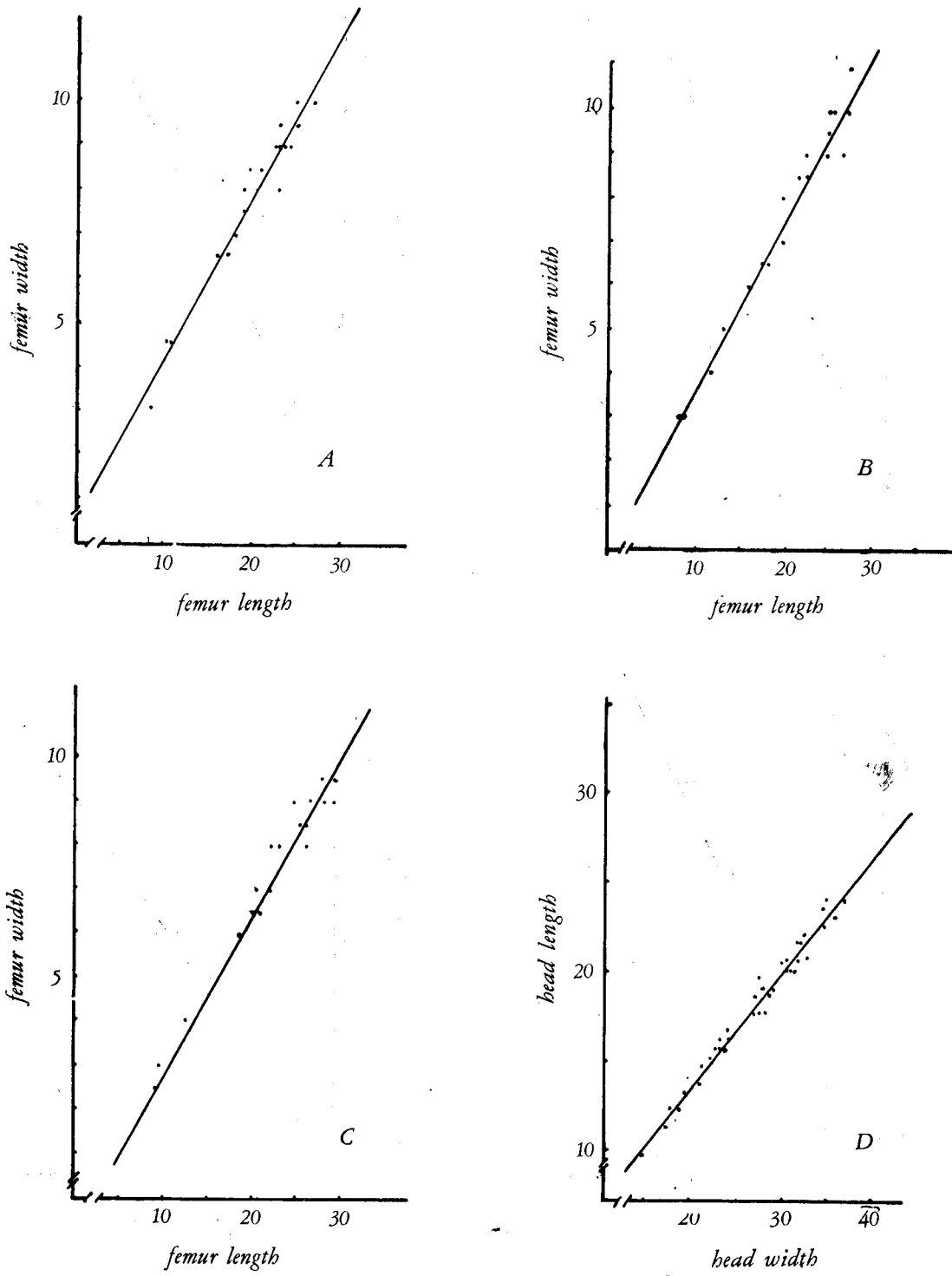


Fig. 3. First, second and third femur ratios (A-C) and head ratio (D) of *A. barnardi*

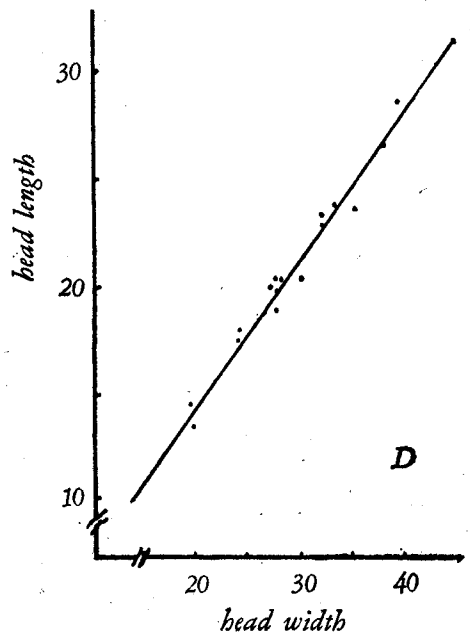
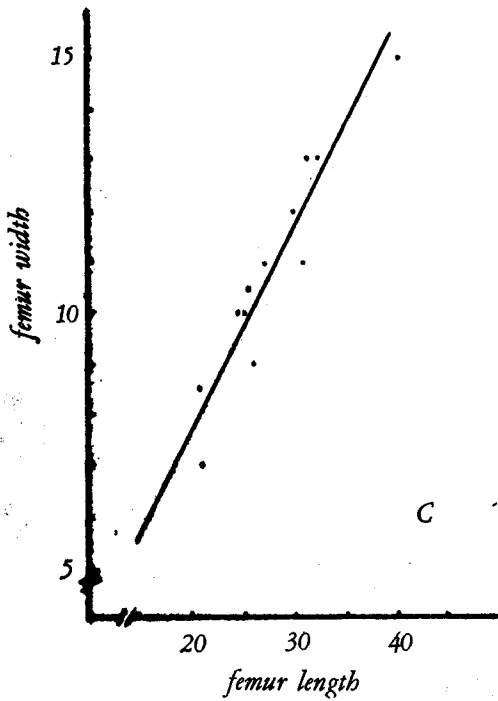
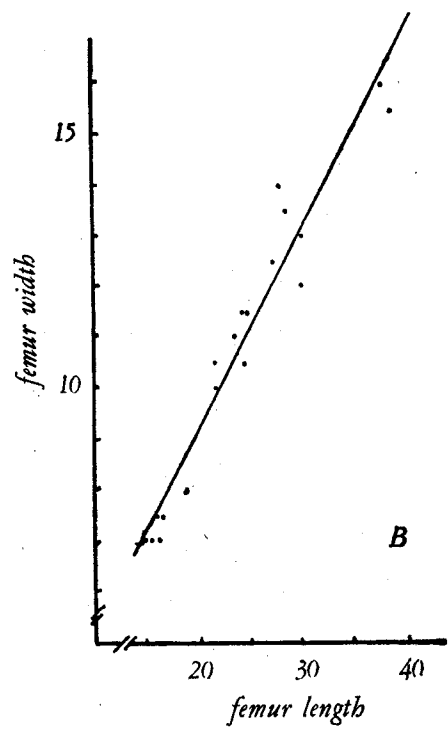
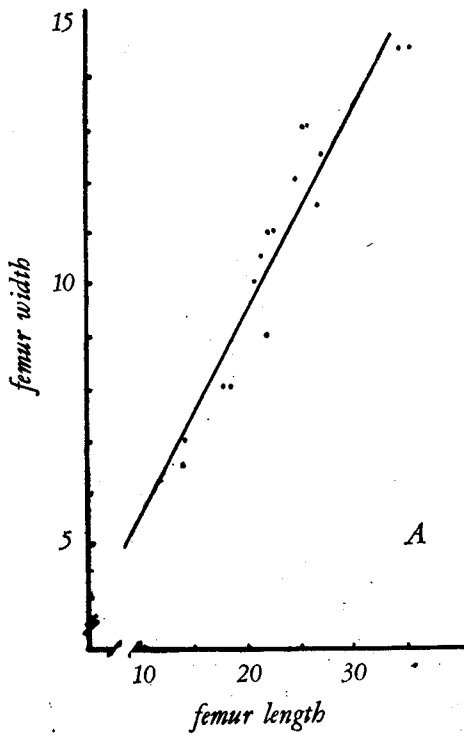


Fig. 4. First, second and third femur ratios (A-C) and head ratio (D) of *A. scotti*

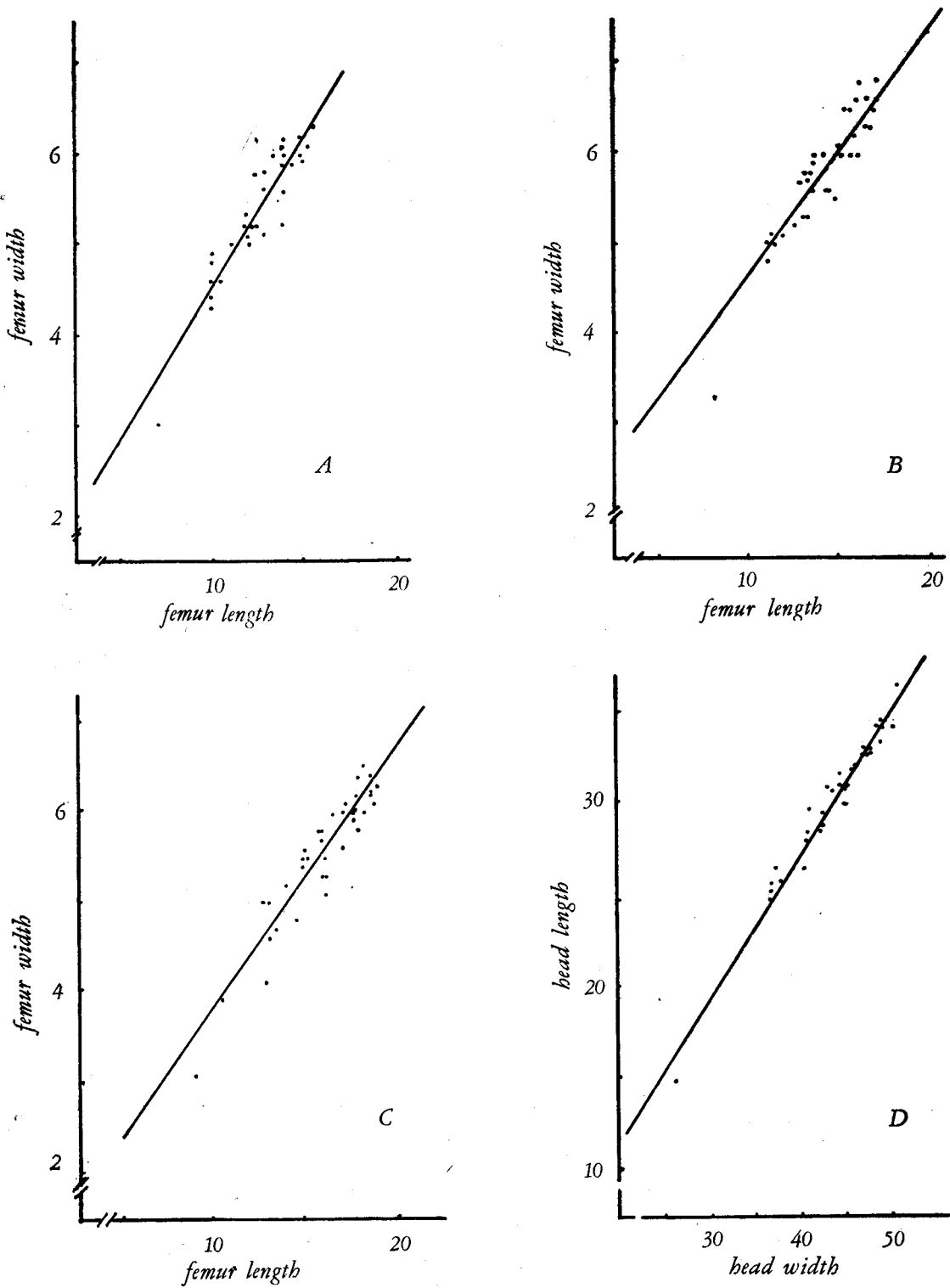


Fig. 5. First, second and third femur ratios (A-C) and head ratio (D) of *A. peringueyi*

1. Values for this ratio increases from the first to the third femur i.e. femur 1 < femur 2 < femur 3, for all the species under consideration. This also implies that the femurs become progressively more slender in this order.

2. The coefficient of variability (C.V., Table II) remains small, and, being less than 10 (usually fluctuating between 4 and 7), also reflects a small but somewhat higher degree of variability than for the corresponding head ratios.

VI. Statistical evaluation of results

Student's t-distribution test was employed in the comparison of the head width/length as well as the femur length/width ratio's. Results of these comparisons are listed in Table III (head ratios) and Tables 4-14 (femur ratios).

In the case of the comparison of the head width/length ratio's between the various species (Table III) it was found that at the 95% level of confidence, highly significant differences were obtained between the species compared, with the exception of the comparisons between *barnardi* (Natal) and *peringueyi*, and *barnardi* (Western Cape) and *oliffi*, where no differences were found. Of great importance was the highly significant difference found between the Cape specimens of *barnardi* and those from Natal. It is in these similarities between some species and differences within the *barnardi*-species group that a possible answer is sought for the particular distribution of the *Afronurus* species in South African rivers.

In the analysis of results on the comparisons of the femur length/width ratio's between the species the following results were obtained:

1. Statistically highly significant differences between *oliffi* and *barnardi* (Tables IV-VI, XIII), *oliffi* and *scotti* (Tables VII-VIII), *barnardi* (all localities) and *scotti* (Tables X, XIII), *barnardi* (all localities) and *peringueyi* (Tables XI and XIII) and *scotti* and *peringueyi* (Table XII).

2. In the comparison of *A. oliffi* and *peringueyi* (Table IX) statistically significant differences were only found for the first femur whilst the *barnardi* specimens from the Cape differs significantly from the Natal material of this species in the third femur ratio (Table XIII).

3. No differences were obtained in the comparison of the femur ratios of *barnardi* specimens collected from the Natal and Transvaal (Table XIV). As this was also found to apply to the head ratios, the species *barnardi* from these areas are considered to be the same with respect to these two parameters.

VII. Discussion

From the results obtained in the comparison of the ratios of head width/length and femur length/width of the *Afronurus* nymphs it was shown that the species of *Afronurus* under consideration differ statistically from each other in either one or both parameters.

The statistical evaluation of these results also points towards similarities between some species e.g. *oliffi* and *barnardi* (Head ratios, Table II), *barnardi* (Transvaal and Natal specimens) and *peringueyi* (Second and third femur ratios, Table XIII) as well as between the Cape specimens of *barnardi* and those of this species from the Transvaal and Natal localities (Head ratio as well as third femur ratio, Tables III and XIII).

One question which now arises from these findings is whether the differences and similarities regarding these parameters between the species have any bearing on their distributional tendencies in rivers i.e. can it perhaps explain why certain species only occur in particular regions of rivers and not in others as was shown by SCHOONBEE (1973). If so, can a wider head relative to head length in these

Table I

Ratios of head width/length in the different South African species of *Afronurus*

SPECIES	LOCALITY	N	\bar{x}	Range	$n-1 Sx^2$	Sx^2	Sx	C.V.
<i>Afronurus oliffi</i>	Small mountain stream, Cathedral Peak, Drakensberg, Natal.	23	1.52	1.469—1.599	0.0292	0.0013273	0.03643	2.39
<i>A. barnardi</i>	Emolweni river, Krantzklouf Nature reserve, Kloof, Natal.	42	1.46	1.375—1.645	0.1093	0.0026659	0.05163	3.53
<i>A. barnardi</i>	Saron, Great Berg river, Western Cape Province.	13	1.52	1.449—1.578	0.0150	0.00125	0.03536	2.33
<i>A. scotti</i>	Umgeni river at Dargle Forestry, Dargle, Natal.	20	1.39	1.33—1.463	0.0297	0.0015632	0.03954	2.85
<i>A. harrisoni</i>	Great Berg river. Western Cape Province.	4	1.59	1.564—1.618	0.0018	0.000600	0.02450	1.54
<i>A. peringueyi</i>	Vaal river, Skandinawië-drift, border between the Transvaal and Orange Free State.	38	1.45	1.379—1.770	0.1386	0.003746	0.06120	4.21

Table II

The ratios of femur length/width of the nymphs of the different South African species of *Afronurus*

SPECIES	LOCALITY	Femur	N	\bar{x}	Range	Sx	C.V.
<i>Afronurus oliffi</i>	Small mountain stream Cathedral Peak, Drakensberg, Natal.	First	23	2.42	2.267—2.600	0.09630	3.98
		Second	23	2.48	2.323—2.886	0.1337	5.39
		Third	23	2.83	2.671—3.129	0.1185	4.19
<i>A. barnardi</i>	Emolweni river, Krantzklouf Nature reserve, Kloof, Natal.	First	39	2.57	2.167—2.947	0.1510	5.87
		Second	40	2.69	2.421—3.286	0.1891	7.01
		Third	39	3.17	2.875—3.971	0.2229	7.03
	Vaal river system, various localities.	First	23	2.56	2.294—2.875	0.1457	5.69
		Second	23	2.64	2.437—2.889	0.1358	5.15
		Third	24	3.07	2.722—3.625	0.2275	7.41
	Vaal river, Skandinawië, border between Transvaal and Orange Free State.	First	6	2.57	2.440—2.773	0.1191	4.63
		Second	5	2.67	2.379—2.933	0.1963	7.36
		Third	6	3.16	3.036—3.448	0.1549	4.90
	Saron. Great Berg river system.	First	13	2.62	2.354—2.910	0.1599	6.11
		Second	13	2.82	2.578—3.116	0.1819	6.46
		Third	13	3.31	2.904—3.846	0.0316	0.95
<i>A. scotti</i>	Umgeni river at Dargle Forestry, Dargle, Natal.	First	19	2.17	2.000—2.483	0.1572	6.12
		Second	19	2.22	1.500—2.548	0.2238	10.07
		Third	16	2.57	2.385—3.000	0.1862	7.24
	Umgeni river system (various localities), Natal.	First	22	2.21	2.091—2.244	0.1221	5.52
		Second	23	2.30	2.158—3.000	0.1395	6.07
		Third	20	2.54	2.158—3.000	0.1835	7.24
<i>A. peringueyi</i>	Vaal river, Skandinawië, border between Transvaal and the Orange Free State.	First	39	2.35	2.061—2.692	0.1333	5.67
		Second	39	2.44	2.138—2.683	0.1430	5.87
		Third	39	2.88	2.560—3.177	0.1512	5.25
<i>A. harrisoni</i>	Great Berg river.	First	4	2.67	2.600—2.732	0.07301	2.74
		Second	4	2.90	2.767—2.957	0.08945	3.08
		Third	4	3.31	3.147—3.438	0.16330	4.94

Table III

A statistical comparison of the ratios head width/head length of the different South African species of *Afronurus* (2-sided t-test)

Species Compared	N	\bar{x}	$n-1 Sx^2$	d. f.	t	P	Differences between sample means
<i>oliffi</i> and <i>barnardi</i> *	23	1.52	0.0292	63	4.880	0.001	highly significant
	42	1.46	0.1093				
<i>oliffi</i> and <i>scotti</i>	23	1.52	0.0292	41	11.808	0.001	highly significant
	20	1.39	0.0297				
<i>oliffi</i> and <i>peringueyi</i>	23	1.52	0.0292	59	4.927	0.001	highly significant
	38	1.45	0.1386				
<i>barnardi</i> and <i>scotti</i> *	42	1.46	0.1093	60	5.927	0.001	highly significant
	20	1.39	0.0297				
<i>barnardi</i> and <i>peringueyi</i> *	42	1.46	0.1093	78	0.799	0.4-0.5	nonsignificant
	38	1.45	0.1386				
<i>scotti</i> and <i>peringueyi</i>	20	1.39	0.0297	56	4.452	0.001	highly significant
	38	1.45	0.1386				
<i>barnardi</i> ** and <i>barnardi</i>	13	1.52	0.0150	53	3.717	0.001	highly significant
	42	1.46	0.1093				
<i>barnardi</i> ** and <i>oliffi</i>	13	1.52	0.0150	34	0.228	0.8-0.9	nonsignificant
	23	1.52	0.0292				
<i>barnardi</i> ** and <i>scotti</i>	13	1.52	0.0150	31	9.906	0.001	highly significant
	20	1.39	0.0297				
<i>barnardi</i> ** and <i>peringueyi</i>	13	1.52	0.0150	49	3.700	0.001	highly significant
	38	1.45	0.1386				

* Emolweni river. Krantzklouf Nature reserve. Kloof, Natal.

** Great Berg river system. Near Saron, Western Cape.

Table IV

Comparison between the femur ratios length/width of the nymphs of the South African species of *Afronurus*: *A. oliffi** and *A. barnardi***

Femur	Species	N	\bar{x}	$n-1 Sx^2$	d. f.	t	P		Differences between sample means	
							2-sided test	1-sided test	2-sided test	1-sided test
First	<i>oliffi</i>	23	2.42	0.204	27	3.350	0.001-0.010	0.0005-0.005	highly significant	highly significant
	<i>barnardi</i>	6	2.57	0.071						
Second	<i>oliffi</i>	23	2.48	0.393	26	2.597	0.01-0.02	0.005-0.010	highly significant	highly significant
	<i>barnardi</i>	5	2.67	0.154						
Third	<i>oliffi</i>	23	2.83	0.309	27	5.768	0.001	0.0005	highly significant	highly significant
	<i>barnardi</i>	6	3.16	0.120						

* Locality: Small mountain stream, Cathedral Peak, Natal.

** Locality: Vaal river, Skandinawie drift, Transvaal — Orange Free State Border

Table V

A comparison between the femur ratios length/width of the nymphs of the South African species of *Afronurus* *A. oliffi** and *A. barnardi***

Femur	Species	N	\bar{x}	n-1 Sx ²	d. f.	t	P		Differences between sample means	
							2-sided test	1-sided test	2-sided test	1-sided test
First	<i>oliffi</i>	23	2.42	0.204	60	4.381	0.001	0.0005	highly significant	highly significant
	<i>barnardi</i>	39	2.57	0.866						
Second	<i>oliffi</i>	23	2.48	0.393	61	4.797	0.001	0.0005	highly significant	highly significant
	<i>barnardi</i>	40	2.69	1.395						
Third	<i>oliffi</i>	23	2.83	0.309	60	6.873	0.001	0.0005	highly significant	highly significant
	<i>barnardi</i>	39	3.17	1.888						

* Locality: Small mountain stream, Cathedral Peak, Natal.

Locality: Emolweni river, Kloof, Natal.

Table VI

Comparison between the femur ratios length/width of the nymphs of the South African species of *Afronurus* *A. oliffi** and *A. barnardi***

Femur	Species	N	\bar{x}	n-1 Sx ²	d. f.	t	P		Difference between sample means	
							2-sided test	1-sided test	2-sided test	1-sided test
First	<i>oliffi</i>	23	2.42	0.204	44	3.839	0.001	0.0005	highly significant	highly significant
	<i>barnardi</i>	23	2.56	0.467						
Second	<i>oliffi</i>	23	2.48	0.393	44	3.878	0.001	0.0005	highly significant	highly significant
	<i>barnardi</i>	23	2.64	0.406						
Third	<i>oliffi</i>	23	2.83	0.309	45	4.597	0.001	0.0005	highly significant	highly significant
	<i>barnardi</i>	24	3.07	1.190						

* Locality: Small mountain stream, Cathedral Peak, Natal.

** Locality: Vaal river. Various localities.

Table VII

Comparison between the femur ratios length/width of the nymphs of the South African species of *Afronurus* *A. oliffi** and *A. scotti***

Femur	Species	N	\bar{x}	n-1 Sx ²	d. f.	t	P		Differences between sample means	
							2-sided test	1-sided test	2-sided test	1-sided test
First	<i>oliffi</i>	23	2.42	0.204	43	6.361	0.001	0.0005	highly significant	highly significant
	<i>scotti</i>	22	2.21	0.313						
Second	<i>oliffi</i>	23	2.48	0.393	44	4.496	0.001	0.0005	highly significant	highly significant
	<i>scotti</i>	23	2.30	0.428						
Third	<i>oliffi</i>	23	2.83	0.309	41	6.262	0.001	0.0005	highly significant	highly significant
	<i>scotti</i>	20	2.54	0.640						

* Locality: Small mountain stream, Cathedral Peak, Natal.

Locality: Umgeni river, (various localities), Natal.

Table VIII

Comparison between the femur ratios length/width of the nymphs of the South African species of *Afronurus* *A. oliffi** and *A. scotti***

Femur	Species	N	\bar{x}	n-1 Sx ²	d. f.	t	P		Differences between sample means	
							2-sided test	1-sided test	2-sided test	1-sided test
First	<i>oliffi</i>	23	2.42	0.204	40	6.270	0.001	0.0005	highly significant	highly significant
	<i>scotti</i>	19	2.17	0.445						
Second	<i>oliffi</i>	23	2.48	0.393	40	4.6360	0.001	0.0005	highly significant	highly significant
	<i>scotti</i>	19	2.22	0.901						
Third	<i>oliffi</i>	23	2.83	0.309	37	5.237	0.001	0.0005	highly significant	highly significant
	<i>scotti</i>	16	2.57	0.520						

* Locality: Small mountain stream, Cathedral Peak, Natal.

** Locality: Umgeni river at Dargle Forestry, Dargle, Natal.

Table IX

Comparison between the femur ratios length/width of the nymphs of the South African species of *Afronurus* *A. oliffi** and *A. peringueyi***

Femur	Species	N	\bar{x}	n-1 Sx ²	d. f.	t	P		Differences between sample means	
							2-sided test	1-sided test	2-sided test	1-sided test
First	<i>oliffi</i>	23	2.42	0.204	60	2.092	0.02-0.05	0.010-0.025	significant	significant
	<i>peringueyi</i>	39	2.35	0.676						
Second	<i>oliffi</i>	23	2.48	0.393	60	1.2013	0.2-0.3	0.10-0.15	nonsignificant	nonsignificant
	<i>peringueyi</i>	39	2.44	0.777						
Third	<i>oliffi</i>	23	2.83	0.309	60	1.466	0.1-0.2	0.05-0.10	nonsignificant	nonsignificant
	<i>peringueyi</i>	39	2.88	0.869						

* Locality: Small mountain stream, Cathedral Peak, Natal.

** Locality: Vaal river, Skandinawie, border of Transvaal and Orange Free State.

nymphs be considered as an adaptation towards a better utilization of poor algal growths (available food) and furthermore, can a wider femur be considered as an adaptation to conditions of a stronger force of flow, which otherwise would have prevented such an organism to invade certain areas? To consider these two possibilities it is necessary to summarize some of the findings on the head/width and femur length/width ratios.

These are:

1. That the head width/length amongst the *Afronurus* nymphs decreases i.e. the heads of the species become progressively narrower in relation to length in the following order: *harrisoni* > *oliffi* > *barnardi* (Cape) > *barnardi* (Transvaal + Natal) > *peringueyi* > *scotti*.

2. The femur length/width ratio decreases for the species i.e. the femur becomes more muscular, robust in the following order: *harrisoni* > *barnardi* (Cape) > *barnardi* (Transvaal + Natal) > *oliffi* > > *peringueyi* > *scotti*.

From 1 and 2 above, indications are that the species with the widest heads in relation to their lengths also appear to possess the more slender, less muscular femurs. What then are the conditions regarding algal growths (available food) and force of flow under which the above mentioned species are found in rivers in South Africa?

Rivers in the Transvaal and Natal are as a rule alkaline from their places of origin (OLIFF, 1960; SCHOONBEE, 1964; CHUTTER, 1963). On their way to the sea, these rivers flow largely over geological

Table X
Comparison of the first, second and third femur ratios length/width of *Afronurus barnardi* and *A. scotti* from different localities in South Africa

Femur	Species	Locality*	N	\bar{x}	n-1 Sx ²	d.f.	t	P		Differences between sample means	
								2-sided test	1-sided test	2-sided test	1-sided test
First	<i>barnardi</i>	Vaal river	23	2.56	0.467	40	8.277	0.001	0.0005	highly significant	highly significant
	<i>scotti</i>	Dargle Forestry	19	2.17	0.445	40	7.362	0.001	0.0005	highly significant	highly significant
Second	<i>barnardi</i>	Vaal river	23	2.64	0.406	40	7.303	0.001	0.0005	highly significant	highly significant
	<i>scotti</i>	Dargle Forestry	19	2.22	0.901	38	7.303	0.001	0.0005	highly significant	highly significant
Third	<i>barnardi</i>	Vaal river	24	3.07	1.190	42	8.485	0.001	0.0005	highly significant	highly significant
	<i>scotti</i>	Dargle Forestry	16	2.57	0.520	43	8.658	0.001	0.0005	highly significant	highly significant
First	<i>barnardi</i>	Vaal river	23	2.56	0.467	43	8.658	0.001	0.0005	highly significant	highly significant
	<i>scotti</i>	Umgeni	22	2.21	0.313	44	8.255	0.001	0.0005	highly significant	highly significant
Second	<i>barnardi</i>	Vaal river	23	2.64	0.406	42	8.485	0.001	0.0005	highly significant	highly significant
	<i>scotti</i>	Umgeni	23	2.30	0.428	56	9.379	0.001	0.0005	highly significant	highly significant
Third	<i>barnardi</i>	Vaal river	24	3.07	1.190	57	8.466	0.001	0.0005	highly significant	highly significant
	<i>scotti</i>	Umgeni	20	2.54	0.640	53	9.502	0.001	0.0005	highly significant	highly significant
First	<i>barnardi</i>	Emolweni	39	2.57	0.866	59	9.598	0.001	0.0005	highly significant	highly significant
	<i>scotti</i>	Dargle Forestry	19	2.17	0.445	61	8.751	0.001	0.0005	highly significant	highly significant
Second	<i>barnardi</i>	Emolweni	40	2.69	1.395	57	8.751	0.001	0.0005	highly significant	highly significant
	<i>scotti</i>	Dargle Forestry	19	2.22	0.901	57	11.000	0.001	0.0005	highly significant	highly significant
Third	<i>barnardi</i>	Emolweni	39	3.17	1.88	57	11.000	0.001	0.0005	highly significant	highly significant
	<i>scotti</i>	Dargle Forestry	16	2.57	0.520	57	11.000	0.001	0.0005	highly significant	highly significant
First	<i>barnardi</i>	Emolweni	39	2.57	0.866	59	9.598	0.001	0.0005	highly significant	highly significant
	<i>scotti</i>	Umgeni	22	2.21	0.313	59	9.598	0.001	0.0005	highly significant	highly significant
Second	<i>barnardi</i>	Emolweni	40	2.69	1.395	61	8.751	0.001	0.0005	highly significant	highly significant
	<i>scotti</i>	Umgeni	23	2.30	0.428	61	8.751	0.001	0.0005	highly significant	highly significant
Third	<i>barnardi</i>	Emolweni	39	3.17	1.888	57	11.000	0.001	0.0005	highly significant	highly significant
	<i>scotti</i>	Umgeni	20	2.54	0.640	57	11.000	0.001	0.0005	highly significant	highly significant

(cont. Tab. X)

First	<i>barnardi</i> <i>scotti</i>	Skandinawië Dargle Forestry	6	2.57	0.071	23	5.738	0.001	0.0005	highly significant	highly significant
			19	2.17	0.445					highly significant	highly significant
Second	<i>barnardi</i> <i>scotti</i>	Skandinawië Dargle Forestry	5	2.67	0.154	22	4.038	0.001	0.0005	highly significant	highly significant
			19	2.22	0.901					highly significant	highly significant
Third	<i>barnardi</i> <i>scotti</i>	Skandinawië Dargle Forestry	6	3.16	0.120	20	6.877	0.001	0.0005	highly significant	highly significant
			16	2.57	0.520					highly significant	highly significant
First	<i>barnardi</i> <i>scotti</i>	Skandinawië Umgeni	6	2.57	0.071	26	6.486	0.001	0.0005	highly significant	highly significant
			22	2.21	0.313					highly significant	highly significant
Second	<i>barnardi</i> <i>scotti</i>	Skandinawië Umgeni	5	2.67	0.154	26	4.970	0.001	0.0005	highly significant	highly significant
			23	2.30	0.428					highly significant	highly significant
Third	<i>barnardi</i> <i>scotti</i>	Skandinawië Umgeni	6	3.16	0.120	24	7.539	0.001	0.0005	highly significant	highly significant
			20	2.54	0.640					highly significant	highly significant

Table XI
Comparison of the first, second and third femur ratios length/width of *Afronurus barnardi* and *A. peringueyi*

Femur	Species	Locality	N	\bar{x}	$n-1 Sx^2$	d.f.	t	P		Difference between sample means	
								2-sided test	1-sided test	2-sided test	1-sided test
First	<i>barnardi</i>	Skandinawië	6	2.57	0.071	43	3.834	0.001	0.0005	highly significant	highly significant
	<i>peringueyi</i>	Skandinawië	39	2.35	0.676					highly significant	highly significant
Second	<i>barnardi</i>	Skandinawië	5	2.67	0.154	42	3.252	0.01—0.001	0.005—0.0005	significant	highly significant
	<i>peringueyi</i>	Skandinawië	39	2.44	0.777					significant	significant
Third	<i>barnardi</i>	Skandinawië	6	3.16	0.120	43	2.026	0.05—0.02	0.025—0.010	significant	significant
	<i>peringueyi</i>	Skandinawië	39	2.88	0.869					highly significant	highly significant
First	<i>barnardi</i>	Vaal river	23	2.56	0.467	50	5.671	0.001	0.0005	highly significant	highly significant
	<i>peringueyi</i>	Skandinawië	39	2.35	0.676					highly significant	highly significant
Second	<i>barnardi</i>	Vaal river	23	2.64	0.406	50	5.597	0.001	0.0005	highly significant	highly significant
	<i>peringueyi</i>	Skandinawië	39	2.44	0.777					highly significant	highly significant
Third	<i>barnardi</i>	Vaal river	24	3.07	0.190	51	3.992	0.001	0.0005	highly significant	highly significant
	<i>peringueyi</i>	Skandinawië	39	2.88	0.869					highly significant	highly significant
First	<i>barnardi</i>	Emolweni	39	2.57	0.866	76	6.835	0.001	0.0005	highly significant	highly significant
	<i>peringueyi</i>	Skandinawië	39	2.35	0.676					highly significant	highly significant
Second	<i>barnardi</i>	Emolweni	40	2.69	1.395	77	8.129	0.001	0.0005	highly significant	highly significant
	<i>peringueyi</i>	Skandinawië	39	2.44	0.777					highly significant	highly significant
Third	<i>barnardi</i>	Emolweni	39	3.17	1.888	76	8.078	0.001	0.0005	highly significant	highly significant
	<i>peringueyi</i>	Skandinawië	39	2.88	0.869					highly significant	highly significant

Table XII
 Comparison on the first, second and third femur ratios length/width of *Afonurus scotti* and *A. peringueyi* from two localities in Natal and the Transvaal

Femur	Species	Locality	N	x	n-1 Sx ²	d.f.	t	P		Difference between sample means	
								2-sided test	1-sided test	2-sided test	1-sided test
First	<i>Scotti</i> <i>peringueyi</i>	Dargle Forestry	19	2.17	0.445	56	4.578	0.001	0.0005	highly significant	highly significant
		Skandinawië	39	2.35	0.676					highly significant	highly significant
Second	<i>Scotti</i> <i>peringueyi</i>	Dargle Forestry	19	2.22	0.901	56	4.433	0.001	0.0005	highly significant	highly significant
		Skandinawië	39	2.44	0.777					highly significant	highly significant
Third	<i>Scotti</i> <i>peringueyi</i>	Dargle Forestry	16	2.57	0.520	53	6.434	0.001	0.0005	highly significant	highly significant
		Skandinawië	39	2.88	0.869					highly significant	highly significant
First	<i>Scotti</i> <i>peringueyi</i>	Umgeni	22	2.21	0.313	59	4.096	0.001	0.0005	highly significant	highly significant
		Skandinawië	39	2.35	0.676					highly significant	highly significant
Second	<i>Scotti</i> <i>peringueyi</i>	Umgeni	23	2.30	0.428	60	3.679	0.001	0.0005	highly significant	highly significant
		Skandinawië	39	2.44	0.777					highly significant	highly significant
Third	<i>Scotti</i> <i>peringueyi</i>	Umgeni	20	2.54	0.640	57	7.712	0.001	0.0005	highly significant	highly significant
		Skandinawië	39	2.88	0.869					highly significant	highly significant

Table XIII

Comparison between the femur ratios length/width of the nymphs of *A. barnardi* from the Cape with *A. oliffi* (Cathedral Peak, Natal), *A. scotti* (Umgeni river, various localities), *A. peringueyi* (Vaal river, Skandinawië drift, Transvaal) and *A. barnardi* (Emolweni river tributary of Umgeni river, Natal)

Femur	Species	N	\bar{X}	$n-1 Sx^2$	d.f.	t	P	Differences between sample means
First	<i>barnardi</i>	13	2.57	0.866	34	2.610	0.01—0.02	Highly significant
	<i>oliffi</i>	23	2.42	0.204				
Second	<i>barnardi</i>	13	2.82	0.397	34	6.326	0.001	Highly significant
	<i>oliffi</i>	23	2.48	0.393				
Third	<i>barnardi</i>	13	3.31	0.012	34	14.432	0.001	Highly significant
	<i>oliffi</i>	23	2.83	0.309				
First	<i>barnardi</i>	13	2.57	0.866	33	5.748	0.001	Highly significant
	<i>scotti</i>	22	2.21	0.313				
Second	<i>barnardi</i>	13	2.82	0.397	34	9.346	0.001	Highly significant
	<i>scotti</i>	23	2.30	0.428				
Third	<i>barnardi</i>	13	3.31	0.012	31	15.090	0.001	Highly significant
	<i>scotti</i>	20	2.54	0.640				
First	<i>barnardi</i>	13	2.57	0.866	50	3.930	0.001	Highly significant
	<i>peringueyi</i>	39	2.35	0.676				
Second	<i>barnardi</i>	13	2.82	0.397	50	7.760	0.001	Highly significant
	<i>peringueyi</i>	39	2.44	0.777				
Third	<i>barnardi</i>	13	3.31	0.012	50	10.220	0.001	Highly significant
	<i>peringueyi</i>	39	2.88	0.869				
First	<i>barnardi</i>	13	2.57	0.866	50	0.872	0.4—0.3	non-significant
	<i>barnardi</i> *	39	2.62	0.307				
Second	<i>barnardi</i>	13	2.82	0.397	51	1.981	0.1—0.05	non-significant
	<i>barnardi</i> *	40	2.69	1.395				
Third	<i>barnardi</i>	13	3.31	0.012	50	2.271	0.05—0.02	significant
	<i>barnardi</i> *	39	3.17	1.888				

* Natal, Emolweni river specimens taken as representative of Transvaal — Natal complex of *barnardi*.

beds such as Beaufort, Ecca and Dwyka, giving rise to waters which are rich in Calcium and Magnesium. pH-values normally range between 7 and 8.5 while concentrations for total dissolved solids may vary from 20, near the source, to well over 500 p.p.m. Nutrients such as PO_4 and NO_3 , largely responsible for biological growth in rivers are always present in these rivers in such concentrations as to allow a proper development of algae. The concentrations of these biological growth nutrients normally increase as the rivers flow towards the sea, accompanied by a resultant increase of algal growths. In the lower reaches of these rivers called the foothill sand bed and flood plain zones the rivers are as a rule turbid due to the presence of suspended particles such as silt and detritus which are largely deposited on the river bed in the latter zone as a result of the sluggish flow of the river. This results in a reduced growth of algae on stones in the stream and therefore also of food available to organisms such as the mayflies.

In contrast to the conditions referred to for the Transvaal and the Natal rivers, the rivers in the Western Cape such as the Great Berg river, runs off poorly mineralized geological strata i.e. Table Mountain Sandstone (HARRISON & ELSWORTH, 1958). The acid in the sandstone soils also give rise to pH-values of the water which are well below 7. The scarcity of nutrients in this type of water furthermore results in poor algal growths, and consequently also of other available food, a condition which occurs over long distances in the upper zones of these rivers. Also, there is a generally slower development of algae in parts of the streams compared to similar regions in the Natal and Transvaal rivers. The

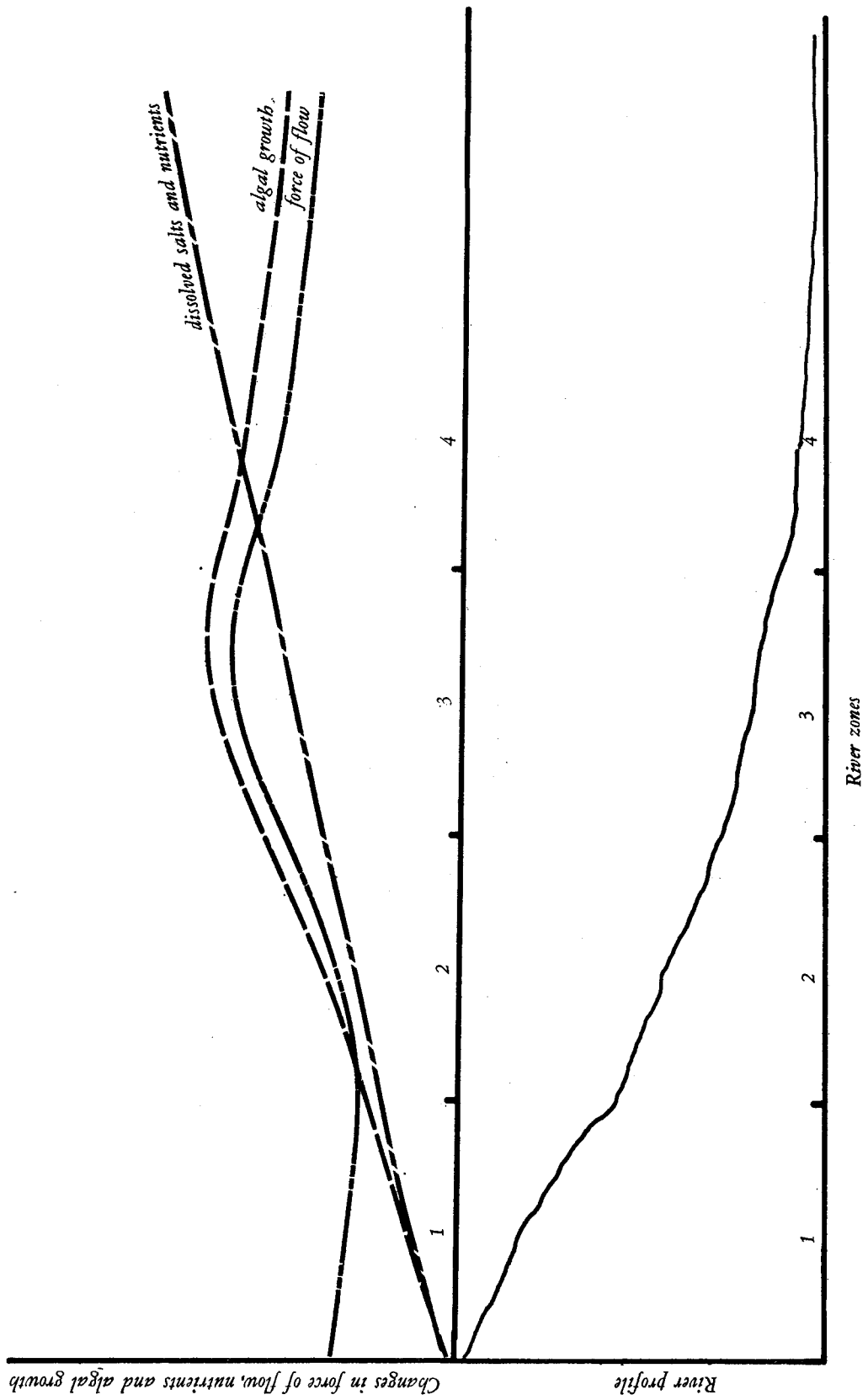


Fig. 6. Schematic presentation of changes in force of river flow, dissolved salts and nutrients, and algal growth in a river such as the Umgeni river, Natal, South Africa

Table XIV

Comparison of the first, second and third femur ratios of length/width of *Afronurus barnardi* from three different localities in South Africa

Femur	Sampling localities	N	\bar{x}	n-1 Sx ²	d.f.	t	P		Difference between sample means	
							2-sided test	1-sided test	2-sided test	1-sided test
First	Emolweni	39	2.57	0.866	60	0.358	0.8—0.7	0.40—0.35	nonsignificant	nonsignificant
	Vaal river	23	2.56	0.467						
Second	Emolweni	40	2.69	1.395	61	1.352	0.2—0.1	0.10—0.05	nonsignificant	nonsignificant
	Vaal river	23	2.64	0.406						
Third	Emolweni	39	3.17	1.888	61	1.737	0.1—0.05	0.05—0.025	nonsignificant	nonsignificant
	Vaal river	24	3.07	1.190						
First	Emolweni	39	2.57	0.866	43	0.019	0.9	0.45	nonsignificant	nonsignificant
	Skandinawië	6	2.57	0.071						
Second	Emolweni	40	2.69	1.395	43	0.322	0.8—0.7	0.40—0.35	nonsignificant	nonsignificant
	Skandinawië	5	2.67	0.154						
Third	Emolweni	39	3.17	1.888	43	0.131	0.9—0.8	0.45—0.40	nonsignificant	nonsignificant
	Skandinawië	6	3.16	0.120						
First	Vaal river	23	2.56	0.467	27	0.235	0.9—0.8	0.45—0.40	nonsignificant	nonsignificant
	Skandinawië	6	2.57	0.071						
Second	Vaal river	23	2.64	0.406	26	0.439	0.7—0.6	0.35—0.30	nonsignificant	nonsignificant
	Skandinawië	5	2.67	0.154						
Third	Vaal river	24	3.07	1.190	28	0.897	0.4—0.3	0.20—0.15	nonsignificant	nonsignificant
	Skandinawië	6	3.16	0.120						

presence of silt loads and detritus and the deposition of there in the lower reaches of the Western Cape rivers have a similar effect in reducing the growth of algae and thus also available food. *A. harrisoni* is confined to the Western Cape rivers whilst *A. barnardi* also occurs there.

The river zones referred to and the general conditions regarding river gradient, force of flow and algal growth are summarized in Table XV.

In order to test the theory that in their distribution in rivers relative to each other, the nymphs of the species of *Afronurus* are in fact largely adapted towards the availability of food (head width) and force of river flow (femur width) and that mainly for this reason each of the species predominates in a particular region of a river (SCHOONBEE, 1973) it is necessary to refer again to the conditions already described and which are summarized in Table XV and illustrated in figure 6.

If food availability is a limiting factor, then, the nymphs of the species of *Afronurus* best suited to survive in zone 1 should in theory possess the widest head (relative to head length) amongst the species under consideration. Also, one may expect such a species not to have the narrowest (= weakest developed) femur, as the steep river gradient encountered in this part of the river allows for some force in the river flow despite a comparatively low volume of water present. Of the species in the Transvaal and Natal rivers, *A. oliffi*, purely on its head and femur ratios best fits these requirements. Similarly, in the Great Berg river, *A. harrisoni* will be the species best adapted to occupy the head water regions of its rivers. The region in the Natal and Transvaal rivers with the highest densities in algal growth (available food) is represented by zone 3. Here the force of the river flow is also at its greatest. The *Afronurus* species with the smallest head width/length ratio but which also possesses the widest femur, according to the results obtained, is *A. scotti*. On this same principle, *A. barnardi* is best placed in zone 2 and *A. peringueyi* in zone 4, respectively, of the Natal and Transvaal rivers. This arrangement of the *Afronurus* species on account of head width and femur width in fact coincides with their actual downstream distribution in the river system concerned, viz. *A. oliffi*, *barnardi*, *scotti* and *peringueyi* in the Transvaal and Natal rivers and *harrisoni* and *barnardi*, in that order, in the rivers of the Western Cape.

Table XV

General conditions and force of flow in Transvaal, Natal and Western Cape rivers

Transvaal & Natal	Western Cape
WATER QUALITY	
1. As a rule alkaline from source. pH: 7-8.5 2. Flows mainly over geological beds of the Beaufort, Ecca and Dwyka series rich in Calcium and Magnesium. 3. Nutrients P and N adequate to encourage increased downstream development of algae and food for organisms.	As a rule acid. pH: 4-6.5 Flows over poorly mineralized beds of Table Mountain Sandstone. Poor in nutrients P & N. Slow downstream development of algae and other food for organisms.

FLOW CONDITIONS

ZONE

1. HEADWATERS

Waterfall conditions at head waters of both river systems. Water volume small but exerts some force due to very steep gradient of over bed. Slight development of algal growth.

2. MOUNTAIN TORRENT ZONE:

River bed gradient less steep than in head water region. Force of flow less, despite slight increase in river volume. Slight development of algae.

3. FOOTHILL TORRENT ZONE:

Further increase in volume of water. Force of flow now stronger than in zones 1 and 2. Considerable algal growth during most seasons of year.

4. FOOTHILL SANDBED ZONE:

Further increase in volume of river flow. River gradient less steep than in zone 3. Deposition of sand particles on riverbed. Reduction in force of flow and algal growth compared with those of zone 3.

5. FLOOD PLAIN ZONE:

Further reduction in river gradient and force of flow. Deposition of silt on stones on river bed which further reduce algal growth.

Table XVI

Number of combs on the maxillae of *Afronurus* nymphs

Species	Number of combs
<i>A. oliffi</i>	24 — 26
<i>A. harrisoni</i>	22 — 26
<i>A. barnardi</i>	< 22
<i>A. scotti</i>	19 — 22
<i>A. peringueyi</i>	< 20

On the assumption that head width has some relationship with the ability to scrape food from stone surfaces, counts were also made of the combs on the maxillae of some nymphs of each of the species of *Afronurus*. Although no constant number of combs were encountered within each species, the preliminary results as summarized in Table XVI further suggest that head width may well have some relation to available food.

SUMMARY

Adaptation towards food availability and force of river flow of the nymphs of the genus Afronurus Lestage (Ephemeroptera: Heptageniidae) in South Africa as a possible explanation for the distribution of its species in rivers

An analysis is made of the ratios head width/length and femur length/width of the nymphs of the species of *Afronurus* LESTAGE in South Africa. On the assumption that variations in head width (relative to head length) and femur width (relative to femur length) are in fact adaptations towards variations in the availability of algal growths and force of river flow along various sections in river systems in South Africa, the species were found to fit into the same order of their actual ecological distribution in these rivers.

DISCUSSION

U. HUMPESCH: Which groups of algae did you find in your rivers? How was the fluctuation of it during the year and how did you estimate the quantity of algae in rivers? I think that from our studies in mountain rivers that the amount of algal growth alone can not explain the presence of animals at different locations, their growths and life cycles.

H. J. SCHOONBEE: My experience of almost 5 years of continuous field work in the Umgeni river basin, Natal, revealed the tendency in algal growths along the lengths of rivers as I have shown. Although I did not carry out a quantitative study on the algal densities, I have no doubt that a study will prove so. There were seasonal fluctuations in algal growths but the nymphs of the different species of *Afronurus* always maintained their positions relative to each other along the length of the rivers.

I do not suggest that the presence and/or abundance of food alone can explain the presence or absence of species at certain localities. There must be several factors which in combination play a role. Food availability and adaptations to optimally utilize it under certain environmental conditions appear to be important factors in the case of the distribution of the *Afronurus* species.

W. P. MCCAFFERTY: According to your correlation of femora width and distribution by force of current, only species with narrow femora would be restricted to slow areas, but species with wide femora should be able to exist in slow currents also.

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